

Modeling of collective dynamics in *Myxococcus xanthus* with congestion constraints

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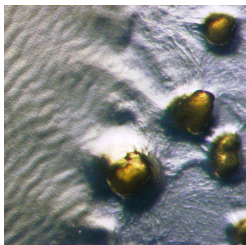
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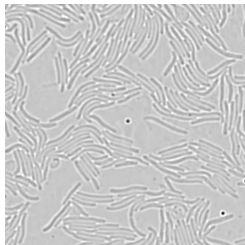
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Myxococcus xanthus



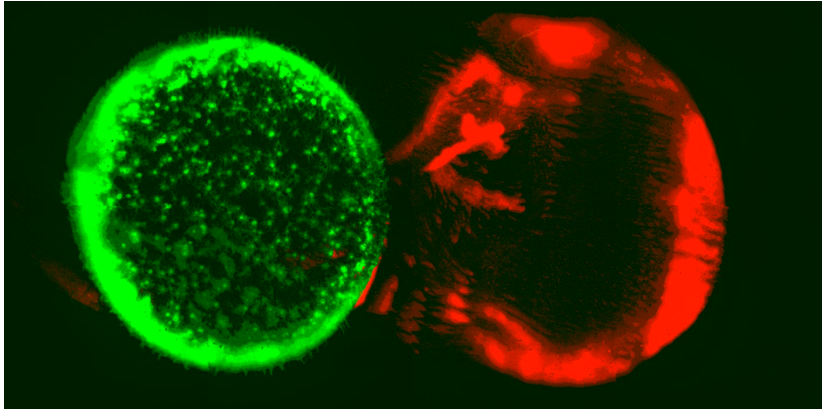
Credits: Z. Vaksman and H. Kaplan



Credits: Y. Deng, P. Coen, *et al.*

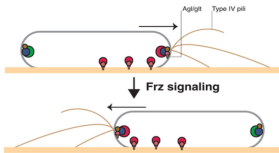
- Type of organism: → **Predatory bacterium** of the soil
- Shape: Rod-shaped (bacillus)
- Scientific interest:
 - → **bacterial cooperation** and pattern formation
 - → **collective motility** and cell differentiation mechanisms.

Collective dynamics: predation of *Escherichia coli*

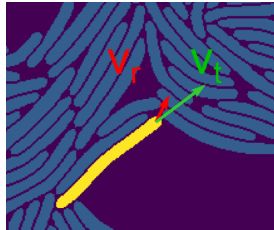


Credits: Saulnier et al. 2024

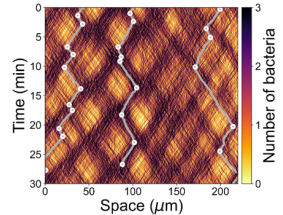
Gliding motility



Credits: Guzzo et al. 2015



Credits: Saulnier et al. 2024



Credits: Saulnier et al. 2024

- Motility: “grapling hooks” (social) or cellular motor (individual)
- → **Persistent motion**
- Polarization mechanism → **refractory period**
- High resolution data → **tracking + experimental kymographs**

- **Nematic alignment**
 - Degond, Manhart, and Yu 2018; Hittmeir et al. 2021
 - Age-structured model and micro-to-macro hierarchy : Degond, Manhart, and Yu 2018; Manhart 2019
 - **Tunable refractory period + frustration** : Saulnier et al. 2024
 - **Review articles** : Eftimie 2012; Hadeler 1999
 - **Local sensing of bacteria** → **Does not fit experimental data !**
- **Goal:** observe pattern formation with a **non local signal** and a **congestion constraint**

A two species congestion model

Approximation of the congestion

The full model

Numerical results

Conclusion and perspectives

A two species congestion model

A two species congestion model

Let $t > 0$, $x \in \mathbb{T}$. The densities $f(t, x)$ and $g(t, x)$ are solution to

$$\begin{cases} \partial_t f + \partial_x ((1 - \partial_x \mathbf{p}) f) = 0 \\ \partial_t g + \partial_x ((-1 - \partial_x \mathbf{p}) g) = 0 \end{cases}$$

The pressure $p(t, x)$ satisfies the complementarity conditions

$$p \geq 0, \quad 1 - \rho \geq 0, \quad p(1 - \rho) = 0$$

with $\rho(t, x) = f(t, x) + g(t, x)$

→ **Crowds modeling**¹

→ **Cross diffusion**³

→ **Porous media/Muskat problem**²

→ **Tumor growth / Hele-Shaw**⁴

¹Maury and Venel 2011; Dambrine et al. 2012; Peyré 2015; Bourdin 2022a.

