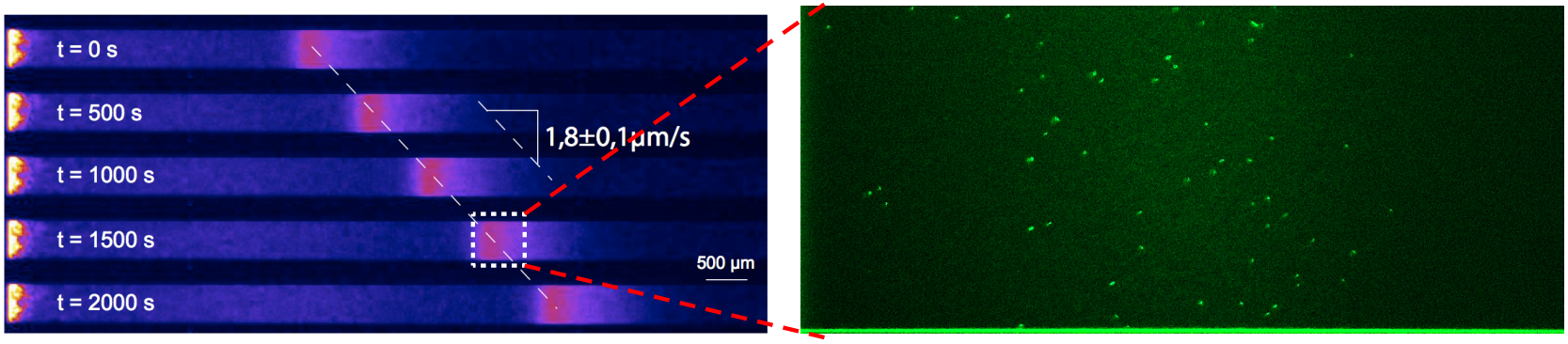
Biological waves at various scales

Vincent Calvez

Institut Camille Jordan, CNRS & Université de Lyon

Congrès SMAI, Juin 2021



Solitary waves of *E. coli* in a microchannel (Curie Institute, Paris)

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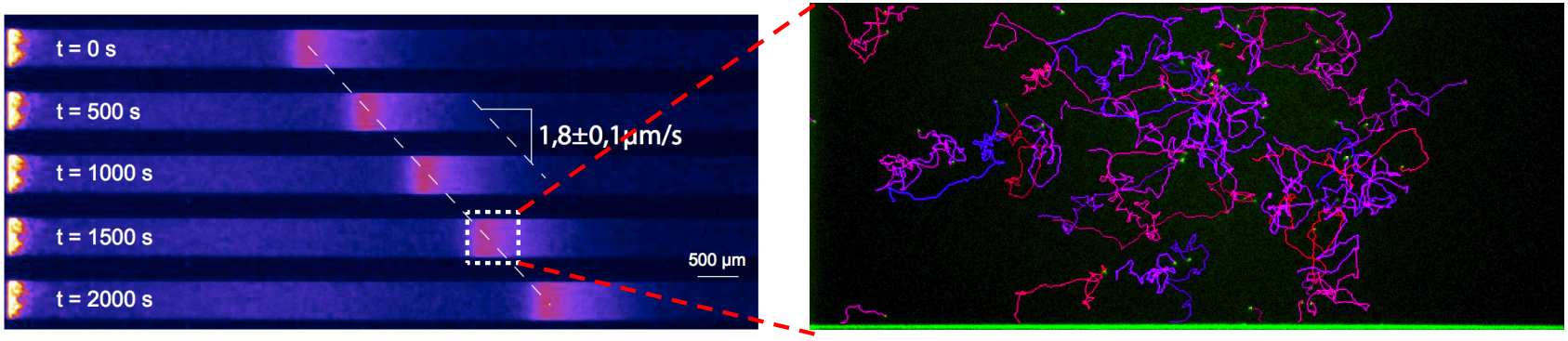


Solitary waves of *E. coli* in a microchannel (Curie Institute, Paris)

Contents

Spreading populations (waves) can be described by PDE models.

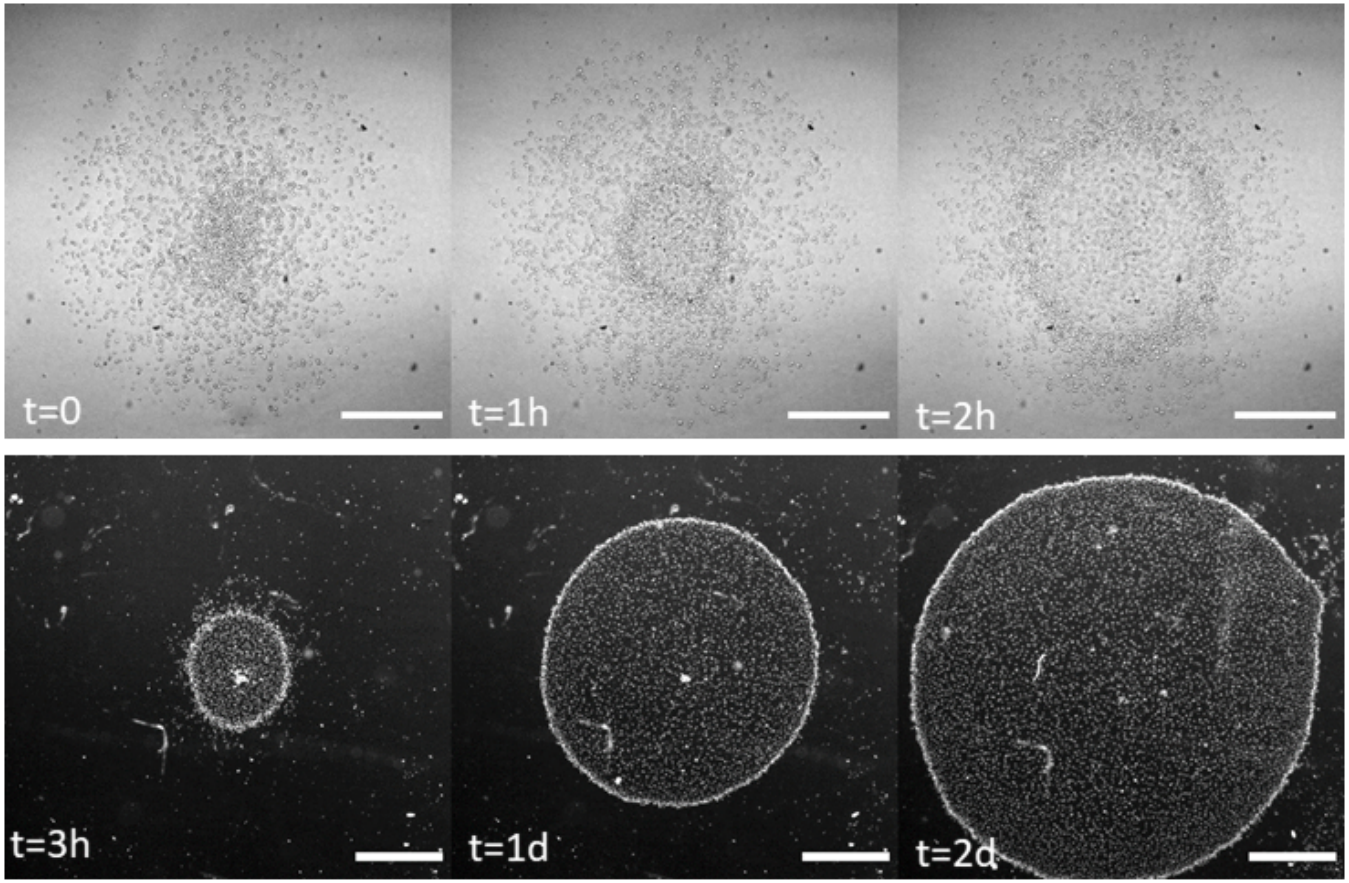
The level of accuracy of the model depends on the nature of data and biological knowledge.

Mathematical content: macroscopic models (i.e. parabolic equations) and mesoscopic models (i.e. kinetic equations and alike)

Biological content: Collective motion following self-generated gradients: two case studies

1. Aerotactic waves of amoeba *Dictyostelium discoideum*
2. Chemotactic waves of bacteria *Escherichia coli*

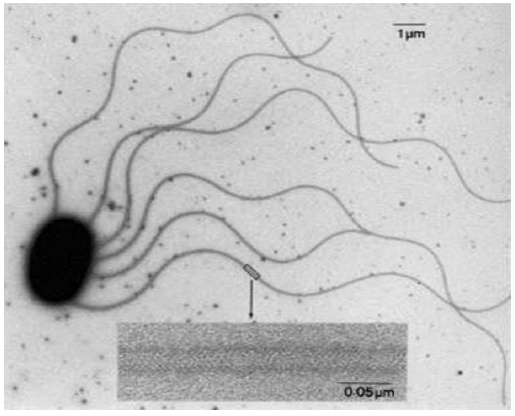
① Aerotactic waves of amoeba *Dicty*

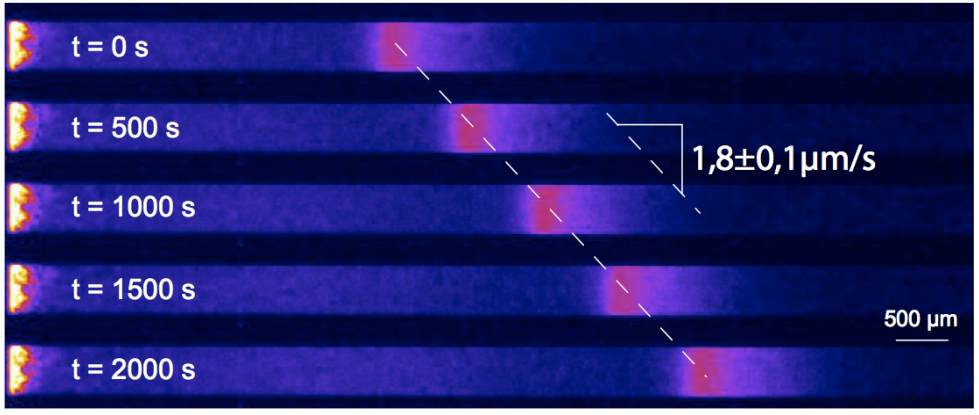


$$\text{Model :} \quad \frac{\partial \rho}{\partial t} - D\frac{\partial^2 \rho}{\partial x^2} = \dots$$

$$\text{Question :} \quad \exists (c, \boldsymbol{\rho}) : \rho(t, x) = \boldsymbol{\rho}(x - ct)?$$

② Chemotactic waves of bacteria *E. coli*





$$\text{Model :} \quad \left(\frac{\partial}{\partial t} + v\frac{\partial}{\partial x}\right) f(t,x,v) = \dots$$

$$\text{Question :} \quad \exists (c,F) : f(t,x,v) = F(x-ct,v)?$$

⓪ Warm-up: the Fisher equation

The Fisher equation is a standard reaction-diffusion equation:

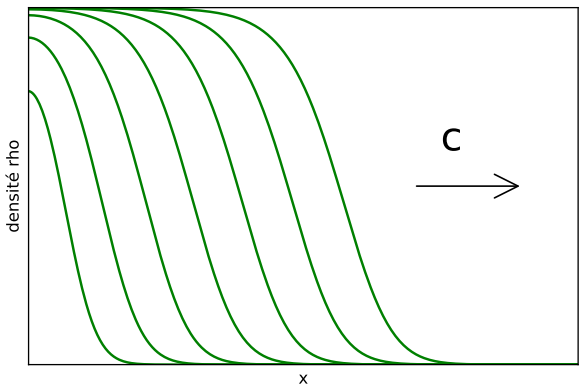
$$\frac{\partial \rho}{\partial t} - D\frac{\partial^2 \rho}{\partial x^2} = r\rho(1-\rho)$$

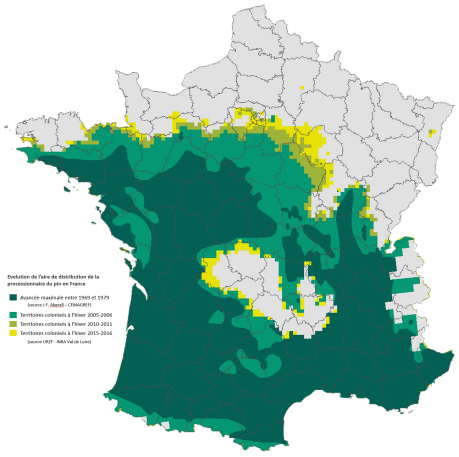
It combines the effects of:

- unbiased random motion: diffusion with coefficient $D > 0$,
- reproduction: logistic growth rate with coefficient $r > 0$).

