# Kinetic Model for Myxobacteria with Directional Diffusion

Laura Kanzler

Laboratoire Jacques-Louis Lions, Sorbonne Université

October 13, 2021

Joint work with C. Schmeiser (UniVie)



# Table of Contents

## 1 Biological Motivation: Myxobacteria

- 2 Kinetic Modelling of Myxobacteria Dynamics
- 3 Existence and Asymptotic Behavior
- ④ Bifurcation Analysis
- **5** Numerical Simulations

# Myxobacteria



 E.M.F. Mauriello, T. Mignot, Z. Yang, and D. R. Zusman, Gliding Motility Revisited: How Do the Myxobacteria Move without Flagella?, Microbiol Mol Biol Rev. 2010 Jun; 74(2): 229–249

## Biological Motivation: Myxobacteria

## 2 Kinetic Modelling of Myxobacteria Dynamics

## 3 Existence and Asymptotic Behavior

④ Bifurcation Analysis



# Kinetic Modelling

**Bacterium:**  $(x, \varphi)$ , center of mass  $x \in \mathbb{R}^2$ , velocity direction  $\varphi \in \mathbb{T}^1$ **Free flight:**  $\mu \ge 0$  diffusion constant

$$\mathrm{d}x = \omega(\varphi)\mathrm{d}t, \ \mathrm{d}\varphi = \sqrt{2\mu}\mathrm{d}B_t$$

## **Bacteria Collisions:**

Collisions between two bacteria  $(x, \varphi), (x_*, \varphi_*) \in \Gamma$  can lead to *alignment*, if the bacteria meet with an angle less than  $\pi/2$ , or to *reversal*, if they meet with an angle greater than  $\pi/2$ :

• Alignment:  $(x,\varphi), (x_*,\varphi_*) \longrightarrow \left(\frac{x+x_*}{2}, \frac{\varphi+\varphi_*}{2}\right), \left(\frac{x+x_*}{2}, \frac{\varphi+\varphi_*}{2}\right)$ 

# Kinetic Equation for Myxobacteria with Directional Diffusion

$$\begin{split} \partial_t f + \omega(\varphi) \cdot \nabla_x f &= \mu \partial_{\varphi}^2 f + Q_{AL}(f, f) + Q_{REV}(f, f) \\ &= \mu \partial_{\varphi}^2 f + 2 \int_{\mathbb{T}^1_{AL}} b(\tilde{\varphi}, \varphi_*) \Big( f(\tilde{\varphi}) f(\varphi_*) - f(\tilde{\varphi}_*) f(\varphi) \Big) \, \mathrm{d}\varphi_* \\ &+ \int_{\mathbb{T}^1_{REV}} b(\varphi, \varphi_*) \Big( f(\varphi + \pi) f(\varphi_* + \pi) - f(\varphi) f(\varphi_*) \Big) \, \mathrm{d}\varphi_*, \end{split}$$

where  $\tilde{\varphi} = 2\varphi - \varphi_*$ . Initial conditions:  $f(x, \varphi, 0) = f_I(x, \varphi)$ 

# Kinetic Equation for Myxobacteria with Directional Diffusion

$$\begin{split} \partial_t f + \omega(\varphi) \cdot \nabla_x f &= \mu \partial_{\varphi}^2 f + Q_{AL}(f, f) + Q_{REV}(f, f) \\ &= \mu \partial_{\varphi}^2 f + 2 \int_{\mathbb{T}^1_{AL}} b(\tilde{\varphi}, \varphi_*) \Big( f(\tilde{\varphi}) f(\varphi_*) - f(\tilde{\varphi}_*) f(\varphi) \Big) \, \mathrm{d}\varphi_* \\ &+ \int_{\mathbb{T}^1_{REV}} b(\varphi, \varphi_*) \Big( f(\varphi + \pi) f(\varphi_* + \pi) - f(\varphi) f(\varphi_*) \Big) \, \mathrm{d}\varphi_*, \end{split}$$

where  $\tilde{\varphi} = 2\varphi - \varphi_*$ . Initial conditions:  $f(x, \varphi, 0) = f_l(x, \varphi)$ 

.

