Spatio-Temporal Chaos in Chemotaxis Models

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Outline

The minimal model (M1)

- Patlak '53
- Keller and Segel, '70

Minimal model

$$\begin{aligned} u_t &= \nabla\left(D\nabla u - \chi u \nabla v\right), \\ v_t &= \Delta v + u - v. \end{aligned} \tag{M1}$$

$u(x,t)$: cell density
$v(x,t)$: chemical signal

Horstmann's review '03

[D. Horstmann, Jahresberichte DMV, 105, 103-165, 2003.]

- model derivations
- steady states
- blow-up
- general mathematical properties
- self similar solutions, traveling waves

(M1) shows finite time blow-up

Theorem (1992-2007)

Childress, Percus, Jäger, Luckhaus, Nagai, Senba, Yoshida, Herrero, Velazquez, Levine, Sleeman, Gajewski, Zacharias, Biler, Post, Horstmann, Suzuki, Yagi, Potapov, Hillen, Perthame, etc

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2-D: *quantized blow-up (Suzuki '05, Hortsmann '03)*
boundary blow-up takes mass $\frac{4\pi}{\chi}$
interior blow-up takes mass $\frac{8\pi}{\chi}$.
Let $\bar{u}_0 = \int u_0(x)dx$. *If* $\|u_0\|_1 < \frac{4\pi}{\chi}$ *then global existence.*

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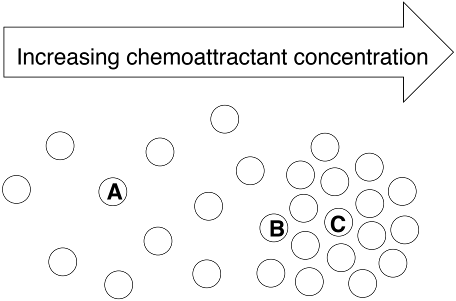
n-D: *There is a threshold in* $L^{n/2}$ *(Perthame et al. 05).*

Outline

The Volume Filling Approach (M3a)



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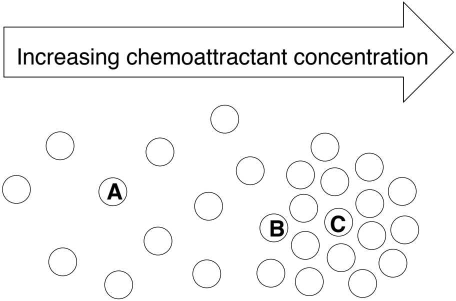

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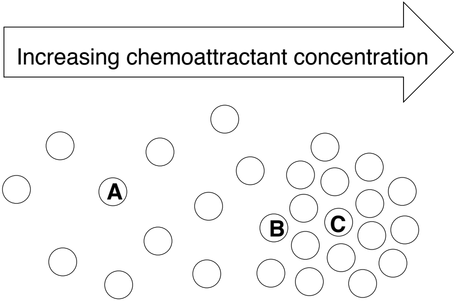

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- Assumption

$$q(U_{\text{max}}) = 0 \text{ and } q(u) \geq 0 \text{ for all } 0 \leq u < U_{\text{max}}.$$

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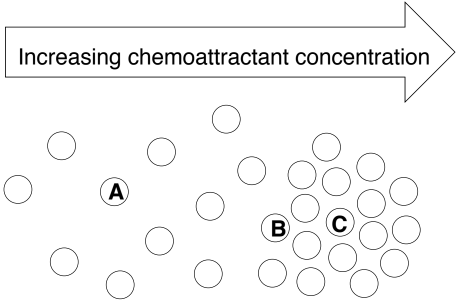

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- Assumption

$$q(U_{\max}) = 0 \text{ and } q(u) \geq 0 \text{ for all } 0 \leq u < U_{\max}.$$

- Standard example: $U_{\max} = 1, \qquad q(u) = 1 - u.$

The Volume Filling Model

We use a Master equation approach to derive:

$$
\begin{aligned}
u_t &= \nabla(D(q(u) - q'(u)u)\nabla u - q(u)u\chi(v)\nabla v) \\
v_t &= \Delta v + u - v
\end{aligned}
$$

Pattern Formation

- H', Painter, AAM, 2000
- Painter, H', CAMQ 2002
  Derivation of the volume filling model; proof of global existence for special cases; pattern formation.

