Pattern formation – Turing instability

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Summer school, Prague, 6–8 August, 2013

Outline

- Motivation
- Turing instability – general conditions
- Schnakenberg system – Turing conditions
- Schnakenberg system – particular example

Motivation

Turing instability

Reaction-diffusion system:

$$\frac{du}{dt} = d_1 \Delta u + f(u, v)$$
$$\frac{dv}{dt} = d_2 \Delta v + g(u, v)$$

Linearisation at (u_0, v_0):

$$\frac{du}{dt} = d_1 \Delta u + A_{11} u + A_{12} v$$
$$\frac{dv}{dt} = d_2 \Delta v + A_{21} u + A_{22} v$$

Homogeneous steady state:

$$f(u_0, v_0) = 0$$
$$g(u_0, v_0) = 0$$

Linearisation matrix:

$$A = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} (u_0, v_0)$$

Turing instability occurs if solution (u_0, v_0) of linearisation is:

(a) stable with respect to spatially homogeneous disturbances

(b) unstable to spatial disturbances

Turing conditions

(a) (u_0, v_0) is stable w.r.t. spatially homogeneous disturbances
if
(T1) $\operatorname{tr} A < 0$
(T2) $\det A > 0$

(b) (u_0, v_0) is unstable to spatial disturbances
if

$$\exists k > 0 :: \ \lambda_k = \frac{1}{2}\left[-b_k + \sqrt{b_k^2 - 4h_k}\right] > 0 \quad \Leftrightarrow \quad h_k < 0$$

where

$b_k = (d_1 + d_2)\mu_k - \operatorname{tr} A$
$h_k = d_1 d_2 \mu_k^2 - (d_2 f_u + d_1 g_v)\mu_k + \det A$
μ_k ... eigenvalue of Laplacian

Remark 1: (b) $\Rightarrow$
(T3) $d_2 f_u + d_1 g_v > 0$
(T4) $4 d_1 d_2 \det A < (d_2 f_u + d_1 g_v)^2$

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where

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$h_k = d_1 d_2 \mu_k^2 - (d_2 f_u + d_1 g_v)\mu_k + \det A$
μ_k ... eigenvalue of Laplacian

Remark 2:
$\mathbf{w}_k(x,t) = \mathrm{e}^{\lambda_k t} z_k(x)\mathbf{U}_k$ is an unstable solution of linearisation.

$$[A - \mu_k D]\mathbf{U}_k = \lambda_k \mathbf{U}_k$$

Schnakenberg model

$$2A + B \overset{k_1}{\rightarrow} 3A \qquad \emptyset \overset{k_2,k_3}{\rightleftharpoons} A \qquad \emptyset \overset{k_4}{\rightarrow} B$$

Notation:

$\overline{u}$, $\overline{v}$ ... number of molecules of A,B

Reaction-diffusion system:

$$\frac{d\overline{u}}{dt} = d_1 \Delta \overline{u} + k_1 \overline{u}^2 \overline{v} + k_2 - k_3 \overline{u},$$
$$\frac{d\overline{v}}{dt} = d_2 \Delta \overline{v} - k_1 \overline{u}^2 \overline{v} + k_4$$

Stationary state:

$$u_s = \frac{k_4 + k_2}{k_3}, \quad v_s = \frac{k_4}{k_1 u_s^2}$$

Schnakenberg model – shifting the system

Shifted variables:

$\overline{u} = u + u_s, \quad \overline{v} = v + u_s$

Shifted system:

$$\frac{du}{dt} = d_1 \Delta u + \alpha u + \beta v + f(u,v)$$
$$\frac{dv}{dt} = d_2 \Delta v - \gamma u - \beta v - f(u,v)$$

where

$\alpha = k_3 \dfrac{k_4 - k_2}{k_4 + k_2}, \quad \beta = \dfrac{k_1}{k_3^2}(k_4 + k_2)^2, \quad \gamma = \dfrac{2k_3 k_4}{k_4 + k_2}$

$f(u,v) = k_1 u^2 v + 2k_1 u_s uv + k_1 v_s u^2$

Schnakenberg – Turing conditions

$$\alpha = k_3 \frac{k_4 - k_2}{k_4 + k_2}, \quad \beta = \frac{k_1}{k_3^2}(k_4 + k_2)^2, \quad \gamma = \frac{2k_3 k_4}{k_4 + k_2}$$