Collision operator:  $Q(f, f) := Q_{AL}(f, f) + Q_{REV}(f, f)$ . Collision kernel:

$$b(\varphi, \varphi_*) = \begin{cases} |\sin(\varphi - \varphi_*)| & \text{(rod shaped bacteria),} \\ 1 & \text{(Maxwellian myxos).} \end{cases}$$

Laura Kanzler

## Literature



### I.M. Gamba, V. Panferov, C. Villani,

On the Boltzmann equation for diffusively excited granular media. Commun. Math. Phys. 246, 503-541 (2004).

## E. Bertin, M. Droz, G. Gregoire,

Hydrodynamic equations for self-propelled particles: microscopic derivation and stability analysis.

J. Phys. A: Math. Theor. 42 (2006), 445001.

## R.J. Alonso .

Existence of global solutions to the Cauchy problem for the inelastic Boltzmann equation with near-vacuum data, JSTOR 58 (2009), pp. 999-1022.



### S. Mischler, C. Mouhot.

Stability, convergence to the steady state and elastic limit for the Boltzmann equation for diffusively excited granular media. Discrete Contin. Dyn. Syst. 24, 1 (2009), 159-185.

### I. Tristani.

Boltzmann equation for granular media with thermal force in a weakly inhomogeneous setting,

Journal of Functional Analysis, Volume 270, Issue 5, 2016, Pages 1922-1970, SSN 0022-1236.

# Table of Contents

Biological Motivation: Myxobacteria

2 Kinetic Modelling of Myxobacteria Dynamics

## 3 Existence and Asymptotic Behavior

④ Bifurcation Analysis



# Diffusion vs. No-Diffusion

Kinetic Equation for Myxobacteria

 $\partial_t f + \omega(\varphi) \cdot \nabla_x f = \mathcal{W} + Q_{AL}(f, f) + Q_{REV}(f, f)$ 

No diffusion  $\mu = 0$ :

- Existence of a unique global solution f ∈ C ([0,∞); L<sup>1</sup><sub>+</sub>(T<sup>1</sup>)) for the spatially homogeneous equation.
- Equilibria:
  - Uniform equilibrium  $f_0 := \frac{M}{2\pi}$  unstable (total mass  $M := \int f d\varphi dx$ )
  - Measure equilibrium  $f_{\infty}(\varphi) \coloneqq M_+ \delta_{\varphi_{\infty}}(\varphi) + M_- \delta_{\varphi_{\infty}-\pi}(\varphi)$  stable (equilibrium angle  $\varphi_{\infty}$ )

## [1] S. Hittmeir, L. Kanzler, A. Manhart, C. Schmeiser,

*Kinetic Modelling of Colonies of Myxobacteria*, Kinteic & Related Models **14** (2021), pp. 1-24

Laura Kanzler

Kinetic Equation for Myxobacteria with Diffusion in Velocity

$$\partial_t f + \omega(\varphi) \cdot \nabla_x f = \mu \partial_{\varphi}^2 f + Q_{AL}(f, f) + Q_{REV}(f, f)$$
(1)

Diffusion  $\mu > 0$ :

- Existence ?
- Equilibria:

• Stability of the uniform equilibrium  $f_0 := \frac{M}{2\pi}$ ?

• Existence and stability of non-trivial equilibria ? In dependence of the diffusivity  $\mu > 0$ !