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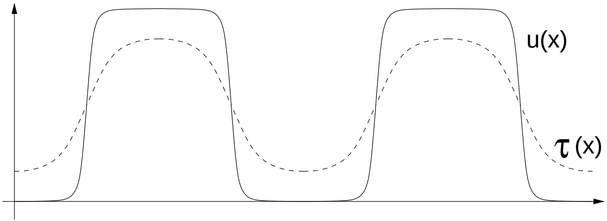
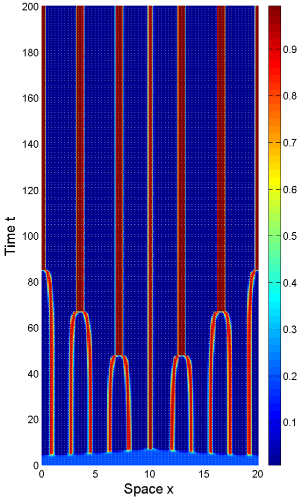
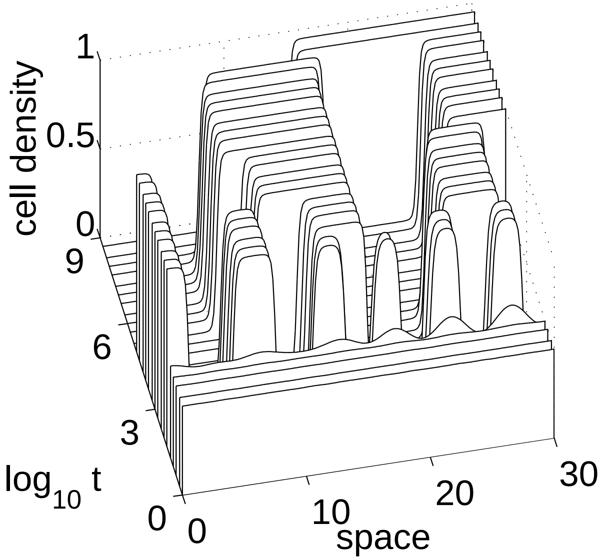
Non trivial steady states:



Z.A. Wang et al '07

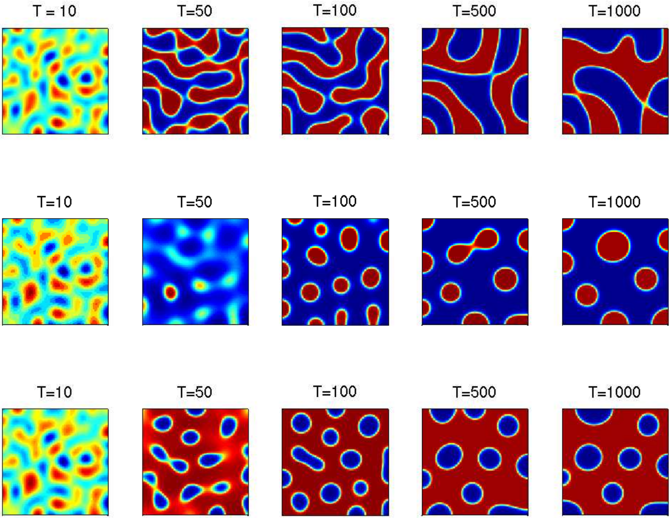


Pattern Formation in 1-D



Pattern Formation in 2-D

$\bar{u}_0 = 0.5$ (top), 0.25 (middle), 0.75 (bottom)



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  Existence of a compact global attractor.

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  Bifurcation diagram, metastability, numerical estimates of leading eigenvalues, scaling analysis and pattern interaction.

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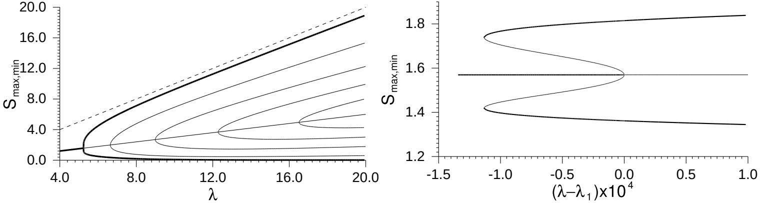
  Bifurcation Diagram



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- Dolak, H' 2003:
  Application to *Dictyostelium discoideum* and to *Salmonella typhimurium*.

Outline

Regularizations

- Signal dependent sensitivity (M2a), (M2b)
- Density dependent sensitivity (M3a), (M3b)
- Non-local gradient (M4)
- Non-linear diffusion (M5)
- Non-linear signal kinetics (M6)
- Non-linear gradient (M7)
- Cell kinetics (M8)

Receptor Model (M2a)

$$
\begin{aligned}
u_t &= \nabla\left(D\nabla u - \frac{\chi u}{(1+\alpha v)^2}\nabla v\right)\\
v_t &= \nabla^2 v + u - v
\end{aligned}
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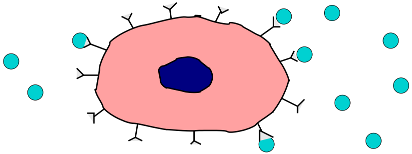
$$u_t = \nabla \left(D\nabla u - \frac{\chi u}{(1+\alpha v)^2} \nabla v \right)$$

$$v_t = \nabla^2 v + u - v$$

- Othmer, Stevens '97
- Segel '76 '77, Ford et al '91, Tyson et al '99, Levine and Sleeman '97