Linearisation matrix:

$$A = \begin{pmatrix} \alpha & \beta \\ -\gamma & -\beta \end{pmatrix}$$

Turing conditions:

(T1) $\operatorname{tr} A = \alpha - \beta < 0$

(T2) $\det A = k_1(k_4 + k_2)^2 / k_3 > 0$

(T3) $d_2\alpha - d_1\beta > 0 \quad \Leftrightarrow \quad \frac{d_2}{d_1} > \frac{\beta}{\alpha} > 1$

(T4) $4 d_1 d_2 \det A < (d_2 f_u + d_1 g_v)^2$

Schnakenberg – particular example

$\Omega = (0, 1)$

$k_1 = 10^{-6}, \quad k_2 = 1, \quad k_3 = 0.02, \quad k_4 = 2 \text{ [sec}^{-1}]$
$d_1 = 10^{-5}, \quad d_2 = 10^{-3} \text{ [mm}^2 \text{ sec}^{-1}]$

Linearisation matrix:

$$A = \frac{1}{100}\begin{pmatrix} 1 & 4 \\ -3 & -4 \end{pmatrix}$$

Turing conditions:

(T1) $\operatorname{tr} A = -0.03 < 0$

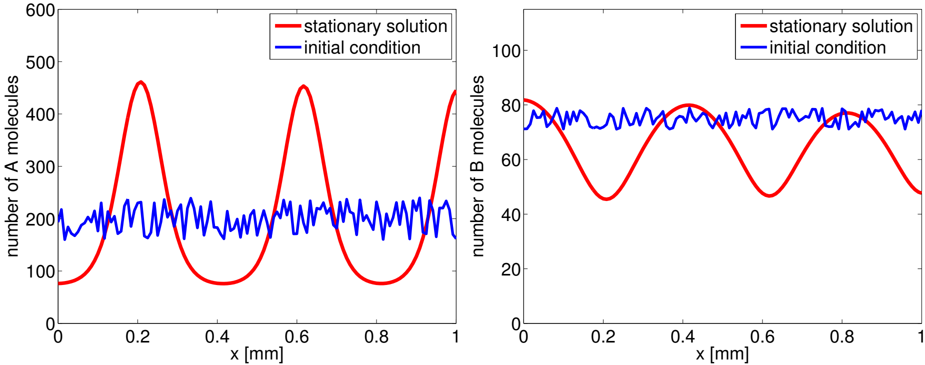
(T2) $\det A = 1/1250 > 0$

(T3) $\dfrac{d_2}{d_1} > 4 \quad \Leftrightarrow \quad d_2 > 4d_1 \quad \Leftrightarrow \quad 10^{-3} > 4 \times 10^{-5}$

(T4) $d_2 > \dfrac{100 d_1}{25 - 8d_1} \quad \Leftrightarrow \quad 10^{-3} > \dfrac{10^{-3}}{25 - 8 \times 10^{-5}} \approx 4 \times 10^{-5}$

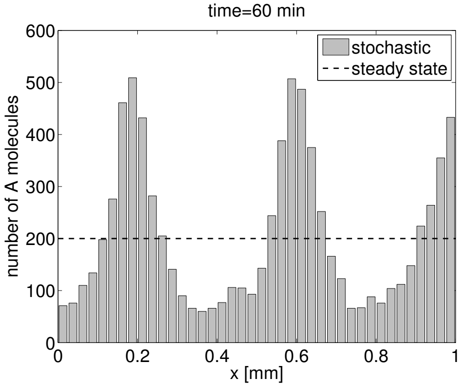
Schnakenberg – deterministic

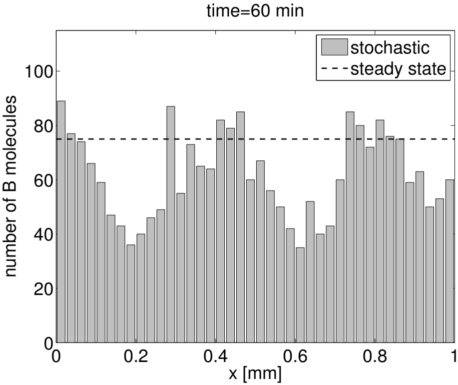
$$\frac{du}{dt} = d_1 u'' + \alpha u + \beta v + f(u,v) \quad \text{in } (0,1), \qquad u'(0) = u'(1) = 0$$
$$\frac{dv}{dt} = d_2 v'' - \gamma u - \beta v - f(u,v) \quad \text{in } (0,1), \qquad v'(0) = v'(1) = 0$$