Theorem (KPP 1937, Aronson-Weinberger 1978...)

There exist nonnegative travelling wave solutions $\rho(t,x) = \mu(x-ct) \geqslant 0$ *for all* $c \geqslant c^* = 2\sqrt{rD}$.

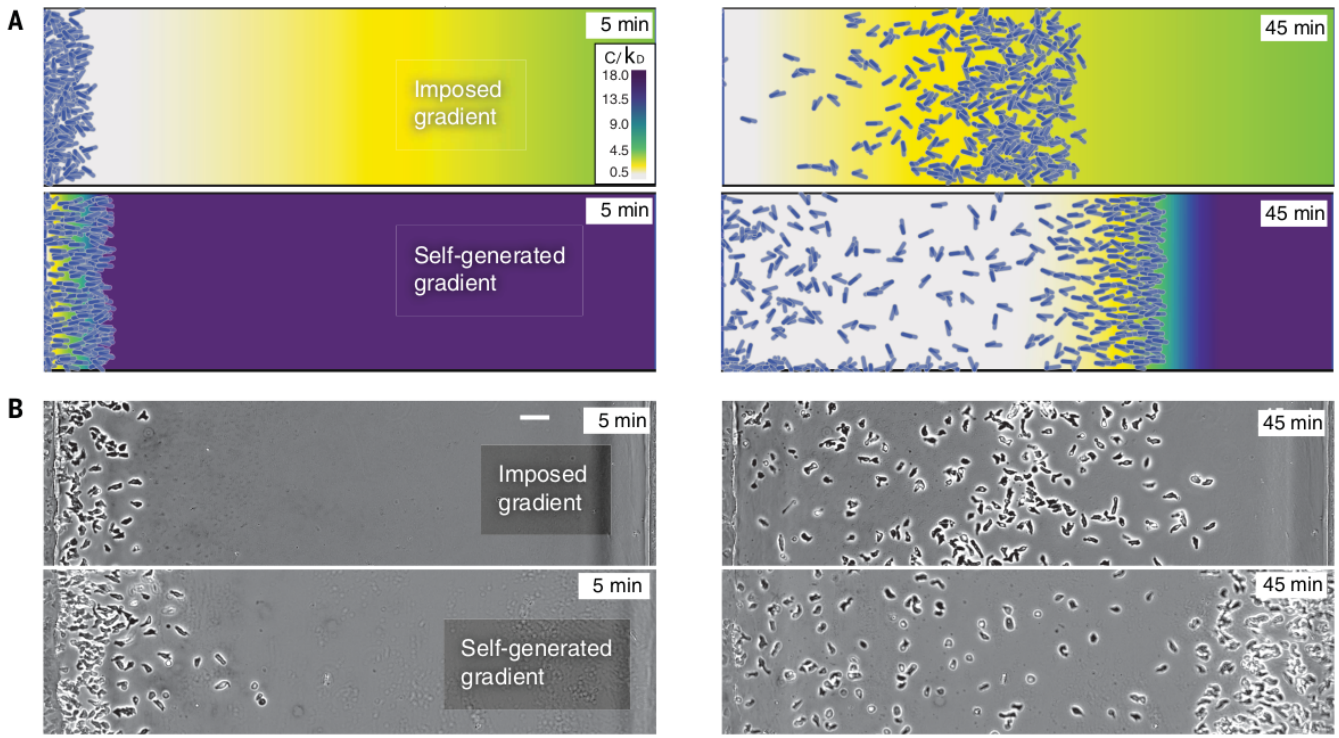




Advertisement: self-generated gradients

Cells can navigate over long distances in complex environments: during development, immune response, metastasis,. . .

It is postulated that they can find their way efficiently using *self-generated gradients*.



Tweedy et al (2016), Cremer et al (2019), Tweedy and Insall (2020), **Tweedy et al, (Science 2020)**

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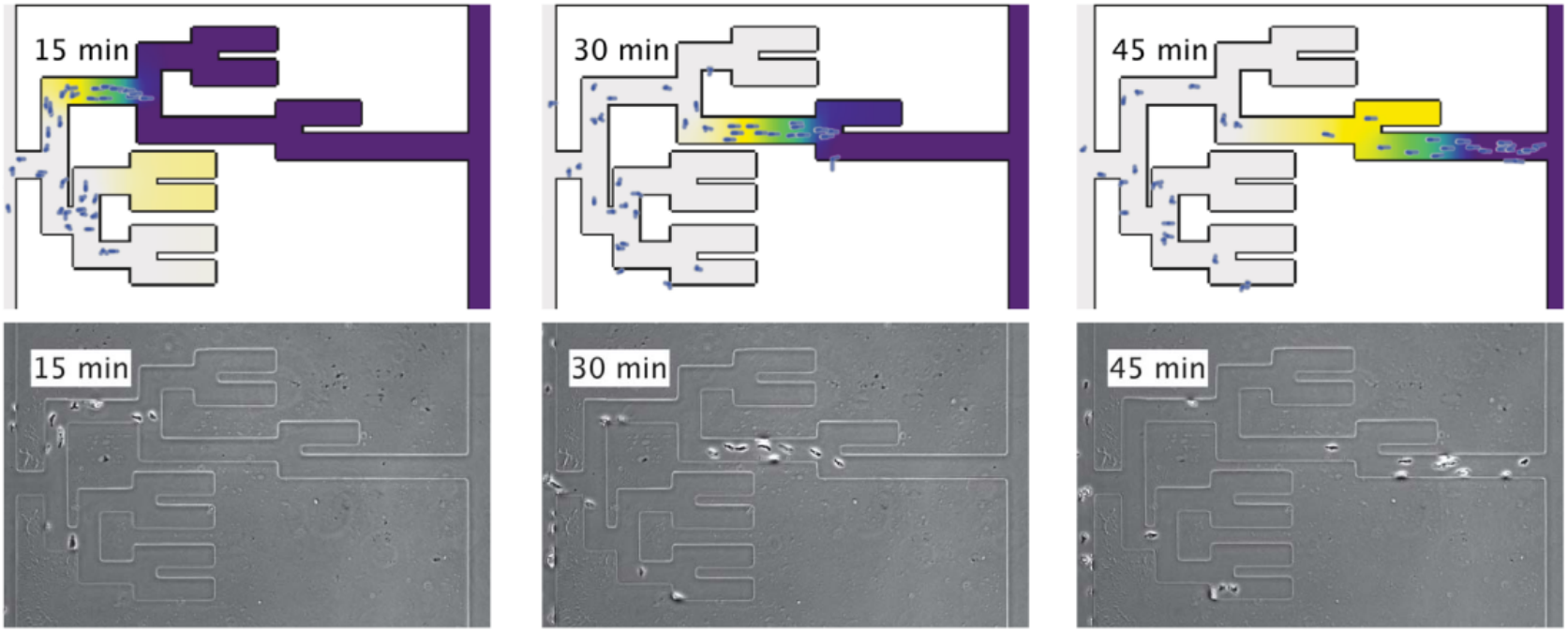

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Tweedy et al (2016), Cremer et al (2019), Tweedy and Insall (2020), **Tweedy et al, (Science 2020)**

Historical background: Adler's experiments (Science 1966)

Chemotaxis in Bacteria

Motile *Escherichia coli* migrate in bands that are influenced by oxygen and organic nutrients.

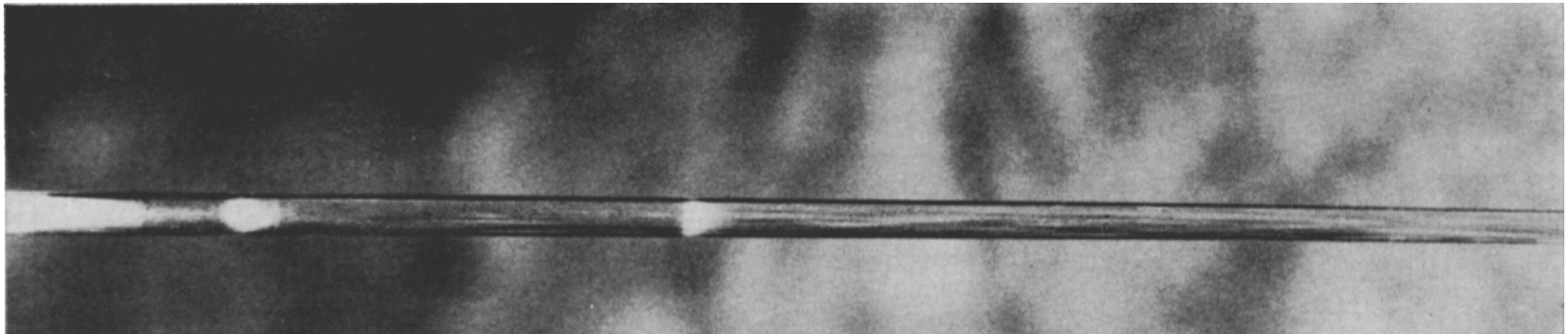
Julius Adler

Chemotaxis is the movement of organisms toward or away from a chemical. This phenomenon has been observed in a wide variety of microorganisms, plants, and animals (*1*, *2*). In bacteria chemotaxis has been known ever since the end of the 19th century, when Engelmann, Pfeffer, and other biologists discovered chemotaxis toward oxygen, minerals, and organic nutrients (for a review see Weibull, *3*). These workers demonstrated chemotaxis microscopically by observing whether bacteria in a suspension accumulated near or away from a gas bubble or a chemical introduced at one point.

In 1893 Beijernck (*4*) demonstrated chemotaxis toward oxygen macroscopically by showing that a variety of motile bacteria placed at the bottom of a test tube filled with water would form a sharp, easily visible band that rose until it came to a stop near the meniscus. The band would then descend if the air above the liquid was replaced by oxygen, and it would ascend if an atmosphere depleted in oxygen was used. Beijerinck interpreted this to mean that the bacteria seek a certain optimum concentration of oxygen. More recently, Sherris, Preston, and Shoesmith (*5*) and Baracchini and Sherris (*6*), using capillary tubes instead of test tubes, confirmed and extended these results.

Very little is understood about the mechanism of chemotaxis in bacteria. In order to learn about this, *Escherichia coli* was chosen for study because the vast knowledge of its biochemistry and genetics could be brought to bear on the problem. Many strains of *E. coli*

The author is an associate professor in the departments of Biochemistry and Genetics at the University of Wisconsin, Madison.