Logistic model (M2b)

$$\begin{aligned} u_t &= \nabla\left(D\nabla u - \chi u \frac{1+\beta}{v+\beta}\nabla v\right) \\ v_t &= \nabla^2 v + u - v \end{aligned}$$

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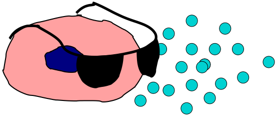
- Keller, Segel '71, Dahlquist et al '72, Nanjundiah '73
- see review in Horstmann '03



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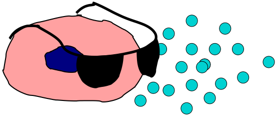

- Popular choice: $\beta = 0$
- Nanjundiah '73: *"... even this fails at both, very small and very large concentrations."*

Volume-Filling (M3a)

$$
\begin{aligned}
u_t &= \nabla\left(D\nabla u - \chi u\left(1-\frac{u}{\gamma}\right)\nabla v\right)\\
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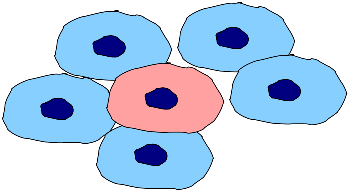
- H, Painter '01 '02, Wang, H '07
- Wrzosek '04, Dolak, Schmeiser '05



Velazquez' model (M3b):

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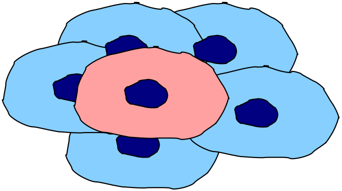
- Velazquez '04



Non-Local Model (M4)

$$
\begin{aligned}
u_t &= \nabla \left(D \nabla u - \chi u \overset{\circ}{\nabla}_\rho v \right) \\
v_t &= \nabla^2 v + u - v
\end{aligned}
$$

Non-local gradient:

$$\overset{\circ}{\nabla}_\rho v(x,t) = \frac{n}{|S^{n-1}|\rho} \int_{S^{n-1}} \sigma v(x + \rho\sigma, t) \, d\sigma,$$

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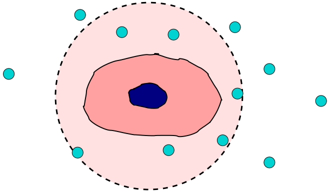
- Othmer, H '02
- H, Painter, Schmeiser '06



Nonlinear Diffusion (M5)

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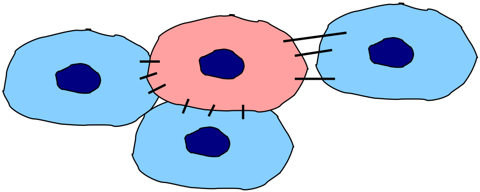
- Kowalczyk '05
- Eberl '01, biofilm, Höfer et al. '95,



Nonlinear Signal Kinetics (M6)

$$
\begin{aligned}
u_t &= \nabla\left(D\nabla u - \chi u \nabla v\right) \\
v_t &= \nabla^2 v + \frac{u}{1+\phi u} - v,
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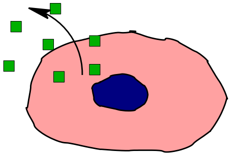
$$

- Höfer et al '95, Woodward et al '95
- Myerscough et al '98, Post '99.



Nonlinear Gradient (M7)

$$\begin{aligned} u_t &= \nabla\left(D\nabla u - \chi u \mathbf{F}_c(\nabla v)\right) \\ v_t &= \nabla^2 v + u - v, \end{aligned}$$

$$\mathbf{F}_c(\nabla v) = \frac{1}{c}\left(\tanh\left(\frac{c v_{x_1}}{1+c}\right), \ldots, \tanh\left(\frac{c v_{x_n}}{1+c}\right)\right).$$

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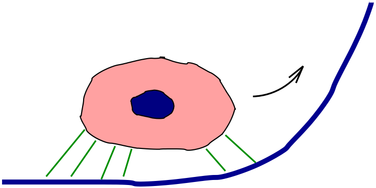
$$

- Rivero et al '89



Cell Kinetics (M8)