²Otto 1999; Jacobs, Kim, and Mészáros 2021.

³Kim and Mészáros 2018; Elbar and Santambrogio 2025; Mészáros and Parker 2026.

⁴Perthame, Quirós, and Vázquez 2014; David and Perthame 2021; Liu et al. 2018.

Explicit pressure

Evolution of $\rho = f + g$ and $m = f - g$:

$$\partial_t \rho + \partial_x [m - \rho \partial_x \rho] = 0, \quad \partial_t m + \partial_x [\rho - m \partial_x \rho] = 0$$

Lemma 1

Let $S(t) = \{x, \rho(t, x) = 1\}$ and assume $S(t) = [a(t), b(t)]$.

Let $x \in [a(t), b(t)]$, then

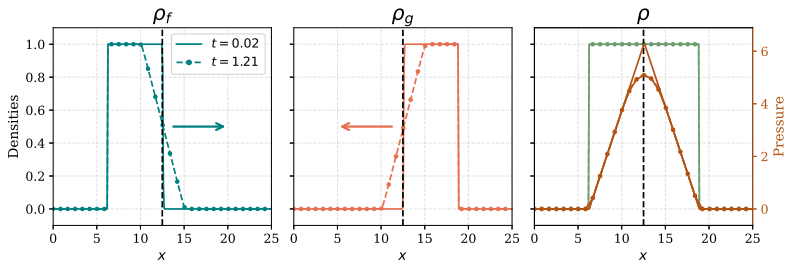
$$\partial_x \rho(t, x) = m(t, x) - \langle m \rangle(t), \quad \langle m \rangle(t) = \frac{1}{b(t) - a(t)} \int_{a(t)}^{b(t)} m(t, x) dx$$

and

$$\partial_t m - \partial_x [m^2 - \langle m \rangle m] = 0$$

- **Unstable numerically**
- **Non-local Burgers equation !**
- **Rarefaction wave structure inside congestion, explicit solutions**

Blocking configuration ?



Approximation of the congestion

- **Variational approach in porous media** : Benamou, Carlier, and Laborde 2016; Cancès et al. 2019; Cancès, Gallouët, and Todeschi 2020
- **JKO schemes in crowd modeling** : Maury, Roudneff-Chupin, and Santambrogio 2010; Peyré 2015; Bourdin 2022a; Bourdin 2022b
- **Pressure regularization + AP schemes** : Liu et al. 2018; David and Ruan 2022; Perrin and Saleh 2022
- → **Splitting schemes** : Maury et al. 2011; Maury and Preux 2017; Bourdin 2022b

→ **Multispecies + hard congestion + independent drifts**

Algorithm 1 One time-step update

1. Prediction without constraint:

Advect f^n and g^n in x at velocities ± 1 to obtain f^* , g^* and ρ^*

2. Pressure computation:

Compute the pressure using ρ^* , yielding p^{n+1}

3. Constrained advection:

Advect f^n and g^n at velocities $(\pm 1 - \partial_x p^{n+1})$ to obtain f^{n+1} , g^{n+1}

→ **Steps 1 and 3** : second order finite volume schemes (explicit)

Solving the pressure

$$\rho \geq 0, \quad 1 - \rho \geq 0, \quad \rho(1 - \rho) = 0$$

→ **Non-smooth problem**, classical for 1st order in time models

Elliptic equation on the pressure:

$$\partial_t \rho + \partial_x [m - \rho \partial_x p] = 0$$

Time discretization: $\rho = \rho^* - \Delta t \partial_x (\rho^* \partial_x p)$

The Fischer-Burmeister function: $\Phi(a, b) = \sqrt{a^2 + b^2} - a - b$

Main property: $\Phi(a, b) = 0 \Leftrightarrow a \geq 0, b \geq 0, ab = 0$

→ **Goal:** Solve $\Phi(\rho, 1 - \rho) = 0$

Newton's method

Jacobian:

$$J = D_a + \Delta t D_b A, \quad D_a := \frac{\partial \Phi}{\partial a}, \quad D_b := \frac{\partial \Phi}{\partial b}$$