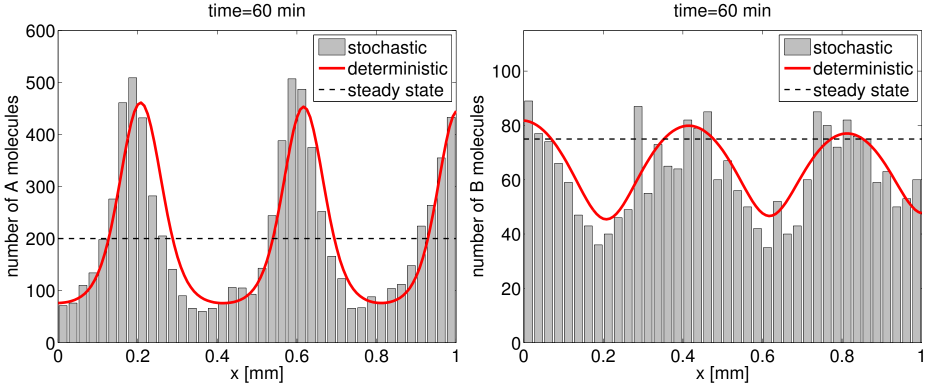
Schnakenberg – stochastic (compartments)

$$2A + B \xrightarrow{k_1} 3A \qquad \emptyset \underset{}{\overset{k_2,k_3}{\rightleftharpoons}} A \qquad \emptyset \xrightarrow{k_4} B$$





Schnakenberg – stochastic vs. deterministic



Schnakenberg – dependence on initial cond.

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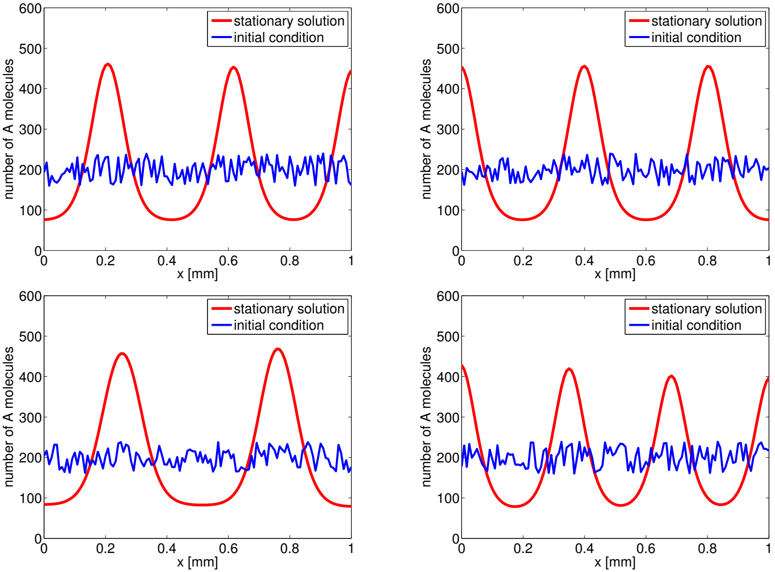
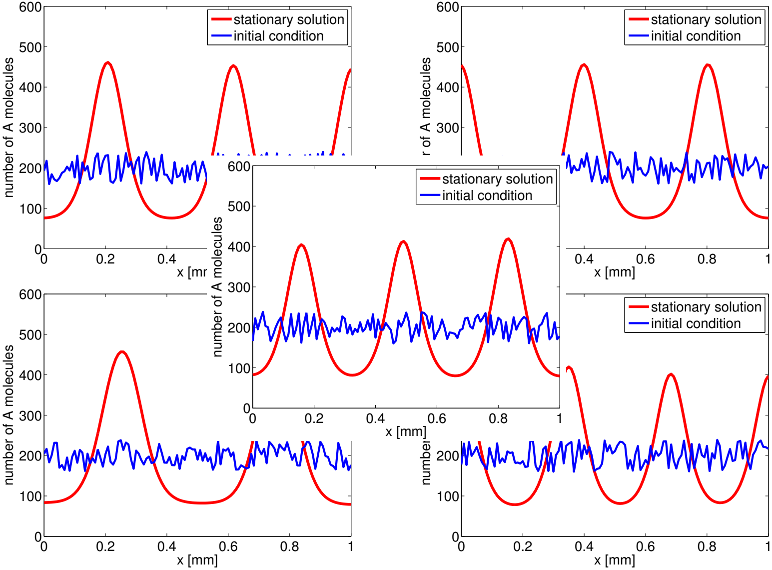


Schnakenberg – dependence on initial cond.