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\begin{aligned}
u_t &= \nabla\left(D\nabla u - \chi u \nabla v\right) + ru(1-u) \\
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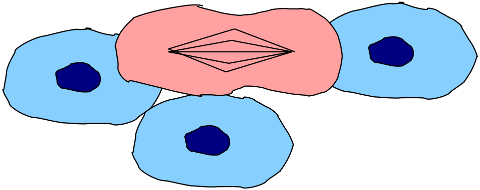
- Tyson '99, Woodward '95, Chaplain, Stuart '93
- Osaki et al '02, Wrzosek '04,



Global Existence

Model	a-priori est.	Lyap. fct.	Reference

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(M4)	Yes		H, Painter, Schmeiser '07

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(M6)		Yes	Horstmann '01

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(M6)		Yes	Horstmann '01
(M7)	Yes		H, Painter, '08

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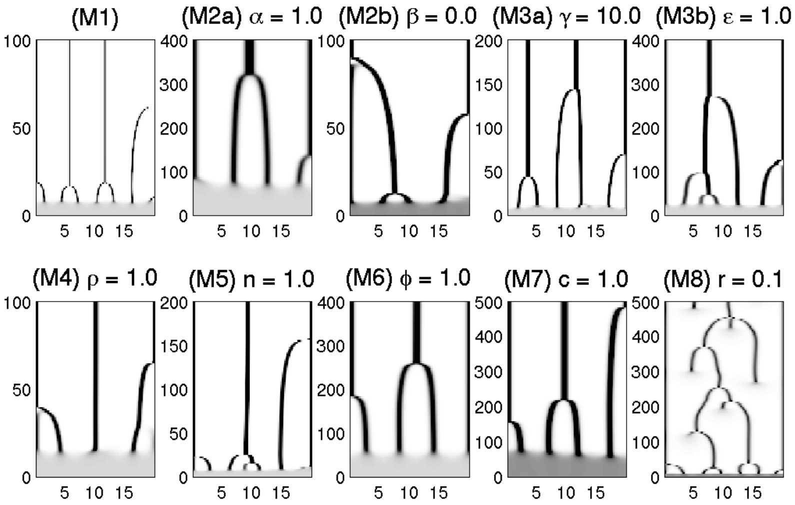
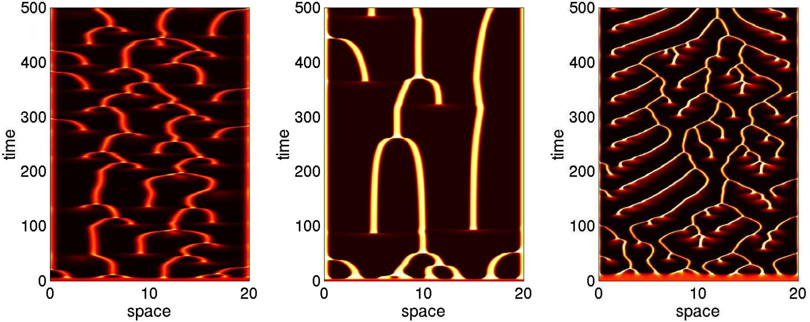
(M7)	Yes		H, Painter, '08
(M8)	Yes	Yes	Osaki et al, '02, Wrzosek '06

Pattern Formation



Merging-Emerging, (M3a) + (M8)



Outline

A chemotaxis model with growth, (M8)

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- Consider on $[0, L]$ with homogeneous boundary conditions.

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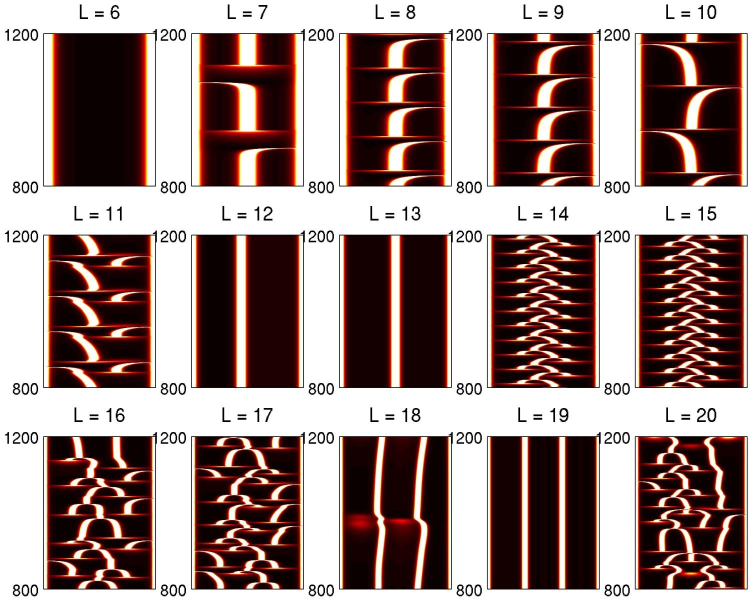
- Fix $\chi = 10$, $D = 1$ and vary L:

Varying Interval Length



Applications

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  - pigmentation of alligator and snake skin

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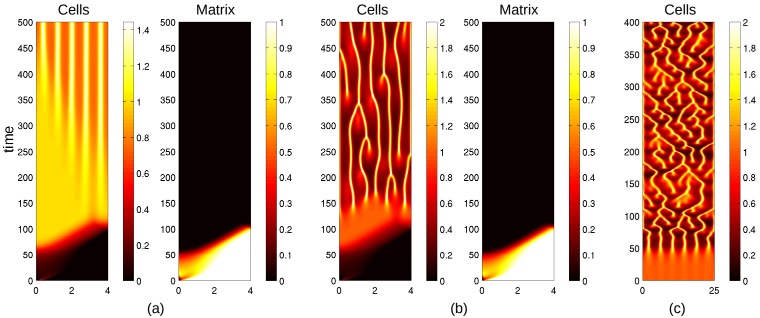
  - embryonic pattern formation
  - pigmentation of alligator and snake skin
- Orme, Chaplan 1996:
  - Capillary sprouting in tumor angiogenesis

Chaplain Lolas model

- Chaplain, Lolas, Gerisch et al. (2005, 06, 10):
  Tumor invasion into extracellular matrix



Mathematically

- Mimura et al. 1996:
  - Allee like nonlinearity $f(u) = u(1-u)(u-a)$.
  - domain separates into regions where the solution
  is close to 1 and regions where the solution is close to 0.
  - they develop an asymptotic theory for movement of the
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- Aida 2006:
  - lower estimate of the fractal dimension of the attractor
  - **Theorem:** $\dim A \geq$ number of unstable modes of $(1,1)$.
  - 2D simulations of periodic or irregular behavior.

Mathematically

- Mimura et al. 1996:
  - Allee like nonlinearity $f(u) = u(1-u)(u-a)$.
  - domain separates into regions where the solution is close to 1 and regions where the solution is close to 0.
  - they develop an asymptotic theory for movement of the transition layers.
- Osaki et al., 2002:
  - existence of a compact global attractor for (1) in $L^2(\Omega) \times H^1(\Omega)$, $\Omega \subset \mathbb{R}^2$.
- Aida 2006:
  - lower estimate of the fractal dimension of the attractor
  - **Theorem:** dim $A \geq$ number of unstable modes of $(1, 1)$.
  - 2D simulations of periodic or irregular behavior.
- Tello, Winkler 2007, Winkler 2010:
  - existence of unique global solutions for (1) in any space dimension, for smooth enough initial data.

Including squeezing

Wang, H', 2007: Include a squeezing probability $q(u)$:

$$\begin{aligned} u_t &= \nabla\left(D(q(u) - q'(u)u)\nabla u - \chi u q(u)\nabla v\right) + ru(1-u) \\ v_t &= \Delta v + u - v\,. \end{aligned}$$

Case 1:

$$q(u) = (2 - u^\gamma)_+, \quad \gamma \geq 1$$

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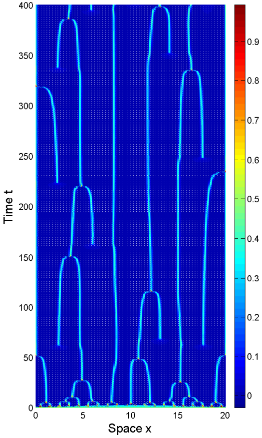
$$q(u) = (2 - u^{\gamma})_+, \quad \gamma \geq 1$$

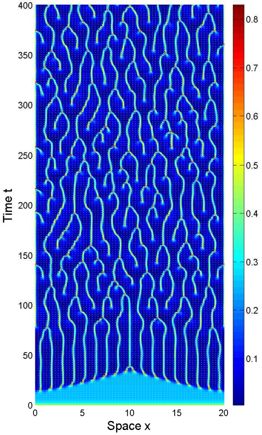
Case 2:

$$q(u) = (2 - u)_+^{\alpha}, \quad \alpha \leq 1$$

Case 2 leads to a fast diffusion problem, see Wrzosek et al.

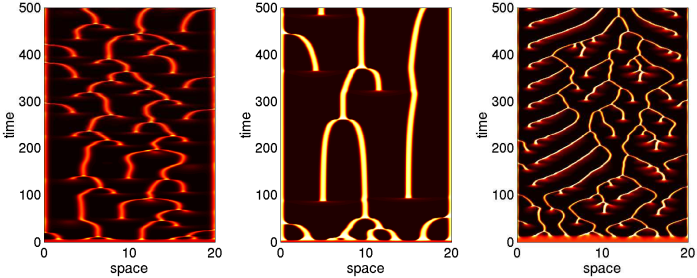
Pattern with squeezing $q(u)$





Merging-Emerging, (M3a) + (M8)

- merging: If two local maxima are close then they join and form one maximum.
- emerging: If two local maxima are far apart, then a new maximum arises between them.