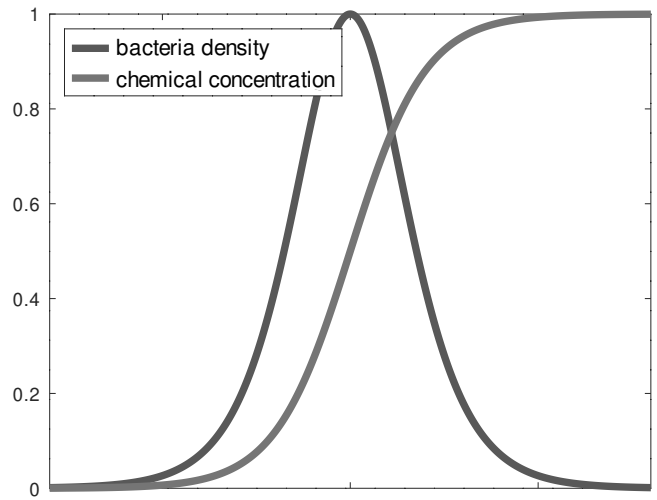


A preliminary attempt by Keller and Segel (1971)

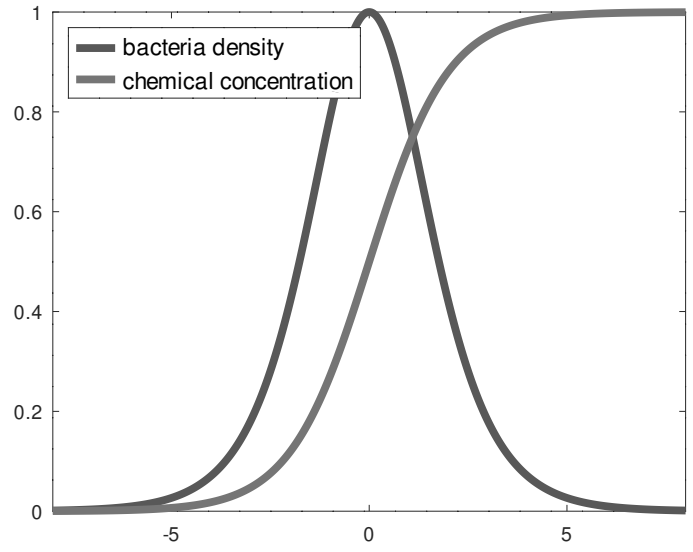
$$\begin{cases} \dfrac{\partial \rho}{\partial t} - D\dfrac{\partial^2 \rho}{\partial x^2} + a\dfrac{\partial}{\partial x}\left(\rho\left(\dfrac{\partial \log C}{\partial x}\right)\right) = 0 & \text{advection-diffusion of bacteria} \\ \dfrac{\partial C}{\partial t} = -\gamma\rho & \text{consumption of the chemical signal} \end{cases}$$

If $a > D$, there is a traveling wave with the limiting values:

$$\begin{cases} \rho(-\infty) = \rho(+\infty) = 0 \\ C(-\infty) = 0 \quad ; \quad C(+\infty) = \text{initial concentration} \end{cases}$$



An elegant result, but...



The wavespeed c can be found immediately:

$$-c\frac{dC}{dz} = -\gamma\rho(z) \quad \longrightarrow \quad c = \frac{\gamma\int\rho}{C(+\infty)}$$

It does not depend on the bacteria response to the chemical signal (advection coefficient a)

Moreover, the wave is unstable (Nagai and Ikeda 1992),
even positivity of $C(z)$ is not guaranteed (numerics not shown)...

A significant modelling effort following KS

[From the review paper by Tindall et al. (Bull. Math. Biol. 2008)]

Appendix A: Comparison of K–S models of bacterial chemotaxis

The generic K–S system of equations is given by

$$\frac{\partial b}{\partial t} = \nabla \cdot \big(\mu(s)\nabla b\big) - \nabla \cdot \big(\chi(s) b \nabla s\big) + g(b,s) - h(b,s) \quad \text{and} \quad \frac{\partial s}{\partial t} = -f(b,s) + D\nabla^2 s.$$

The table below provides a summary of the above terms included in the cited references and lists the functional forms used where necessary.

Reference	$\mu(s)$	$\chi(s)$	$g(b,s)$	$h(b,s)$	$f(b,s)$	D
Keller and Segel (1971b)	$\surd$	χ/s	0	0	$k_f b$	$\surd$
Segel and Jackson (1973)[b]	$\surd$	χ/s	0	0	0	0
Nossal and Weis (1973)	$\surd$	χ/s	0	0	0	0
Lapidus and Schiller (1974)[b]	$\surd$	χ/s	0	0	0	0
Lapidus and Schiller (1975)	$\surd$	χ/s	0	0	$k_f b$	0
Lapidus and Schiller (1976)[c]	$\surd$	$\frac{\chi}{(K_d+s)^2}$	0	0	0	0
Lapidus and Schiller (1978)	$\surd$	$\frac{\chi}{(K_d+s)^2}$	$k_g b$	0	0	0
Rosen (1974)	$\surd$	χ/s	0	0	$k_f b s^p$	$\surd$
Rosen (1975)	$\surd$	χ/s	0	0	$k_f b s^p$	$\surd$
Rosen and Baloga (1975)	$\surd$	χ/s	0	0	$k_f b s^p$	0
Rosen (1976)	$\surd$	χ	0	0	$k_f b$	0
Rosen and Baloga (1976)	$\surd$	χ/s	0	0	$k_f b s^p$	0
Kennedy and Aris (1980)	$\surd$	0	$\frac{k_g b s^p}{K^p+s^p}$	$k_f b$	$\frac{k_f b s^p}{K^p+s^p}$	$\surd$
Lauffenburger et al. (1982)	$\surd$	χ	$\frac{k_g b s}{K+s}$	$k_h b$	$\frac{k_g b s}{K+s}$	$\surd$
Lauffenburger et al. (1984)	$\surd$	χ, χ/s and $\frac{\chi K_d}{(K_d+s)^2}$	$\frac{k_g b s}{K+s}$	$k_h b$	$\frac{k_f b s}{K_s+s}$	$\surd$

A significant modelling effort following KS (ctd.)

[From the review paper by Tindall et al. (Bull. Math. Biol. 2008)]

Reference	$\mu(s)$	$\chi(s)$	$g(b,s)$	$h(b,s)$	$f(b,s)$	D
Rosen (1983)	$\surd$	χ/s	0	0	$k_f b$	$\surd$
Novick-Cohen and Segel (1984)	$\surd$	$\frac{\chi}{(K_d+s)}$	0	0	$k_f b$	$\surd$
Boon and Herpigny (1986)[d]	$\surd$	$\frac{\chi 2 s_i K_d}{(K_d+s_i)^2}$	0	0	$\frac{k_{f1} b s_1}{(K_{s1}+s_1)(K_{s2}+s_2^4)} + \frac{k_{f2} b s_1 s_2}{(K_{s1}+s_1)(K_{s2}+s_2)}$	D_i
Rivero-Hudec and Lauffenburger (1986)	$\frac{1}{2} T v^2$	$\frac{\chi_0 K_d}{(K_d+s)^2}$	0	0	0	$\surd$
Ford and Lauffenburger (1991b)	$\frac{v^2}{(1-\vartheta)p_0} \exp(\sigma \frac{dC}{ds} \frac{\partial s}{\partial t}) \times \operatorname{sech}(\sigma v \frac{dC}{ds} \frac{\partial s}{\partial x})$	$v \tanh(\sigma v \frac{dC}{ds} \frac{\partial s}{\partial x})$	0	0	$\frac{k_f b s}{K_s+s}$	$\surd$
Ford et al. (1991)	$\mu_0 \exp\big(\sigma \frac{R_T K_d}{(K_d+s)^2} \frac{\partial s}{\partial t}\big) \times \operatorname{sech}\big(\sigma \frac{R_T K_d}{(K_d+s)^2} \frac{\partial s}{\partial x}\big)$	$\frac{\chi_0 K_d}{(K_d+s)^2}$	0	0	$\frac{k_f b s}{K_s+s}$	$\surd$
Widman et al. (1997)[a]	$\surd$	$\frac{\chi_0 K_d}{(K_d+s)^2}$	$\frac{k_g N b}{K+N}$	0	$\frac{k b s}{K_s+s}$	$\surd$
Chiu and Hoppensteadt (2001)[a]	$\surd$	$\frac{\chi_0 K_d}{(K_d+s)^2}$	$\frac{k_g N b}{K+N}$	0	$\frac{k b s}{K_s+s}$	$\surd$
Marx and Aitken (1999)	$\surd$	$\frac{2v}{3} \tanh\big(\frac{\chi_0}{2v} \frac{K_d}{(K_d+s)^2} \lvert\nabla s\rvert\big)$	0	0	0	$\surd$
Marx and Aitken (2000)	$\surd$	$\frac{2v}{3} \tanh\big(\frac{\chi_0}{2v} \frac{K_d}{(K_d+s)^2} \lvert\nabla s\rvert\big)$	0	0	$\frac{k b s}{K_s+s}$	$\surd$
Pedit et al. (2002)	$\surd$	$\frac{2v}{3} \tanh\big(\frac{\chi_0}{2v} \frac{K_d}{(K_d+s)^2} \lvert\nabla s\rvert\big)$	$\frac{k_g b s}{K+s}$	$k_h b$	$\frac{k s b}{K_s+s}$	$\surd$
Hilpert (2005)	$\surd$	$\frac{2v}{3} \tanh\big(\frac{\chi_0}{2v} \frac{K_d}{(K_d+s)^2} \lvert\nabla s\rvert\big)$	$\frac{k_g b s}{K+s}$	0	$\frac{k_f b s}{K_s+s}$	$\surd$

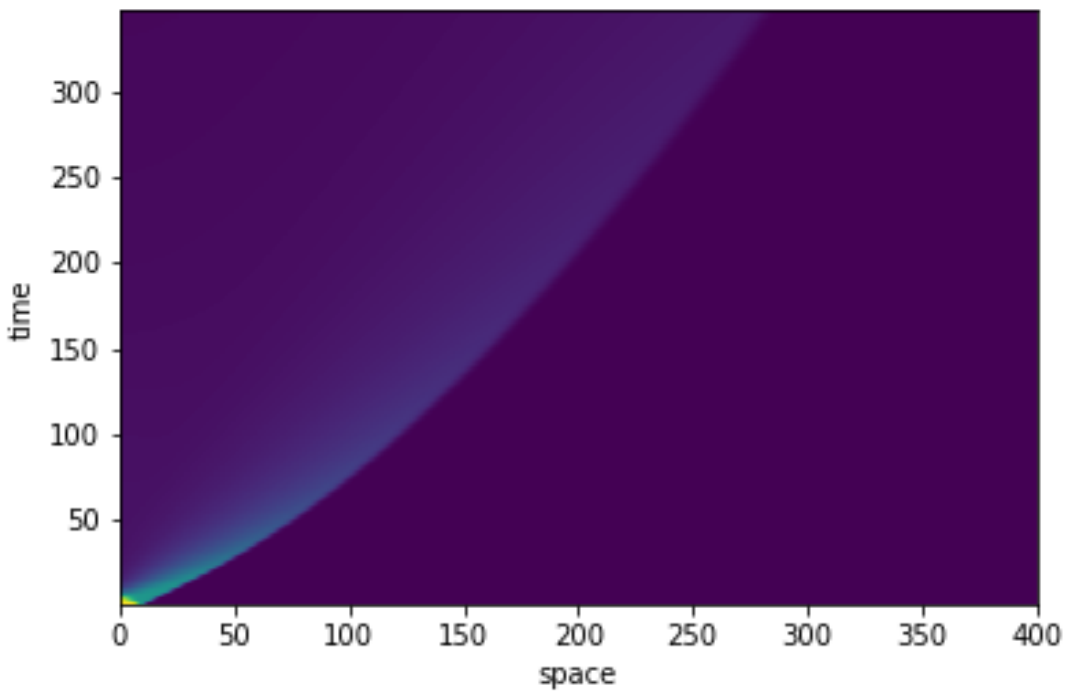
A major issue

One of the main obstacle to the existence of traveling waves is the conservation of mass (number of bacteria is constant).