Schnakenberg – sharper conditions

(b) (u_0, v_0) is unstable to spatial disturbances if $\exists k > 0$:

$$\lambda_k = \frac{1}{2}\left[-b_k + \sqrt{b_k^2 - 4h_k}\right] > 0 \ldots \text{ dispersion relation}$$

$$\Leftrightarrow$$

$$h_k = d_1 d_2 \mu_k^2 - (d_2 f_u + d_1 g_v)\mu_k + \det A < 0 \ldots \text{ hyperbolas}$$

Solutions of linearization: $\begin{pmatrix} u \\ v \end{pmatrix}(x,t) = \mathbf{w}_k(x,t) = \mathrm{e}^{\lambda_k t} z_k(x) \mathbf{U}_k,$

where

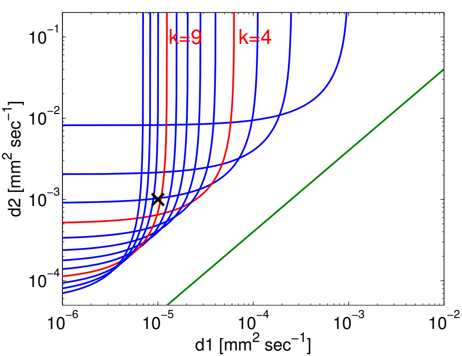
$$\left.\begin{array}{l} -z_k'' = \mu_k z_k \quad \text{in } (0,1) \\ z_k(0) = z_k(1) = 0 \end{array}\right\} \Leftrightarrow \left\{\begin{array}{l} z_k = \cos(k\pi x), \quad k = 0, 1, 2, \ldots \\ \mu_k = k^2\pi^2 \end{array}\right.$$

$$[A - \mu_k D]\mathbf{U}_k = \lambda_k \mathbf{U}_k, \quad D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}$$

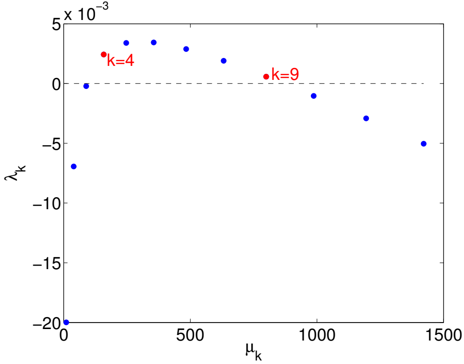
General solution of linearization: $\mathbf{w}(x,t) = \sum_{k=0}^{\infty} c_k \mathbf{w}_k(x,t)$