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U_t &= DU_{xx} - rU\,, \\
V_t &= V_{xx} + U - V\,. \\
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0 &= V_x(0,t) = v_x(l,t)
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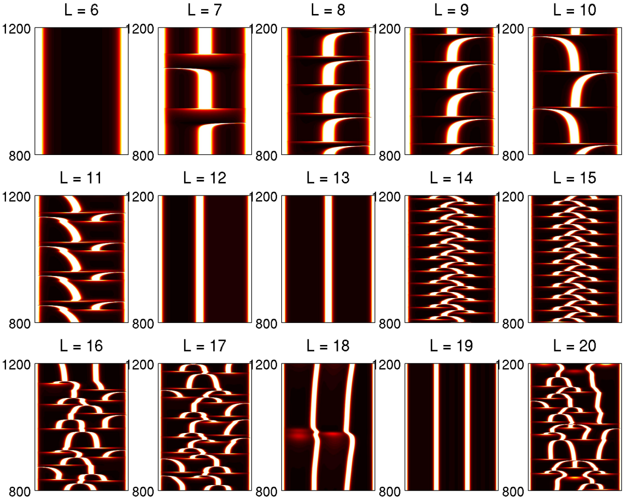
- Nontrivial solutions exist for

$$
l > l_e := 2\pi\sqrt{\frac{D}{r}}.
$$

Example

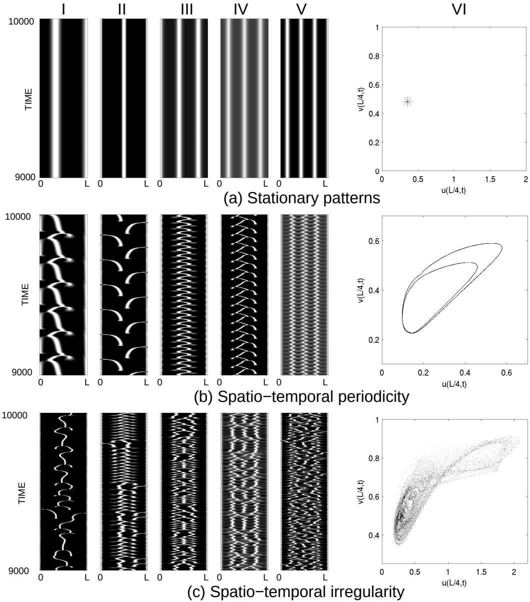
$$\chi = 10, \quad D = r = 1, \quad l_e = 2\pi \approx 6.28$$



Classification of Solutions

- H-solutions: homogeneous steady states (no pattern)
- S-solutions: stationary patterns
- P-solutions: periodic patterns
- I-solutions: irregular patterns

Solution Types



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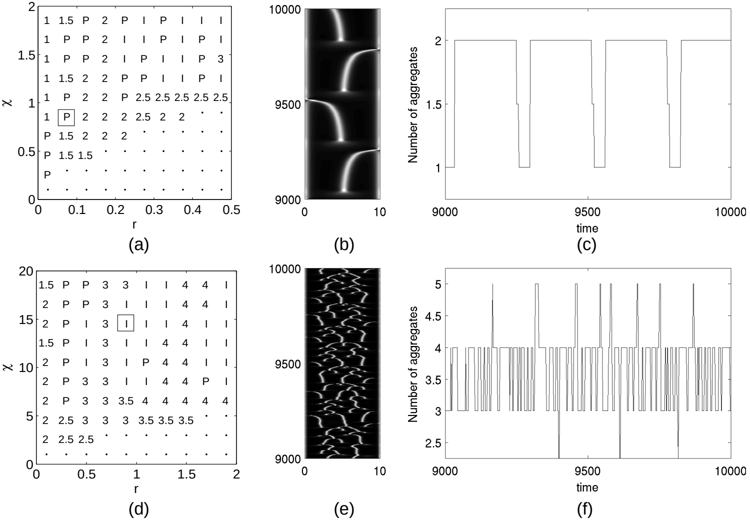