Cells should not get lost at the back of the wave!

Example:

$$\begin{cases} \dfrac{\partial \rho}{\partial t} - D\dfrac{\partial^2 \rho}{\partial x^2} + a\dfrac{\partial}{\partial x}\left(\rho\left(\dfrac{\partial \log C}{\partial x}\right)\right) = 0 \\ \dfrac{\partial C}{\partial t} = -\gamma\rho C \end{cases}$$



① Aerotactic waves of amoeba *Dicty*

Close collaboration with:

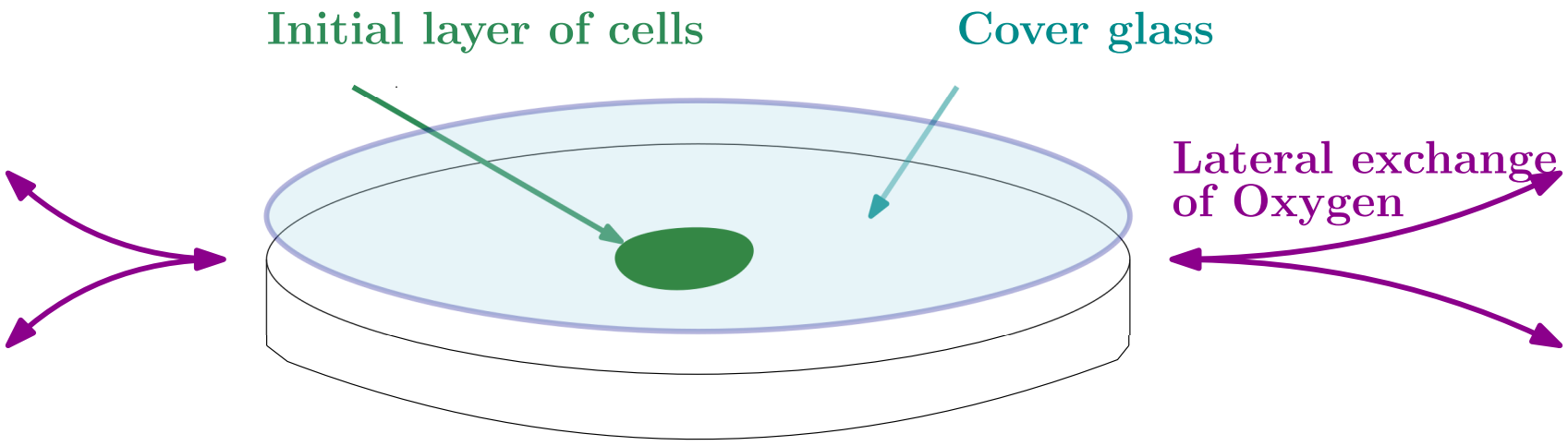
- Christophe Anjard, Olivier Cochet-Escartin, Jean-Paul Rieu (Institut Lumière Matière, Lyon)
- Mete Demircigil (PhD student) for most of the mathematical contribution

This section is a *subpart* of the following preprint:

O. Cochet-Escartin, M. Demircigil, S. Hirose, B. Allais, P. Gonzalo, I. Mikaelian, K. Funamoto, C. Anjard, V. Calvez, J.-P. Rieu,

Hypoxia triggers collective aerotactic migration in Dictyostelium discoideum, bioRxiv 2020

A long-lasting traveling ring (I)



Experiment performed at Institut Lumière Matière with Dicty cells.

Main objective: a simple experimental set-up to generate ultra low concentrations of oxygen

Previously performed at CRCL (Lyon) with mammary epithelial cells (Deygas et al, Nature Comm. 2018)

Further experiments with motility assays in controlled oxygen environments (results not shown, see preprint)

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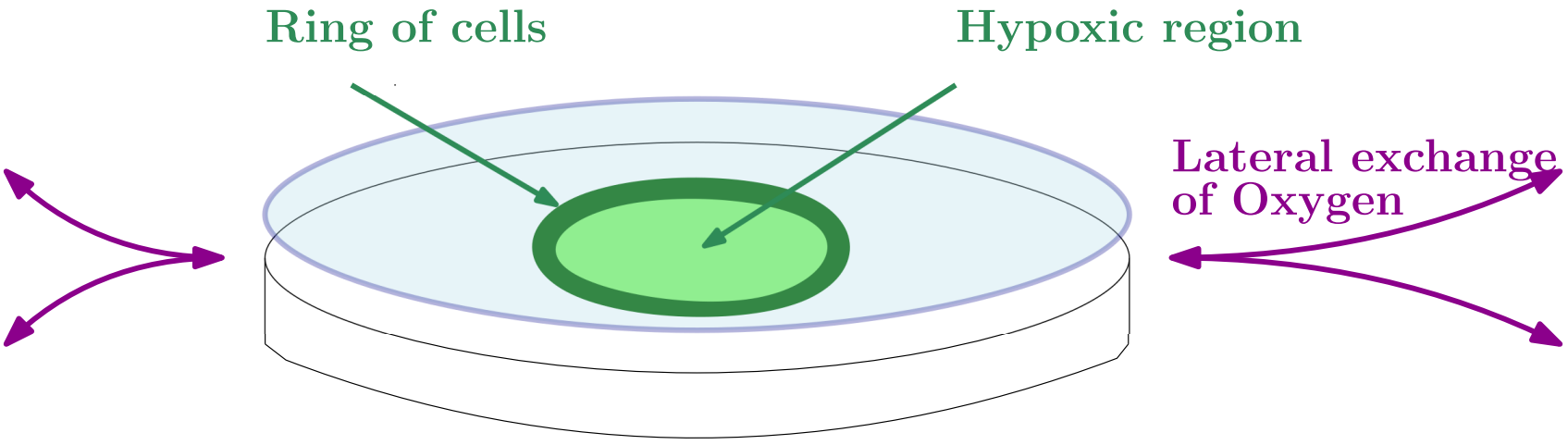

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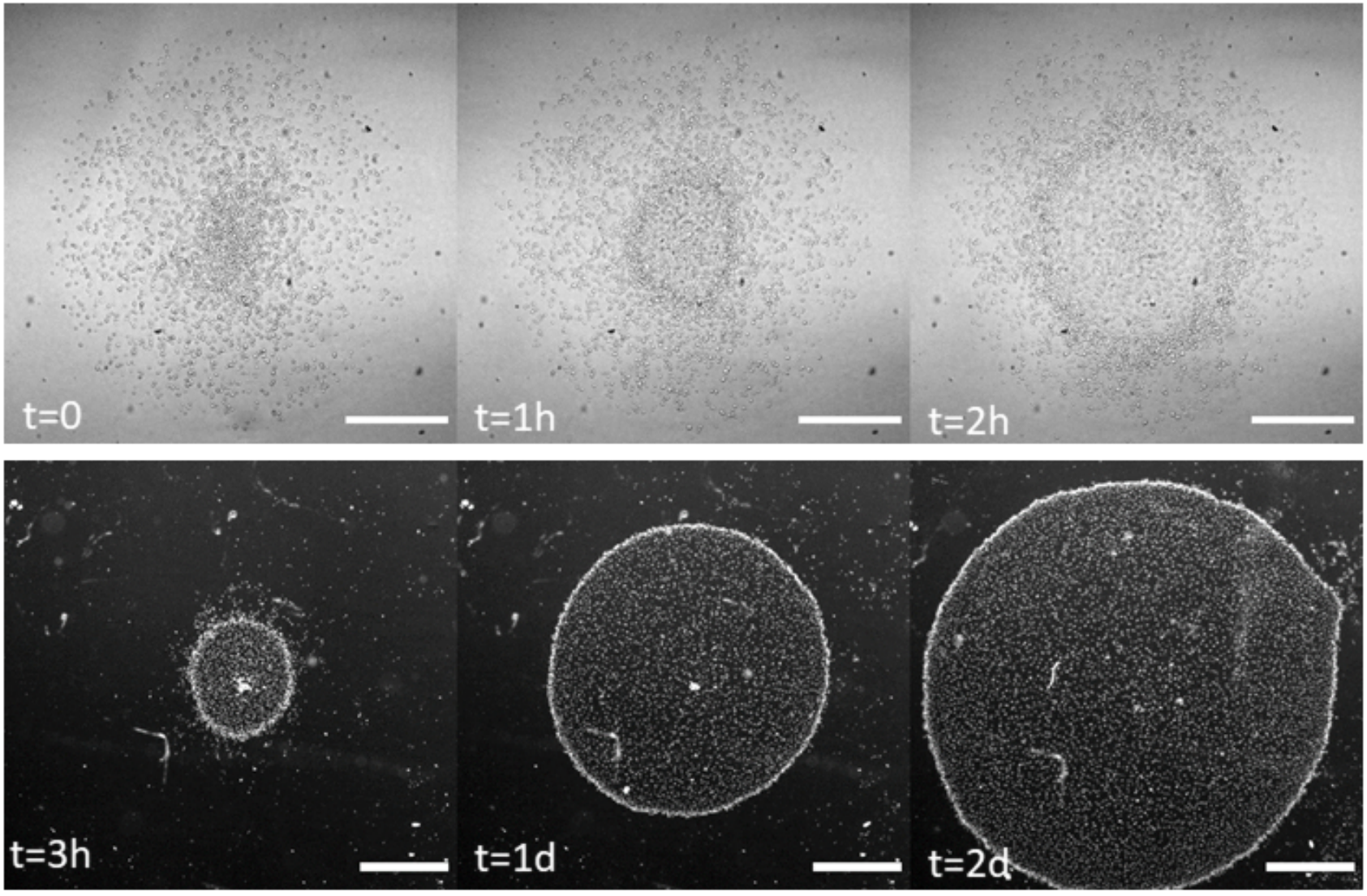
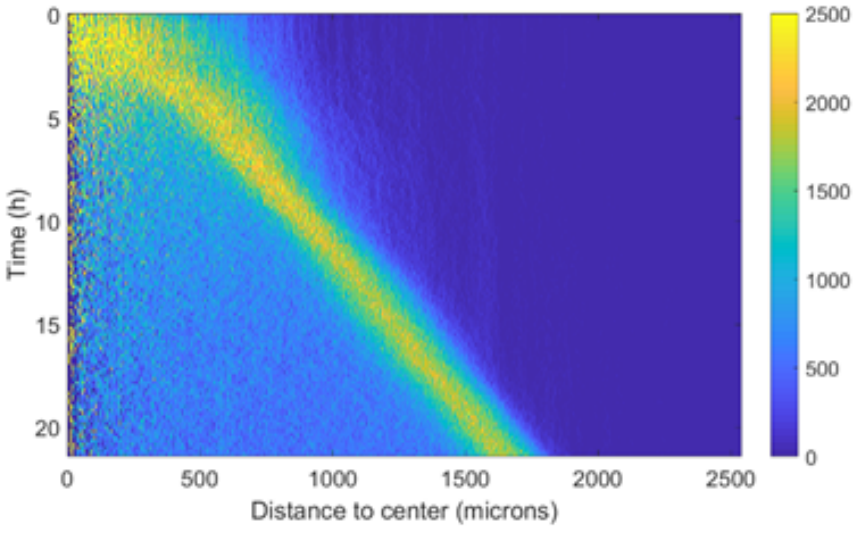
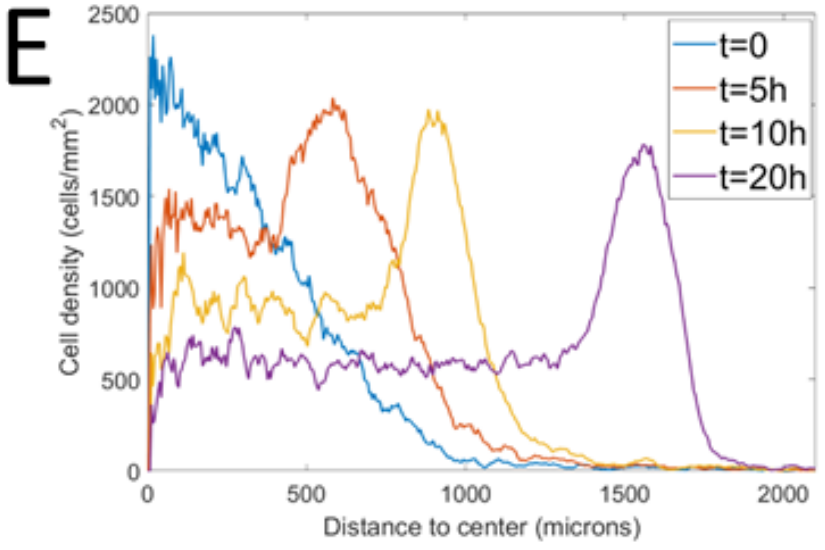
A long-lasting traveling ring (II)