Schnakenberg

Hyperbolas



Dispersion relation

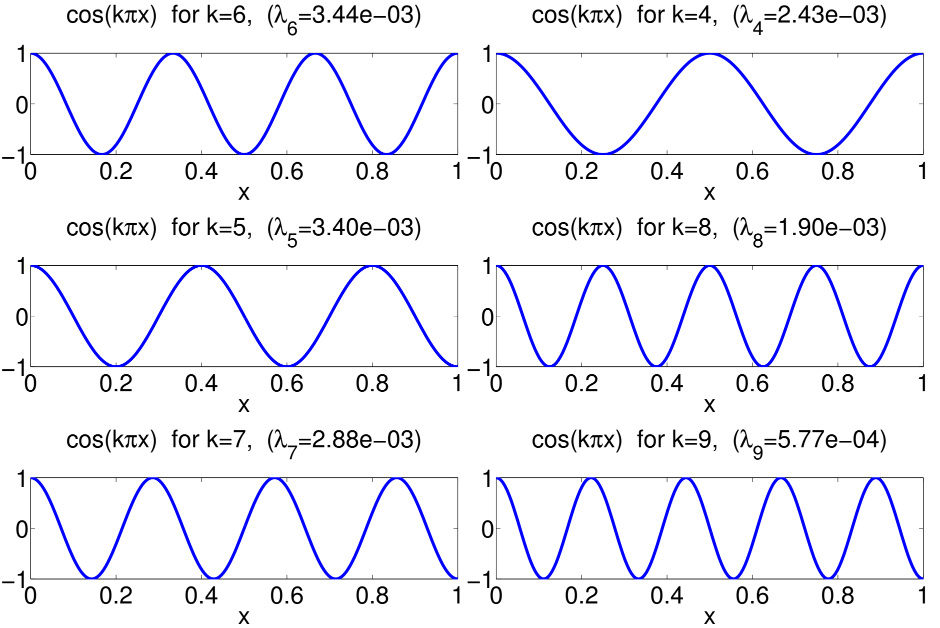


$d_1 = 10^{-5}$ $d_2 = 10^{-3}$ [mm^2 sec^{-1}]

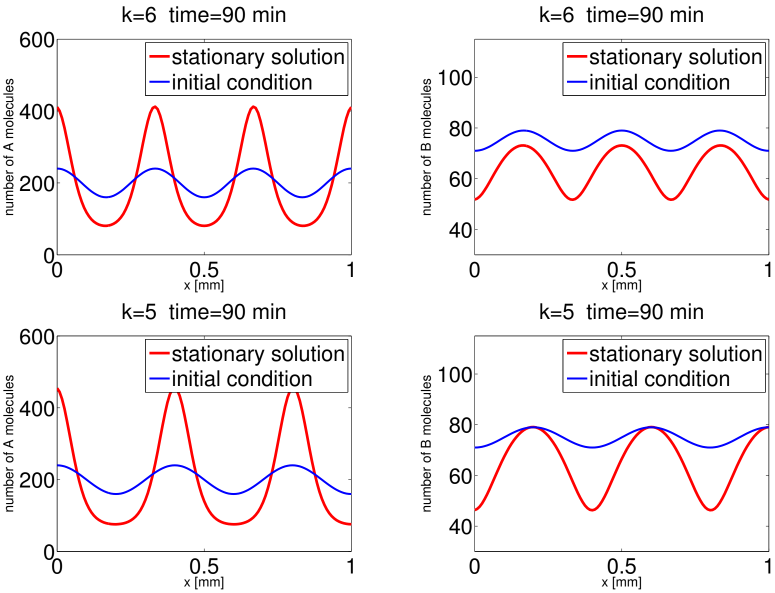
Point (d_1, d_2) lies inside hyperbolas for $k = 4, 5, \ldots, 9$.

$\lambda_6 > \lambda_5 > \lambda_7 > \lambda_4 > \lambda_8 > \lambda_9$

Schnakenberg – Laplace eigenmodes



Schnakenberg – dependence on initial cond.



Schnakenberg – dependence on initial cond.