## Decay to the uniform equilibrium

## Theorem

Let  $f_I \in H^2_{x,\varphi}(\mathbb{T}^2 \times \mathbb{T}^1)$ ,  $f_I \ge 0$ , and let  $\mu/M$  be "large enough". Let furthermore  $||f_I - f_0||_{H^2_{x,\varphi}(\mathbb{T}^2 \times \mathbb{T}^1)}$  be "small enough". Then equation (1) subject to the initial condition  $f(t = 0) = f_I$  has a unique global mild solution  $f \in C([0, \infty), H^2_{x,\varphi}(\mathbb{T}^2 \times \mathbb{T}^1))$ , satisfying

$$\|f(t)-f_0\|_{H^2_{x,\varphi}(\mathbb{T}^2\times\mathbb{T}^1)}\leq Ce^{-\lambda t}\|f_l-f_0\|_{H^2_{x,\varphi}(\mathbb{T}^2\times\mathbb{T}^1)},\qquad C,\lambda>0.$$

# Decay to the uniform equilibrium

## Theorem

Let  $f_I \in H^2_{x,\varphi}(\mathbb{T}^2 \times \mathbb{T}^1)$ ,  $f_I \ge 0$ , and let  $\mu/M$  be "large enough". Let furthermore  $||f_I - f_0||_{H^2_{x,\varphi}(\mathbb{T}^2 \times \mathbb{T}^1)}$  be "small enough". Then equation (1) subject to the initial condition  $f(t = 0) = f_I$  has a unique global mild solution  $f \in C([0, \infty), H^2_{x,\varphi}(\mathbb{T}^2 \times \mathbb{T}^1))$ , satisfying

$$\|f(t)-f_0\|_{H^2_{x,\varphi}(\mathbb{T}^2\times\mathbb{T}^1)}\leq Ce^{-\lambda t}\|f_I-f_0\|_{H^2_{x,\varphi}(\mathbb{T}^2\times\mathbb{T}^1)},\qquad C,\lambda>0.$$

**Proof** (essentials):

- Spectral stability of  $f_0$  by  $L^2$ -hypocoercivity
- Nonlinear stability of f<sub>0</sub> by control of quadratic nonlinearities in H<sup>2</sup>, existence by Picard-argument

Linearization of (1) around  $f_0$ :

 $\partial_t f + Tf = (L + Q_L)f,$ 

(2)

## with

- the dissipative operator  $L \coloneqq \mu \partial_{\varphi}^2$
- the conservative transport operator  $\mathcal{T} \coloneqq \omega(\varphi) \cdot \nabla_{\mathsf{X}}$
- linearized collision operator Q<sub>L</sub>f := Q(f<sub>0</sub>, f) + Q(f, f<sub>0</sub>) (perturbation).

## [1] J. Dolbeault, C. Mouhot, C. Schmeiser,

*Hypocoercivity for linear kinetic equations conserving mass*, Trans. AMS 367 (2015), pp. 3807-3828.

•  $L + Q_L - T$  generates the strongly continuous semigroup  $e^{(L+Q_L-T)t}$  on  $\mathcal{H}$ , with

$$\mathcal{H} := \left\{ f \in L^2(\mathbb{T}^2 \times \mathbb{T}^1) : \ \int_{\mathbb{T}^2 \times \mathbb{T}^1} f \mathrm{d}\varphi \mathrm{d}x = 0 \right\} \,.$$

• Orthogonal projection to the nullspace  $\mathcal{N}(L)$  of L is given by the average with respect to the angle:

$$\Pi f \coloneqq \frac{1}{2\pi} \int_{\mathbb{T}^1} f \mathrm{d}\varphi.$$

Modified entropy

$$H[f] \coloneqq \frac{1}{2} \|f\|^2 + \varepsilon \langle Af, f \rangle,$$

fulfilling  $\frac{1-\varepsilon}{2} \|f\|^2 \le H[f] \le \frac{1+\varepsilon}{2} \|f\|^2$  with an appropriately chosen small parameter  $0 < \varepsilon < 1$ , with the operator

$$A = (1 + (T\Pi)^* T\Pi)^{-1} (T\Pi)^*.$$
(3)

$$\begin{split} \frac{\mathrm{d}H}{\mathrm{d}t} &= -D[f] \coloneqq \langle Lf, f \rangle + \langle Q_L f, f \rangle - \varepsilon \langle AT\Pi f, f \rangle \\ &- \varepsilon \langle AT(1-\Pi)f, f \rangle + \varepsilon \langle ALf, f \rangle + \varepsilon \langle TAf, f \rangle + \varepsilon \langle AQ_L f, f \rangle \end{split}$$

$$\begin{split} \frac{\mathrm{d}H}{\mathrm{d}t} &= -D[f] := \langle Lf, f \rangle + \langle Q_L f, f \rangle - \varepsilon \langle AT\Pi f, f \rangle \\ &- \varepsilon \langle AT(1-\Pi)f, f \rangle + \varepsilon \langle ALf, f \rangle + \varepsilon \langle TAf, f \rangle + \varepsilon \langle AQ_L f, f \rangle \end{split}$$