A nearly perfect ring

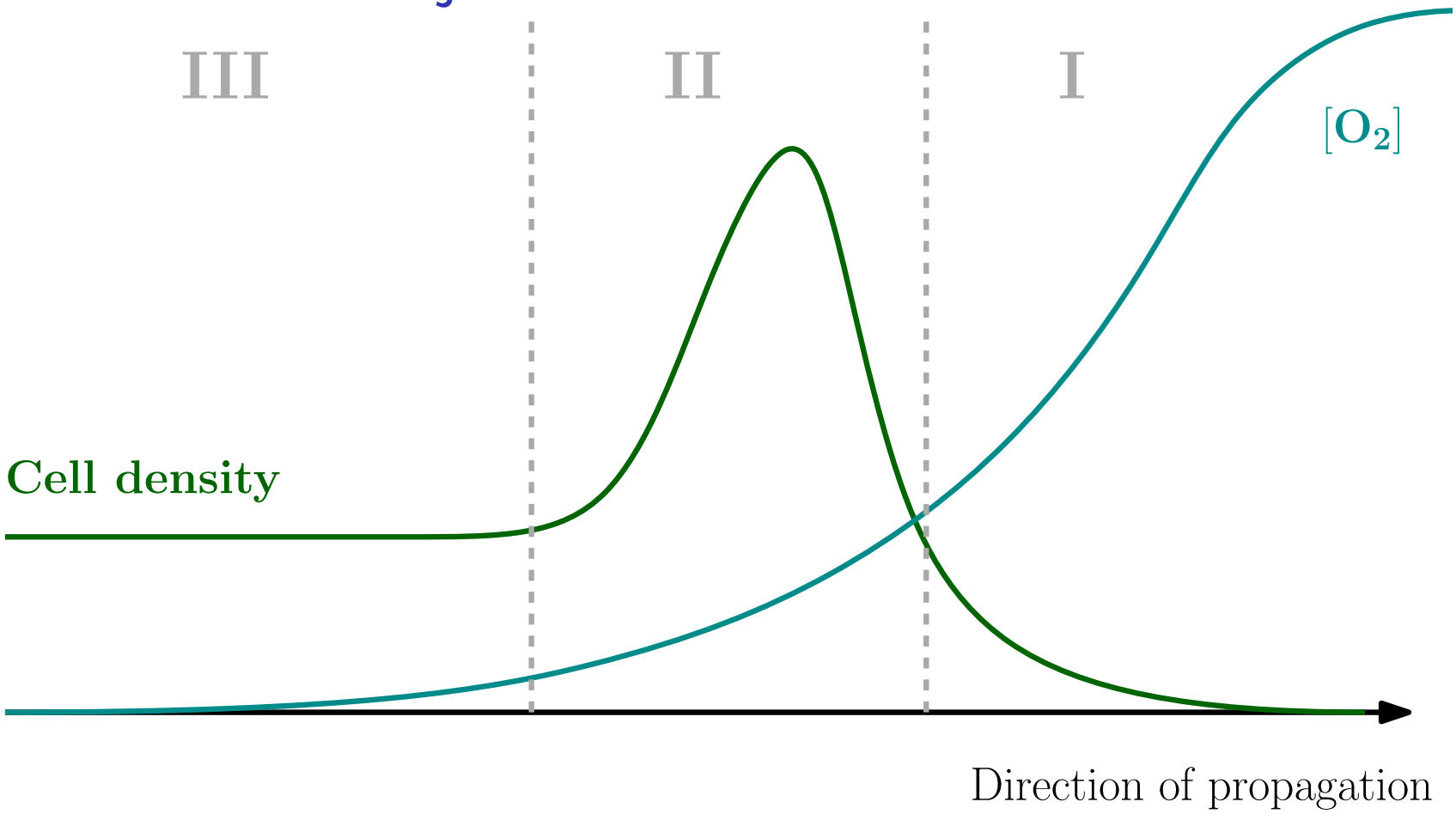


Kymograph



Snapshots of the radial density

Cell trajectories: various behaviours



I Unbiased motion

II Biased motion

III Unbiased motion, strong persistence

Main hypotheses

We supposed that the collective motion results from a **self-generated gradient of oxygen**.

No other signal.

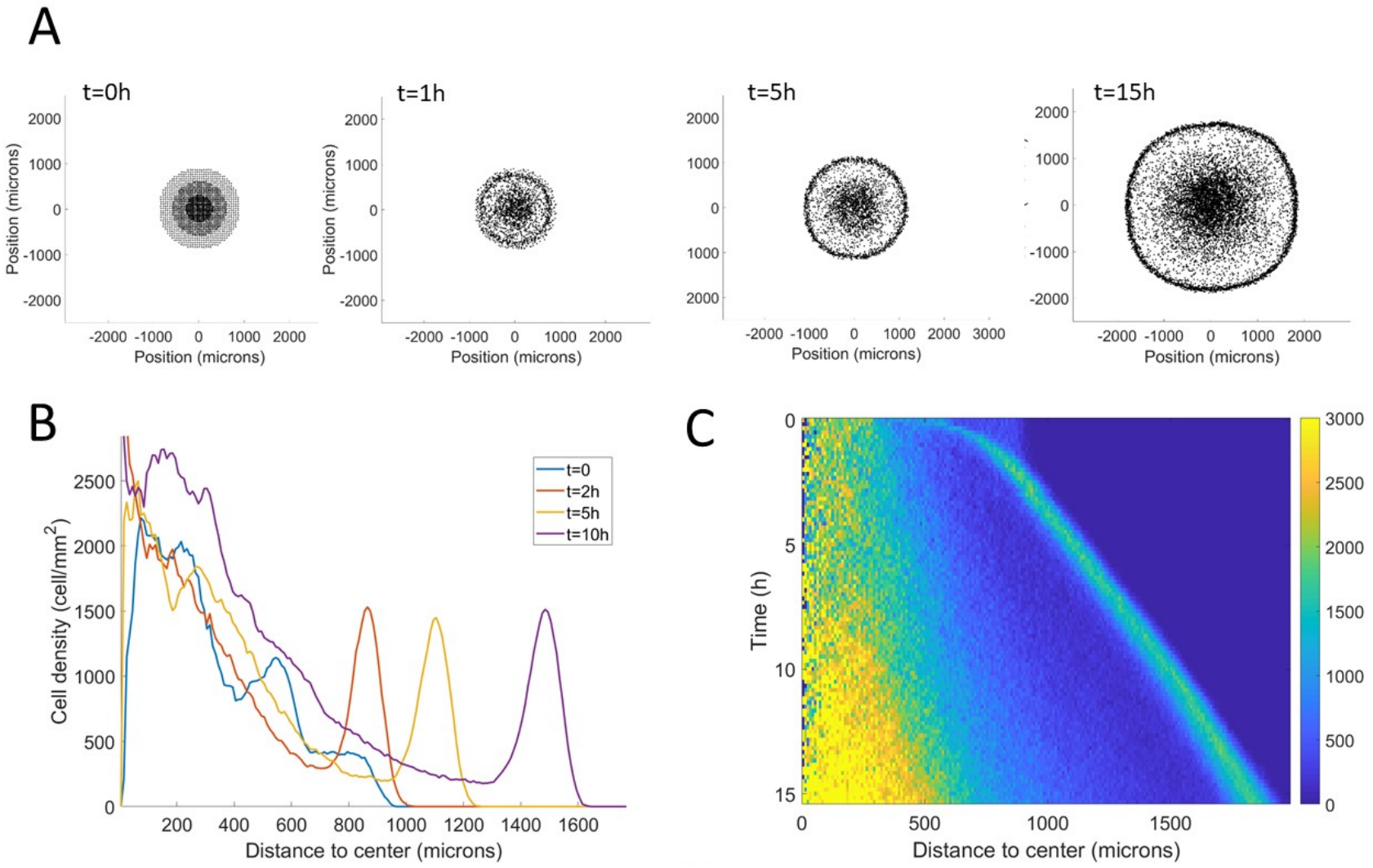
Cell response depends on both the gradient and the level of oxygen:

- If $[O_2]$ is large $\rightarrow$ cell division, unbiased motion
- If $[O_2]$ is small $\rightarrow$ no cell division, biased motion
- If $[O_2]$ is very small $\rightarrow$ no cell division, unbiased motion

Higher persistency in the hypoxic region was neglected.

Self-generated gradients are omnipresent in chemotaxis models (Tweedy et al, Curr Opinion Cell Biol 2016); Saragosti et al, PNAS 2011 (Traveling bands of chemotactic bacteria, following Adler, Science 1966)

Individual based simulations (Potts cellular model)



The model was parametrized based on microfluidic experiments: cell behaviour was measured in a controlled gradient of O_2

Mathematical objectives

So far the set of hypotheses is validated.

However, the Potts model is not amenable to analysis.

Alternatively, we designed a minimal and tractable model to answer simple questions:

- Is it possible to describe traveling waves with a single self-generated gradient?
- Growth is necessary for the sustainability of the wave, but what is the contribution to the wave speed?