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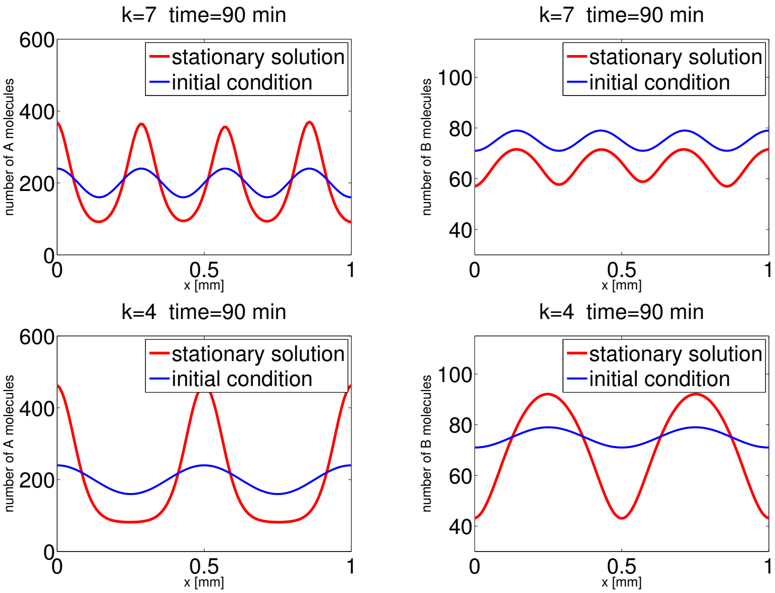
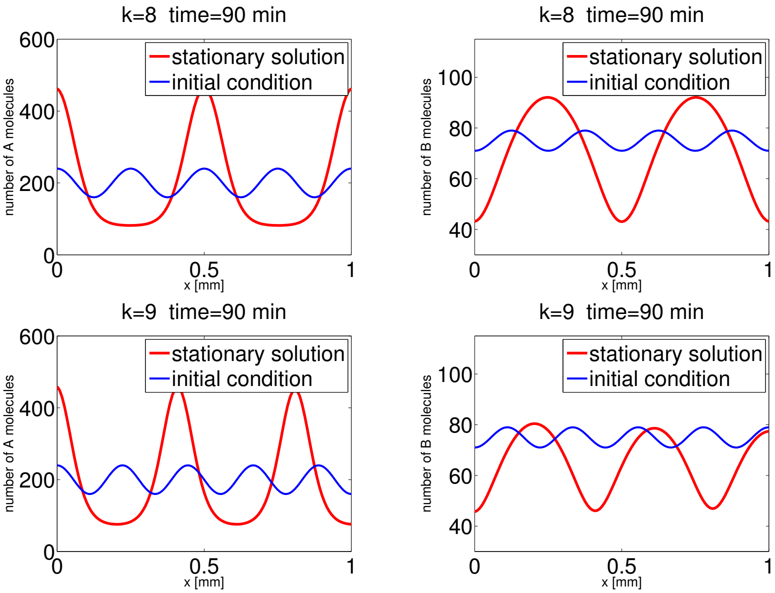


Schnakenberg – dependence on initial cond.



Schnakenberg 2D – sharper conditions

(b) (u_0, v_0) is unstable to spatial disturbances if $\exists k, \ell > 0$:

$$\lambda_{k,\ell} = \frac{1}{2}\left[-b_{k,\ell} + \sqrt{b_{k,\ell}^2 - 4h_{k,\ell}}\right] > 0 \ \ldots \ \text{dispersion relation}$$

$$\Leftrightarrow$$

$$h_{k,\ell} = d_1 d_2 \mu_{k,\ell}^2 - (d_2 f_u + d_1 g_v)\mu_{k,\ell} + \det A < 0 \ \ldots \ \text{hyperbolas}$$

Solutions of linearization: $\begin{pmatrix} u \\ v \end{pmatrix}(x,t) = \mathbf{w}_{k,\ell}(x,t) = \mathrm{e}^{\lambda_{k,\ell} t} z_{k,\ell}(x)\mathbf{U}_{k,\ell}$,

where $\Omega = (0,1)^2,\ k, \ell = 0, 1, 2, \ldots$

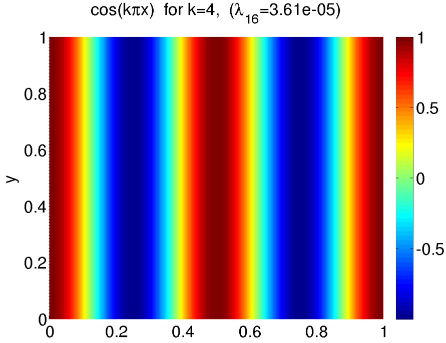
$$\left.\begin{array}{ll} -\Delta z_{k,\ell} = \mu_{k,\ell} z_{k,\ell} & \text{in } \Omega \\ \partial z_{k,\ell}/\partial \mathbf{n} = 0 & \text{on } \partial\Omega \end{array}\right\} \Leftrightarrow \left\{\begin{array}{l} z_{k,\ell} = \cos(k\pi x)\cos(\ell\pi x) \\ \mu_{k,\ell} = (k^2 + \ell^2)\pi^2 \end{array}\right.$$

$$[A - \mu_{k,\ell} D]\mathbf{U}_{k,\ell} = \lambda_{k,\ell}\mathbf{U}_{k,\ell}, \quad D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}$$

General solution of linearization: $\mathbf{w}(x,t) = \sum_{k,\ell=0}^{\infty} c_{k,\ell}\mathbf{w}_{k,\ell}(x,t)$