Newton update: Solve

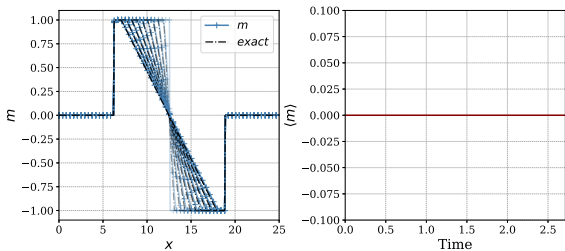
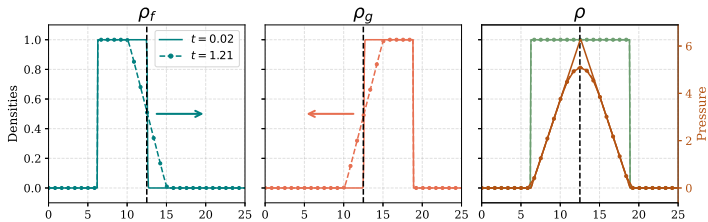
$$J \left(p^{(k+1)} - p^{(k)} \right) = -\Phi \left(p^{(k)}, \rho(p^{(k)}) \right)$$

→ **Non-smooth ! What are $\frac{\partial \Phi}{\partial a}$ and $\frac{\partial \Phi}{\partial b}$ near $(0,0)$?**

In practice: → **Regularized F-B function**

$$\phi_\epsilon(a, b) = \sqrt{a^2 + b^2 + \epsilon^2} - a - b, \quad \epsilon \approx 10^{-8}$$

Exact solution



The full model

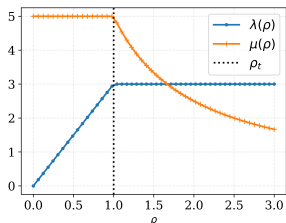
A structured PDE model with local sensing⁵

An age structured model. Let $t > 0$, $x \in \mathbb{T}$ and $r \in \mathbb{R}^+$. The densities $f(t, x, r)$ and $g(t, x, r)$ are solution to

$$\left\{ \begin{array}{l} \partial_t f + \partial_x f + \partial_r f = -\lambda(\rho) f H(r - \mu(\rho)) \\ \partial_t g - \partial_x g + \partial_r g = -\lambda(\rho) g H(r - \mu(\rho)) \\ f(t, x, 0) = \lambda(\rho) \int_{\mathbb{R}^+} g H(r - \mu(\rho)) dr \\ g(t, x, 0) = \lambda(\rho) \int_{\mathbb{R}^+} f H(r - \mu(\rho)) dr \end{array} \right.$$

where

- $\rho(t, x) = \int_{\mathbb{R}^+} f + g dr$ is the density
- λ is the reversal rate
- H is the Heaviside function
- μ modulates the refractory period



⁵Saulnier et al. 2024.

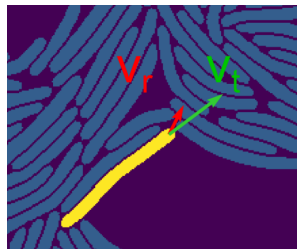
From local IBM to non-local constrained PDE

IBM in Saulnier et al. 2024:

Individual frustrations



“Lagrange multipliers”



Credits: Saulnier et al. 2024

Modeling assumptions:

1. One-dimensional motion of bacteria
2. Right/left polarization with a target velocity equal to ± 1
3. → **Congestion constraint** → **Non-local interactions** → **Pressure**
4. Reorientation rate : $\lambda(\text{pressure})$
5. Refractory period : $\mu(\text{pressure})$

A non-local sensing model with congestion

New hypothesis: **non-local** sensing via **congestion** ($\rho \leq 1$)

Let $t > 0$, $x \in \mathbb{T}$ and $r \in \mathbb{R}^+$. The densities $f(t, x, r)$ and $g(t, x, r)$ are solution to

$$\begin{cases} \partial_t f + \partial_x ((1 - \partial_x \mathbf{p}) f) + \partial_r f = -\lambda(\mathbf{p}) f H(r - \mu(\mathbf{p})) \\ \partial_t g + \partial_x ((-1 - \partial_x \mathbf{p}) g) + \partial_r g = -\lambda(\mathbf{p}) g H(r - \mu(\mathbf{p})) \\ f(t, x, 0) = \lambda(\mathbf{p}) \int_{\mathbb{R}^+} g H(r - \mu(\mathbf{p})) dr \\ g(t, x, 0) = \lambda(\mathbf{p}) \int_{\mathbb{R}^+} f H(r - \mu(\mathbf{p})) dr \end{cases}$$