The minimal framework

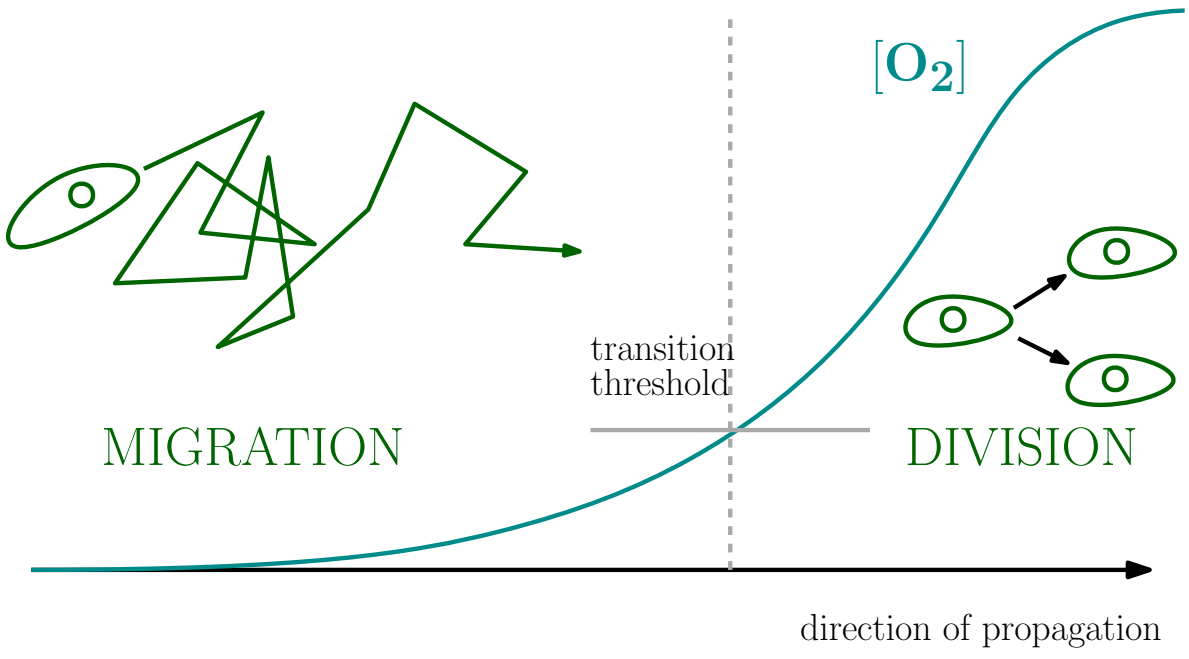
We restrict to the one-dimensional case

Cell density is denoted by $\rho(t,x)$, $t>0$, $x\in\mathbb{R}$

Oxygen concentration is denoted by $C(t,x)$

We further assume:

- 1 threshold C_0
- 2 behaviours: growth ($C>C_0$) *vs.* migration ($C<C_0$).



A simple go-or-grow model

Cells can either go or grow, depending on the level of oxygen.

- Growth rate is either zero or a constant rate $r > 0$
- Directed part of motion is either zero or a constant advection speed $a > 0$

$$\frac{\partial \rho}{\partial t} - D\frac{\partial^2 \rho}{\partial x^2} + \frac{\partial}{\partial x}\left\{ \begin{array}{ll} 0 & \text{if } C > C_0 \\ a\,\text{sign}\left(\frac{\partial C}{\partial x}\right)\rho & \text{if } C < C_0 \end{array} \right\}$$

$$= \left\{ \begin{array}{ll} r\rho & \text{if } C > C_0 \\ 0 & \text{if } C < C_0 \end{array} \right\}$$

Oxygen is consumed by the cells:

$$\frac{\partial C}{\partial t} - D_{\text{ox}}\frac{\partial^2 C}{\partial x^2} = -\gamma \rho C$$

See also Hatzikirou et al, Math. Med. Biol. (2012), but density-dependent switch

Traveling waves are explicit solutions!

We seeked traveling wave solutions $\rho(t,x) = \rho(z)$, $C(t,x) = C(z)$; $z = x - ct$.
The equation on $\rho(z)$ has piecewise constant coefficients:

$$-c\frac{d\rho}{dz} - D\frac{d^2\rho}{dz^2} + \frac{d}{dz}\left\{\begin{array}{ll} 0 & \text{if } C > C_0 \\ a\rho & \text{if } C < C_0 \end{array}\right\}$$

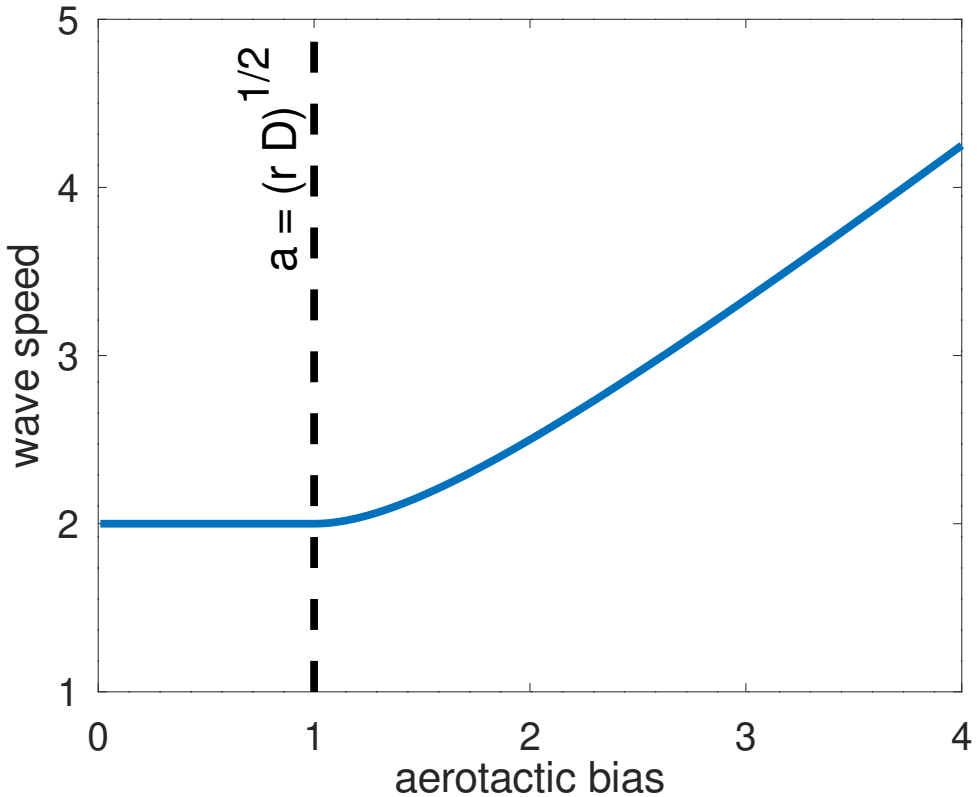
$$= \left\{\begin{array}{ll} r\rho & \text{if } C > C_0 \\ 0 & \text{if } C < C_0 \end{array}\right\}$$

It has an *admissible* solution for

$$c = \begin{cases} 2\sqrt{rD} & \text{if } a < \sqrt{rD} \\ a + \dfrac{rD}{a} & \text{if } a > \sqrt{rD} \end{cases}$$

The speed is independent of O_2 dynamics!

The wave speed



In the case of small aerotactic bias ($a < \sqrt{rD}$),
the wave speed coincides with the Fisher wave speed: $c = 2\sqrt{rD}$.

In the case of large bias ($a > \sqrt{rD}$), $c = a + \dfrac{rD}{a} > 2\sqrt{rD}$.

At the transition, growth contributes to half of the speed.

Further investigation

The model is very attractive, yet too simple!

The constant advection speed is quite unrealistic.

The following extension can be handled analytically
(very preliminary results, in collaboration with Mete Demircigil and a master student Roxana Sublet).

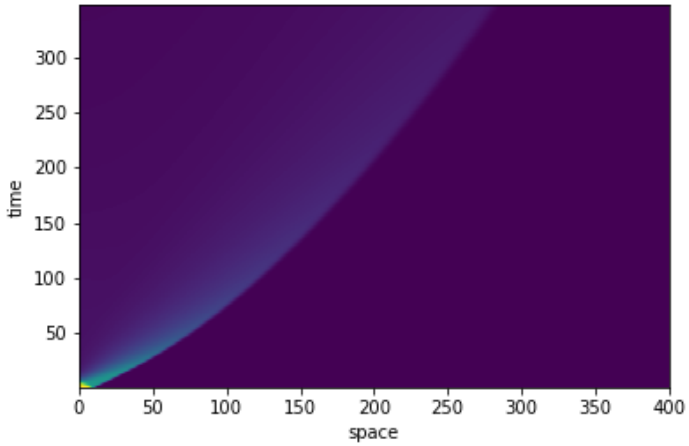
$$\frac{\partial \rho}{\partial t} - D\frac{\partial^2 \rho}{\partial x^2} + \frac{\partial}{\partial x}\left\{ \begin{array}{ll} 0 & \text{if } C > C_0 \\ a\,\dfrac{\partial(\log C)}{\partial x}\rho & \text{if } C < C_0 \end{array} \right\}$$

$$= \left\{ \begin{array}{ll} r\rho & \text{if } C > C_0 \\ 0 & \text{if } C < C_0 \end{array} \right\}$$

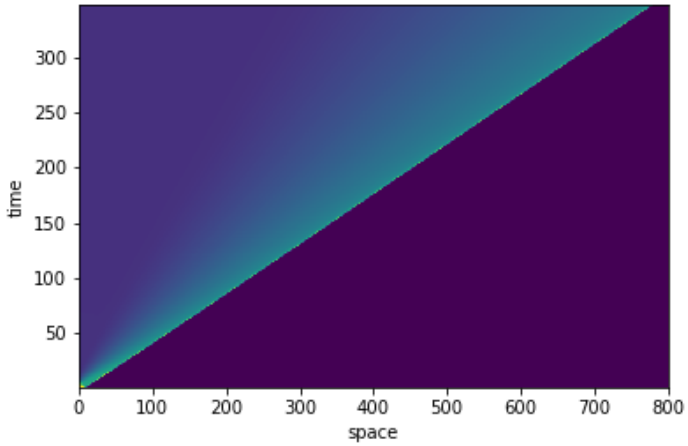
coupled with Oxygen consumption (without diffusion $D_{\mathrm{ox}} = 0$) :

$$\frac{\partial C}{\partial t} = -\gamma \rho C$$

Preliminary result



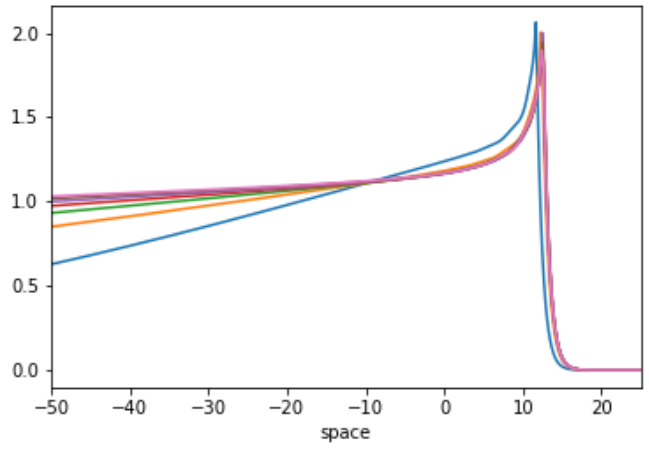
(without growth)



(with limited growth)