• Microscopic- and macroscopic coercivity

$$-\langle Lf, f \rangle + \varepsilon \langle AT\Pi f, f \rangle \ge \mu \| (1 - \Pi) f \|^2 + \varepsilon \frac{4\pi^2}{1 + 4\pi^2} \| \Pi f \|^2$$

- $||Af|| \le \frac{1}{2} ||(1 \Pi)f||$ ,  $||TAf|| \le ||(1 \Pi)f||$  due to  $\Pi T \Pi = 0$
- AT bounded due to elliptic regularity

$$\begin{split} \frac{\mathrm{d}H}{\mathrm{d}t} &= -D[f] \coloneqq \langle Lf, f \rangle + \langle Q_L f, f \rangle - \varepsilon \langle AT\Pi f, f \rangle \\ &- \varepsilon \langle AT(1-\Pi)f, f \rangle + \varepsilon \langle ALf, f \rangle + \varepsilon \langle TAf, f \rangle + \varepsilon \langle AQ_L f, f \rangle \end{split}$$

- Boundedness of the collision kernel  $0 \le b \le 1$
- Conservation of total mass M

$$\begin{split} \frac{\mathrm{d}H}{\mathrm{d}t} &= -D[f] \coloneqq \langle Lf, f \rangle + \langle Q_L f, f \rangle - \varepsilon \langle AT\Pi f, f \rangle \\ &- \varepsilon \langle AT(1-\Pi)f, f \rangle + \varepsilon \langle ALf, f \rangle + \varepsilon \langle TAf, f \rangle + \varepsilon \langle AQ_L f, f \rangle \\ &\leq - \left(\mu - \frac{13}{2}M - \varepsilon\right) \| (1-\Pi)f \|^2 - \varepsilon \frac{8\pi^3}{1+8\pi^3} \| \Pi f \|^2 \\ &+ \varepsilon \left(\sqrt{2} + \frac{\mu}{2} + 3M \left(\sqrt{\frac{2}{\pi}} + \frac{1}{2}\right)\right) \| \Pi f \| \| (1-\Pi)f \| \,. \end{split}$$

For  $\mu/M$  "big enough" and for  $\varepsilon$  small enough, we have

$$\frac{d}{dt}H[f] \le -2\lambda H[f],$$

hence *spectral stability* of  $f_0$  in  $\mathcal{H}$ .

Spectral stability of  $f_0$  in  $H^2 \cap \mathcal{H} \subset L^{\infty}$  via recursive arguments.

- Decay for *x*-derivatives analogous.
- Decay of derivatives involving φ via recursive arguments: E.g.: g := ∂<sub>φ</sub>f solves the equation

$$\partial_t g + (T - L)g = -\omega(\varphi)^{\perp} \cdot \nabla_x f + Q_L g$$

## Lemma (Spectral stability in $H^2$ )

For  $\mu/M$  large enough there exist positive constants  $\lambda$  and C, such that for any initial datum  $f_I \in H^2(\mathbb{T}^2 \times \mathbb{T}^1) \cap \mathcal{H}$ , we have

$$\|e^{t(L+Q_L-T)}f_I\|_{H^2(\mathbb{T}^2\times\mathbb{T}^1)} \le Ce^{-\lambda t}\|f_I\|_{H^2(\mathbb{T}^2\times\mathbb{T}^1)}, \qquad t\ge 0.$$

## Nonlinear stability of the uniform equilibrium

The perturbation  $h \coloneqq f - f_0 \in H^2(\mathbb{T}^2 \times \mathbb{T}^1) \cap \mathcal{H}$ , satisfies

 $\partial_t h + Th = Lh + Q_Lh + Q(h, h),$ 

with Q being local  $\overline{Q}$ -Lipschitz continuous on  $H^2(\mathbb{T}^2 \times \mathbb{T}^1) \cap \mathcal{H}$ .