The pressure p satisfies the complementarity conditions

$$p \geq 0, \quad 1 - \rho \geq 0, \quad p(1 - \rho) = 0$$

Numerical results

Algorithm 2 One time-step update

1. Prediction without constraint:

Advect f^n and g^n in x at velocities ± 1 to obtain f^* , g^*

2. Pressure computation:

Compute the pressure using f^* and g^* , yielding p^{n+1}

3. Constrained advection:

Advect f^n and g^n at velocities $(\pm 1 - \partial_x p^{n+1})$ to obtain f^{**} , g^{**}

4. Reversals:

Apply reversals implicitly (diagonal operator) to obtain f^{***} , g^{***}

5. Aging:

Advect f^{***} and g^{***} at velocity 1 in r to obtain f^{n+1} , g^{n+1}

→ **Steps 1, 3 and 5** : second order finite volume schemes (explicit)

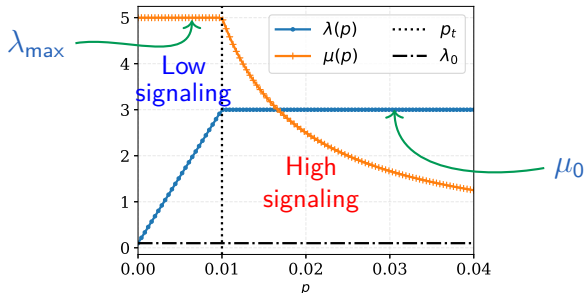
Setup

Parameters:

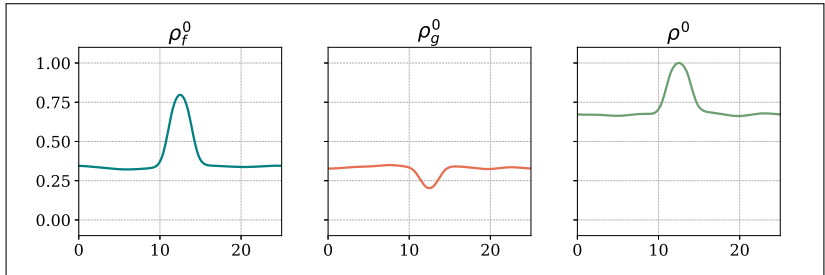
- $x_* = 25, r_* = 6$
- Threshold signal: $p_t = 0.01$
- Spontaneous reversals: $\lambda_0 = 0$
- Max reversal rate: $\lambda_{\max} = 3$
- Base refractory period: $\mu_0 = 5$

Numerical parameters:

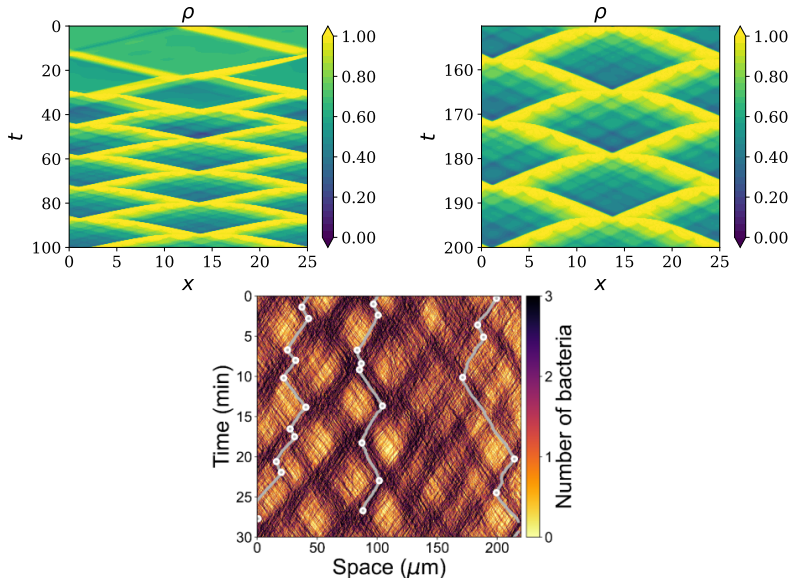
- $N_x = 200, N_r = 51$
 - $\Delta t = C \min\{\Delta x, \Delta r\}$
 $C = 0.005$
- **Stability + congestion**