We have accumulated evidence that the speed should be

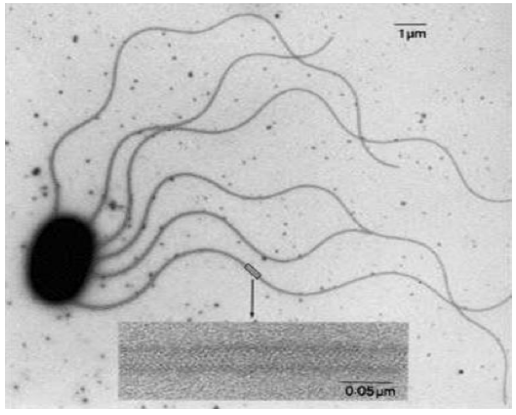
$$c = 2\sqrt{r \max\left(D, a \log\left(\frac{C(+\infty)}{C_0}\right)\right)}$$

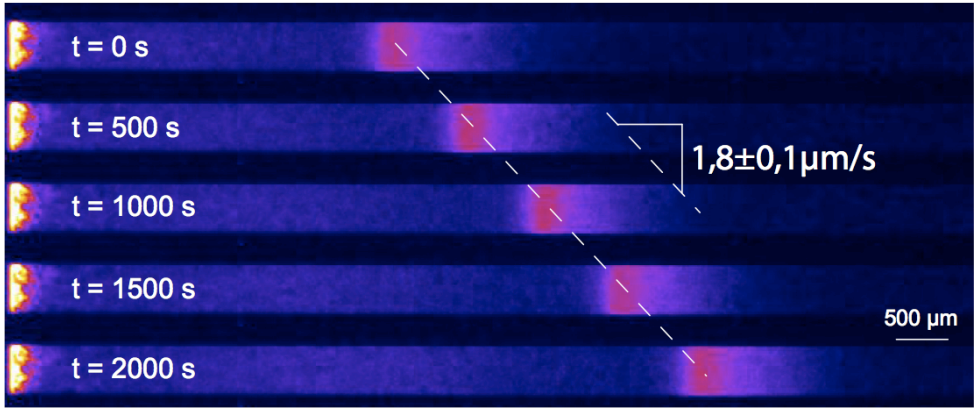


② Chemotactic waves of bacteria *E. coli*

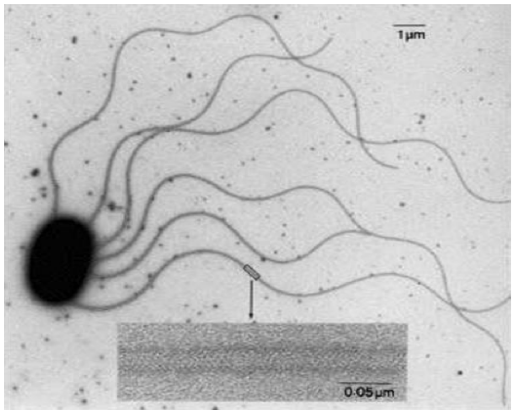
Joint work with:

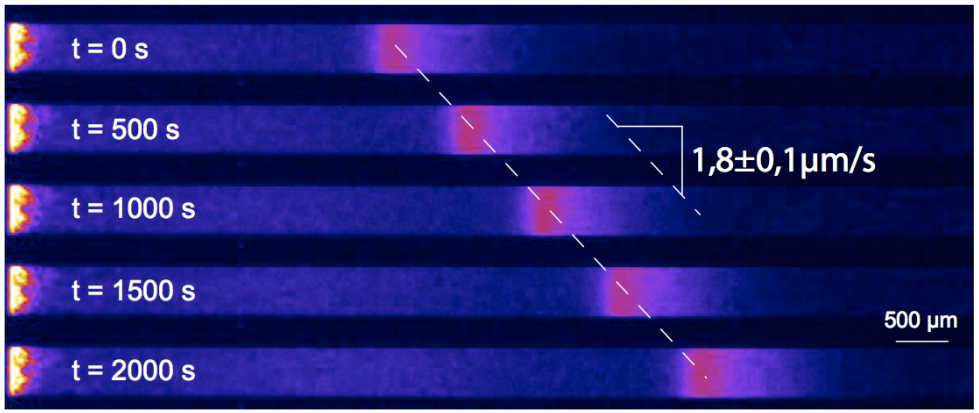
- N. Bournaveas, A. Buguin, B. Perthame, J. Saragosti, P. Silberzan,
- G. Raoul, C. Schmeiser,
- L. Gosse, M. Twarogowska.