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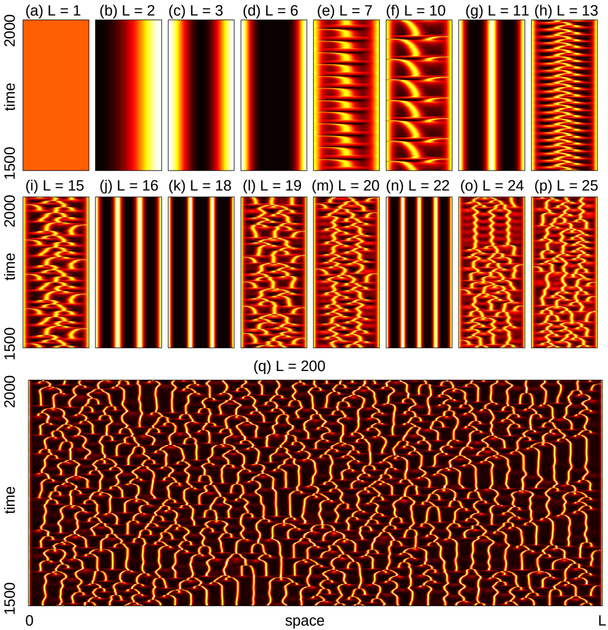

Lyapunov Exponent $\mathcal{L}$

The Lyapunov exponent is a measure for the sensitive dependence on intitial conditions.

Take two solutions $u(x,t)$, and $u_{pert}(x,t)$, then

$$\mathcal{L}(t) = \log_{10}\left(\frac{1}{L}\int_0^L |u(x,t) - u_{pert}(x,t)|dx\right)$$

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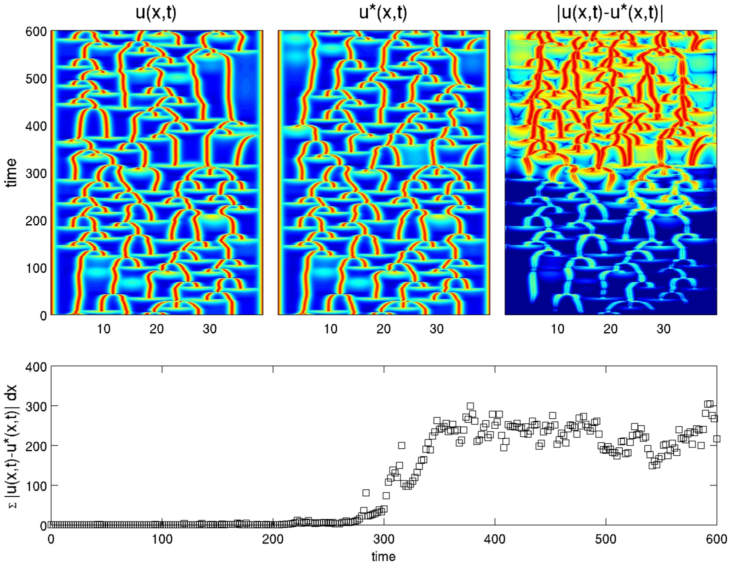
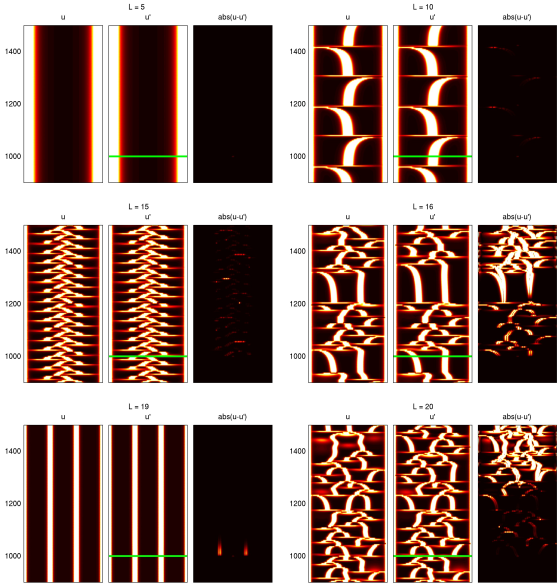
Fit $\mathcal{L}(t)$ by a linear curve with slope λ.

- If $\lambda < 0$, then solutions converge exponentially (stability).
- If $\lambda \approx 0$, then solutions keep their distance (e.g. periodic).
- If $\lambda > 0$, then solutions diverge exponentially.