Evolution of the densities

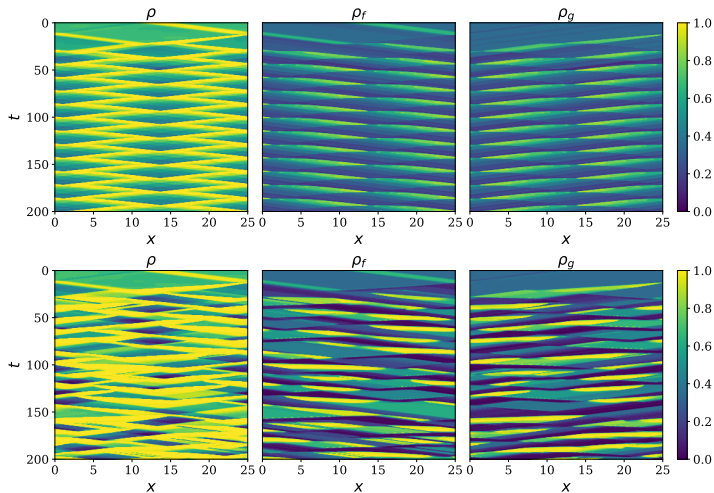


Pattern formation: kymographs



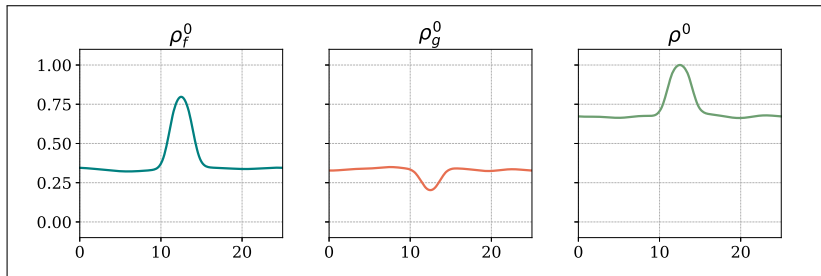
Simulations (Top) and experiment from [Saulnier et al. 2024](#) (Bottom)

Pattern formation: impact of modulation



Modulated (Top) and fixed refractory period

Evolution in the (x, r) -phase space



Conclusion and perspectives

Summary:

- New PDE model for *Myxococcus xanthus* including
 1. Congestion constraint
 2. Non-local sensing
- Numerical simulations exhibit the emergence of collective dynamics

Perspectives:

- Data fitting $\rightarrow \lambda, \mu, p_t$
- Numerical analysis / comparison with other schemes
- Analysis of the pure congestion model
- Hard congestion limit: $p = \rho^\gamma, \gamma \rightarrow \infty^6$, AP scheme⁷

⁶David and Perthame 2021; Dalibard and Perrin 2024.

⁷Liu et al. 2018; Perrin and Saleh 2022.

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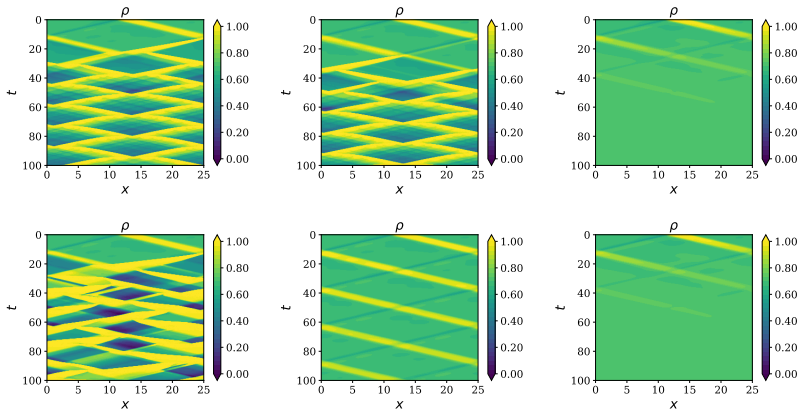
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Thank you for your attention !

⁶David and Perthame 2021; Dalibard and Perrin 2024.

⁷Liu et al. 2018; Perrin and Saleh 2022.

Spontaneous reversals



Kymographs with (Top) and without (Bottom) modulation,
 $\lambda_0 = 0, 0.003, \text{ and } 0.05.$