## Nonlinear stability of the uniform equilibrium

The perturbation  $h \coloneqq f - f_0 \in H^2(\mathbb{T}^2 \times \mathbb{T}^1) \cap \mathcal{H}$ , satisfies

 $\partial_t h + Th = Lh + Q_Lh + Q(h, h),$ 

with Q being local  $\overline{Q}$ -Lipschitz continuous on  $H^2(\mathbb{T}^2 \times \mathbb{T}^1) \cap \mathcal{H}$ .

• Local existence and uniqueness of a *mild solution*.

## Nonlinear stability of the uniform equilibrium

The perturbation  $h \coloneqq f - f_0 \in H^2(\mathbb{T}^2 \times \mathbb{T}^1) \cap \mathcal{H}$ , satisfies

 $\partial_t h + Th = Lh + Q_Lh + Q(h,h),$ 

with Q being local  $\overline{Q}$ -Lipschitz continuous on  $H^2(\mathbb{T}^2 \times \mathbb{T}^1) \cap \mathcal{H}$ .

- Local existence and uniqueness of a mild solution.
- Estimating the mild formulation gives

$$\begin{split} \|h(t)\|_{H^2(\mathbb{T}^2\times\mathbb{T}^1)} &\leq C e^{-\lambda t} \|f_l - f_0\|_{H^2(\mathbb{T}^2\times\mathbb{T}^1)} \\ &+ C \bar{Q} \int_0^t e^{\lambda(s-t)} \|h(s)\|_{H^2(\mathbb{T}^2\times\mathbb{T}^1)}^2 \mathrm{d}s \,. \end{split}$$

for  $\|f_I - f_0\|_{H^2(\mathbb{T}^2 \times \mathbb{T}^1)} \le \frac{\lambda}{4C^2 \bar{Q}}$ , Picard iteration preserves the inequality

$$\|h(t)\|_{H^{2}(\mathbb{T}^{2}\times\mathbb{T}^{1})} \leq 2Ce^{-\lambda t}\|f_{l}-f_{0}\|_{H^{2}(\mathbb{T}^{2}\times\mathbb{T}^{1})}.$$

# Table of Contents

## Biological Motivation: Myxobacteria

2 Kinetic Modelling of Myxobacteria Dynamics

## 3 Existence and Asymptotic Behavior

- 4 Bifurcation Analysis
- 5 Numerical Simulations

# Bifurcation form the Uniform Equilibrium

Linearization of (1) around  $f_0$ :

$$\partial_t f + Tf = (L + Q_L)f,$$

## Fourier series expansion

$$\begin{split} f(\varphi,t) &= \sum_{n=1}^{\infty} a_n(t) \cos(n\varphi) + \sum_{n=1}^{\infty} b_n(t) \sin(n\varphi) \text{ leads to} \\ \dot{a}_n &= \lambda_n a_n, \qquad \dot{b}_n = \lambda_n b_n, \end{split}$$

with

- $\lambda_n(\mu/M) < 0$  for  $n \neq 2$ •  $\lambda_2(\mu/M) \begin{cases} > 0 & \text{for } \mu/M < c_* \\ < 0 & \text{for } \mu/M > c_* \end{cases}$
- Occurrence of a supercritical pitchfork bifurcation



# Table of Contents

- Biological Motivation: Myxobacteria
- 2 Kinetic Modelling of Myxobacteria Dynamics
- 3 Existence and Asymptotic Behavior
- ④ Bifurcation Analysis
- **5** Numerical Simulations

# Numerical Simulations: Spatially Homogeneous Equation



## [1] L. Kanzler, C. Schmeiser,

# Kinetic Model for Myxobacteria with Directional Diffusion, arXiv:2109.13184.

Laura Kanzler