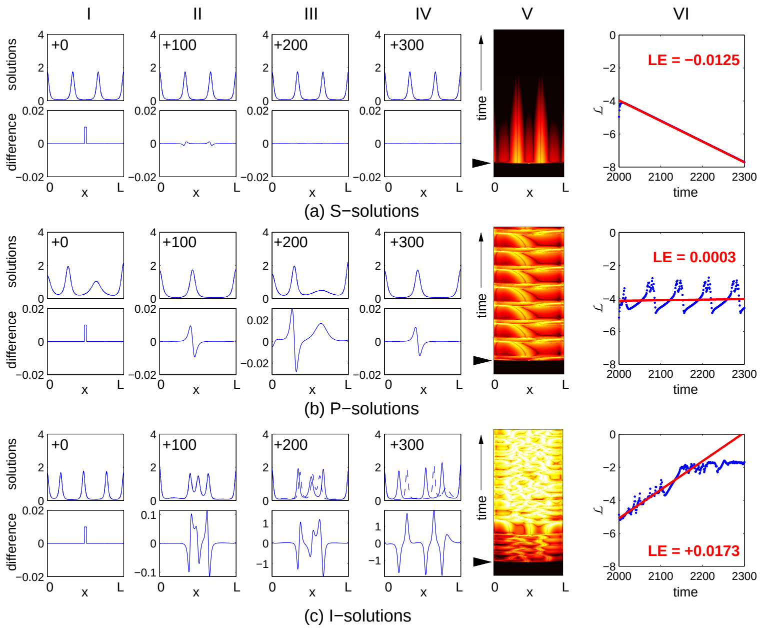
Comparison


u(x,t)
u*(x,t)
|u(x,t)-u*(x,t)|
time
600
500
400
300
200
100
0
10
20
30
Σ |u(x,t)-u*(x,t)| dx
400
300
200
100
0
0
100
200
300
400
500
600
time

Comparison

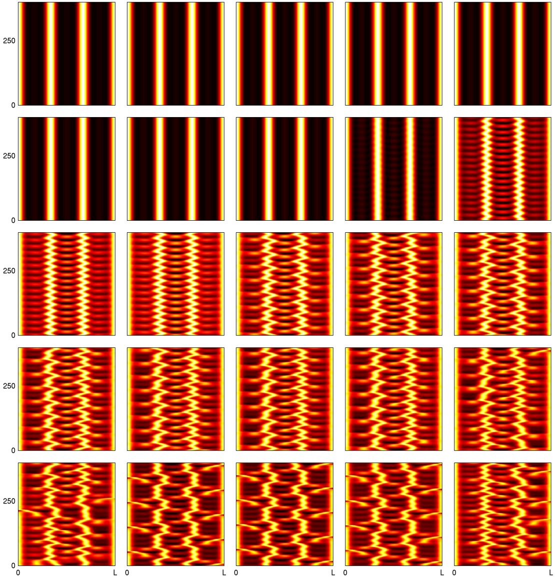

L = 5
u
u'
abs(u-u')
1400
1200
1000
L = 10
u
u'
abs(u-u')
1400
1200
1000
L = 15
u
u'
abs(u-u')
1400
1200
1000
L = 16
u
u'
abs(u-u')
1400
1200
1000
L = 19
u
u'
abs(u-u')
1400
1200
1000
L = 20
u
u'
abs(u-u')
1400
1200
1000

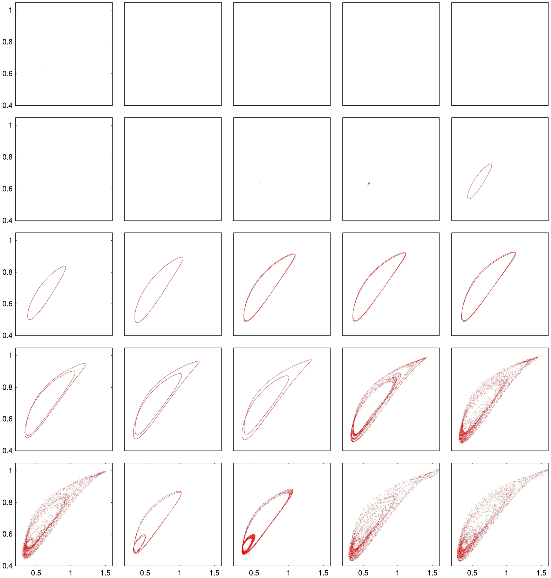
Comparison



I
II
III
IV
V
VI
solutions
difference
+0
+100
+200
+300
time
x
L
LE = −0.0125
LE = 0.0003
LE = +0.0173
(a) S−solutions
(b) P−solutions
(c) I−solutions

Period Doubling, increase χ





1
0.8
0.6
0.4
0.5
1
1.5

Outline

Conclusions

- Merging dynamics is common to all regularizations studied.

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Conclusions

- Merging dynamics is common to all regularizations studied.
- The logistic chemotaxis model (M8) shows many characteristics which are typically associated to chaotic dynamics.
- We gave some evidence of chaotic like behavior (positive Lyapunov exponent, period doubling). We tested many more parameter sets and they show the same behavior.
- There are many routes for further investigation:
  - Is there a way to characterize a merging distance?
  - Better understand steady states and their stability
  - Geometric analysis of the attractor?
  - Higher dimensions

Thank You

- Thanks to you
- Thanks to the organizers
- Thanks to my coauthor K.J. Painter
- My work is supported by NSERC and MITACS