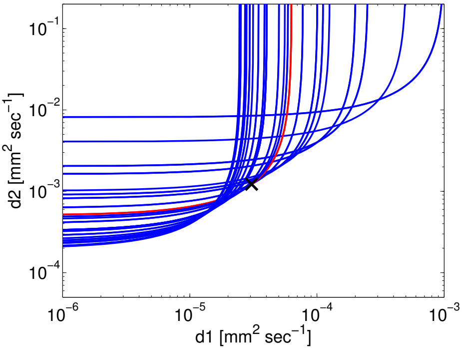
Schnakenberg 2D

Laplace eigenmode:

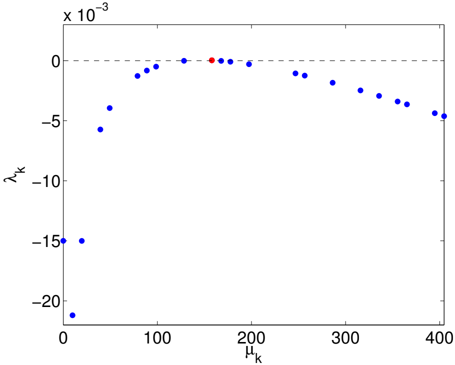


Schnakenberg 2D

Hyperbolas



Dispersion relation



$d_1 = 3.055 \times 10^{-5}$ $d_2 = 1.225 \times 10^{-3}$ [mm^2 sec^{-1}]

Point (d_1, d_2) lies inside the hyperbola for $k = 4$, $\ell = 0$.

Schnakenberg 2D

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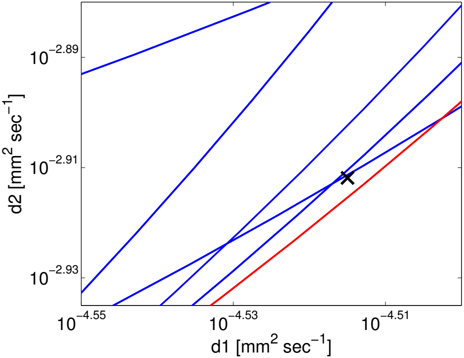
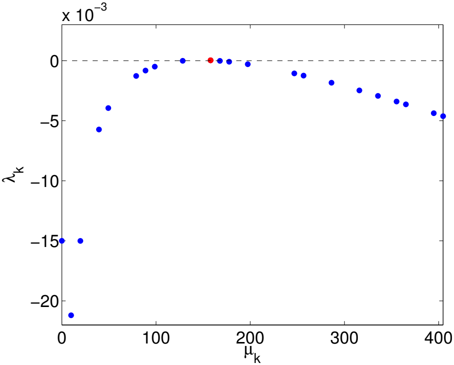
Hyperbolas



Dispersion relation

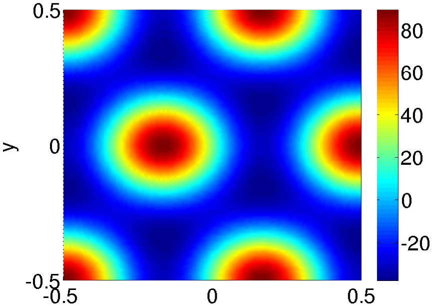


$d_1 = 3.055 \times 10^{-5}$ $d_2 = 1.225 \times 10^{-3}$ [mm^2 sec^{-1}]

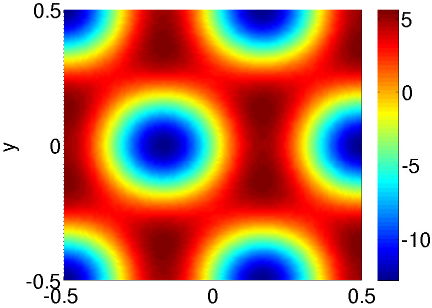
Point (d_1, d_2) lies inside the hyperbola for $k = 4$, $\ell = 0$.

Schnakenberg 2D – stationary state

Number of A molecules



Number of B molecules



Summary

- General conditions for Turing instability
- Schnakenberg system in 1D – stochastically and deterministically
- Schnakenberg system in 2D

Acknowledgement

I am thankful to Radek Erban and Philip K. Maini for their support and fruitful discussions about the topics presented during this summer school.

Marie Curie Fellowship, StochDetBioModel

EUROPEAN COMMISSION

The research leading to these results has received funding from the People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme (FP7/2007-2013) under REA grant agreement no. 328008.

Thank you for your attention

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