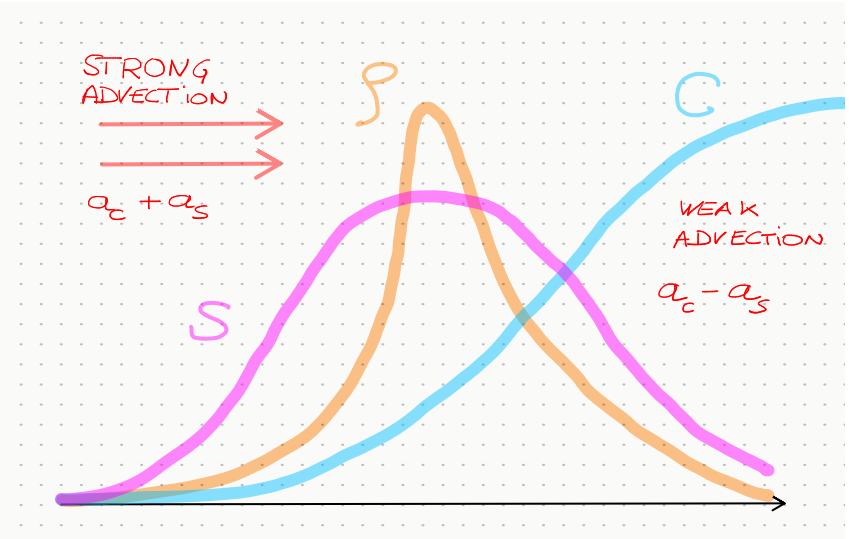


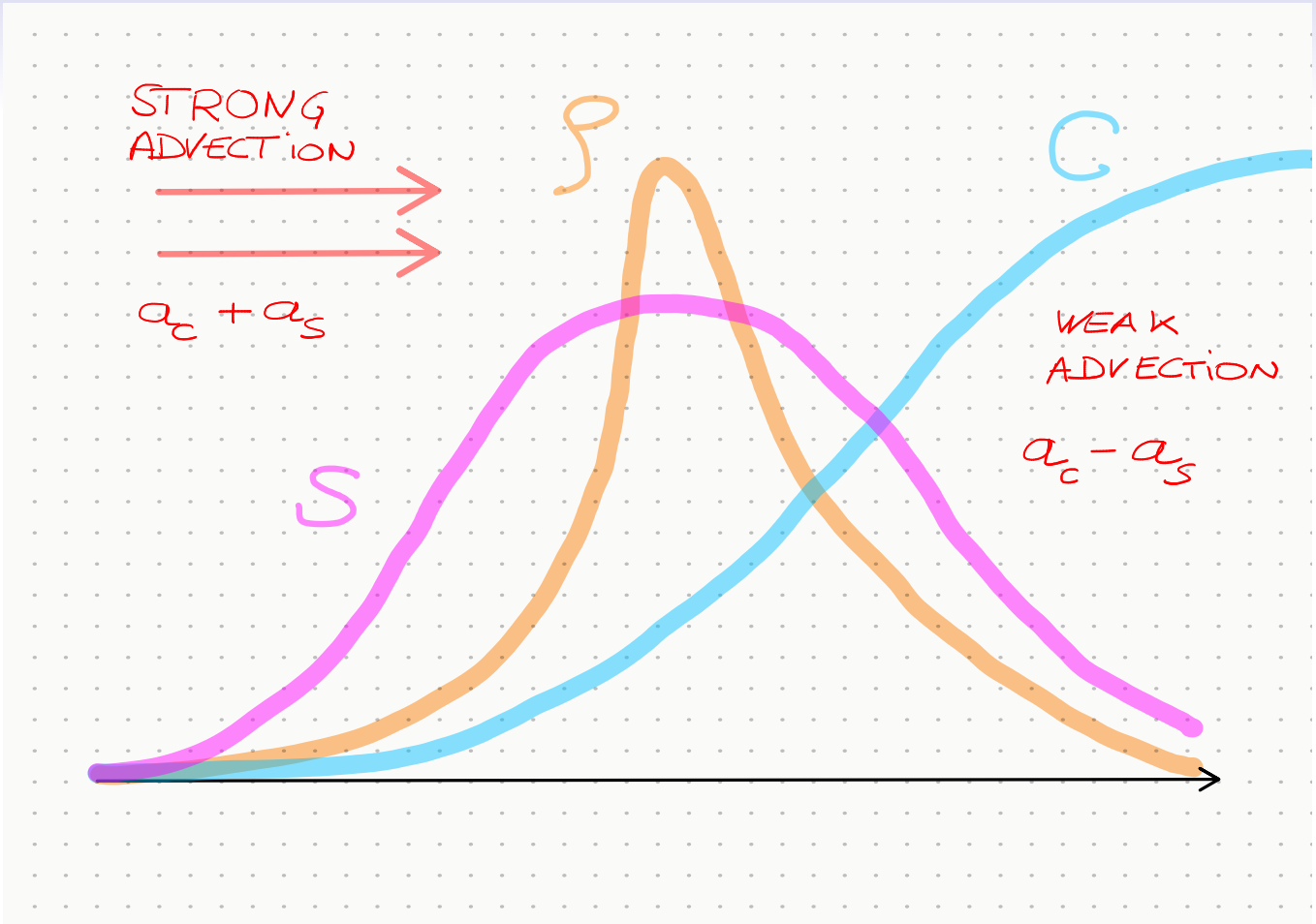
A scenario with two signals



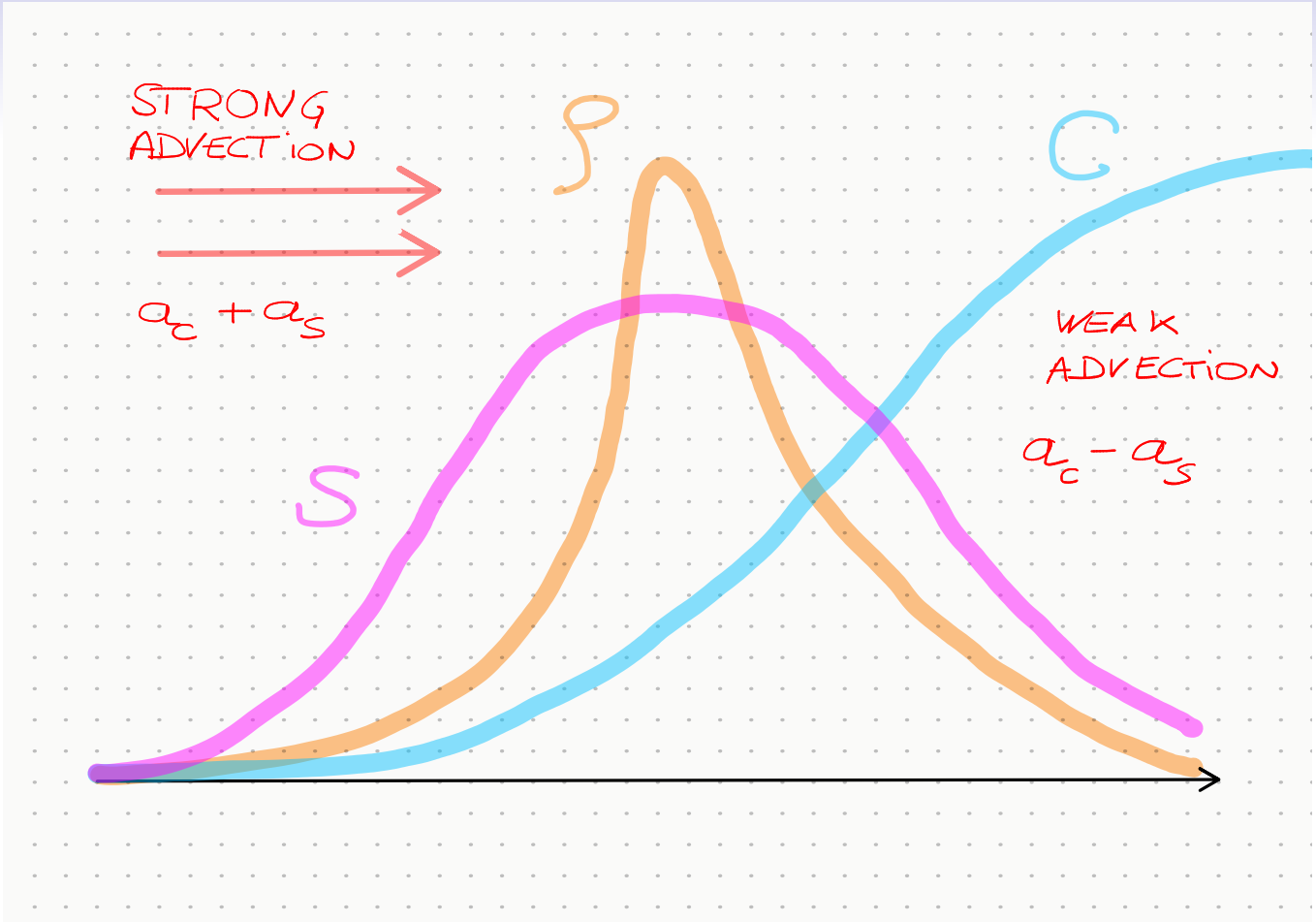


$$\begin{cases} \dfrac{\partial \rho}{\partial t} - D\dfrac{\partial^2 \rho}{\partial x^2} + \dfrac{\partial}{\partial x}\left(\left(a_C \mathrm{sign}\left(\dfrac{\partial C}{\partial x}\right) + a_S \mathrm{sign}\left(\dfrac{\partial S}{\partial x}\right)\right)\rho\right) = 0 \\ \dfrac{\partial C}{\partial t} = D_C \dfrac{\partial^2 C}{\partial x^2} - \gamma \rho C \\ \dfrac{\partial S}{\partial t} = D_S \dfrac{\partial^2 S}{\partial x^2} - \alpha S + \beta \rho \end{cases}$$





- Common point: strong advection (bias) at the back of the wave; essentially diffusion ahead
- Main difference : no growth, but a communication signal S that keeps the population aggregated.

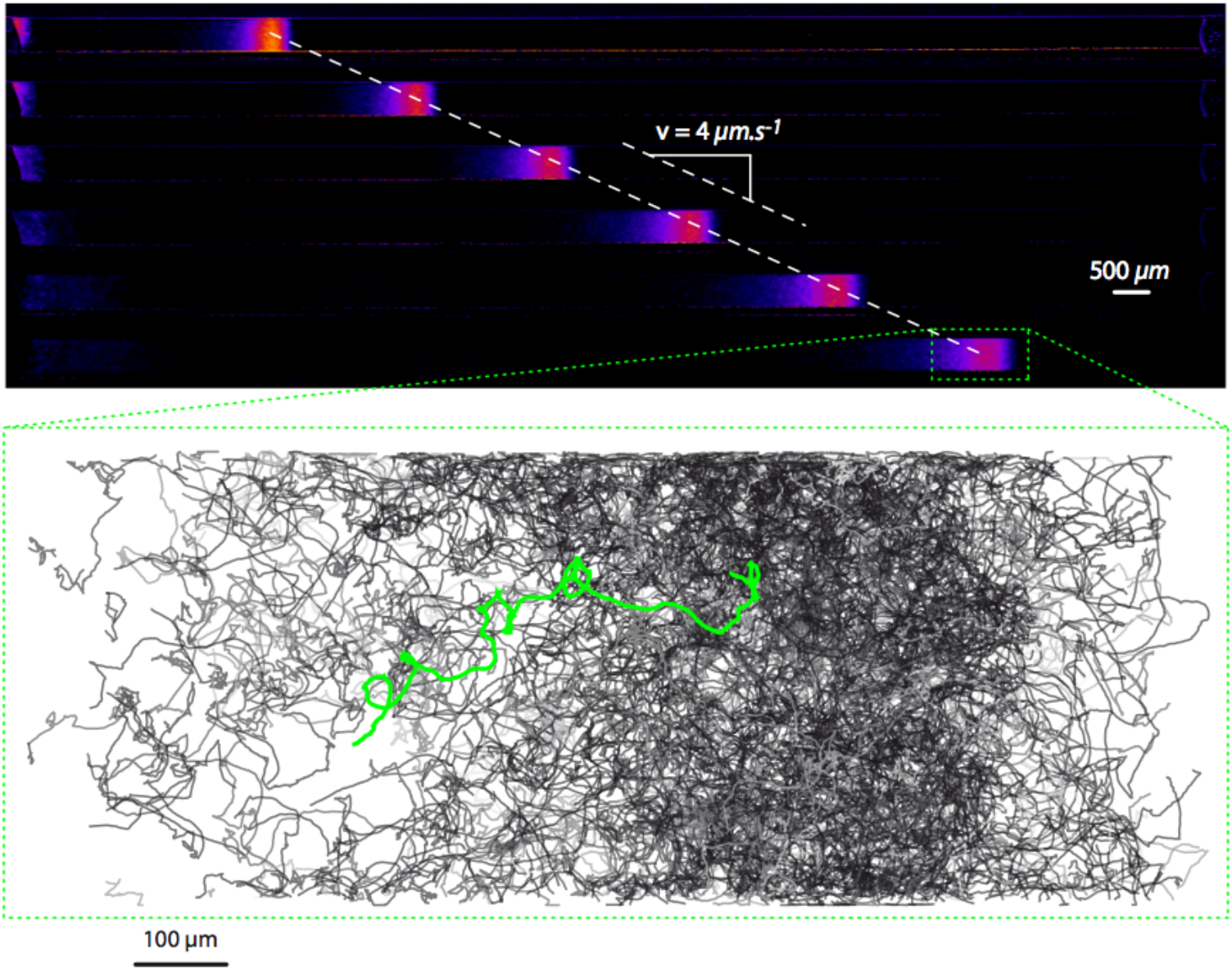


There exists a traveling wave $\rho(x - ct), C(x - ct), S(x - ct)$.
The wave speed is given by an implicit formula:

$$a_C - c = a_S \frac{c}{\sqrt{4D_S\alpha + c^2}}$$

Adler, Science (1966), Keller and Segel, J. Theor. Biol. (1971);
Saragosti et al, PLOS Comput. Biol. (2010), Saragosti et al, PNAS 2011

A multiscale picture

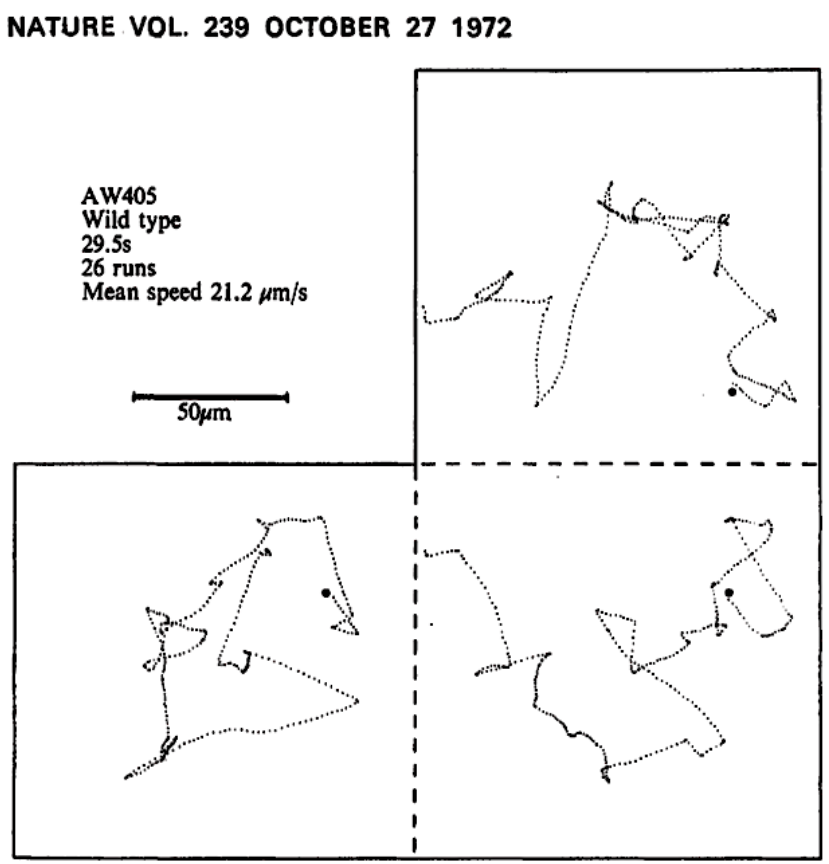


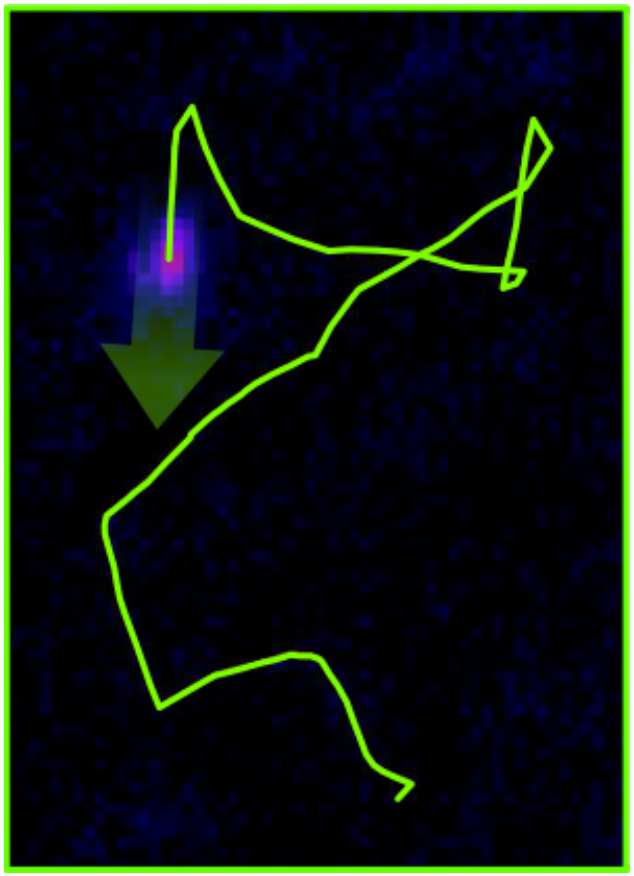
Experiments and pictures by J. Saragosti

From individual motion...

$x \in \mathbb{R}^d$, $v \in V$ compact set of velocities, normalized to $|V| = 1$.

- $\dot{x} = v$
- at rate $\mathbf{T}(t, x, v)$, take a new velocity uniformly at random.





Trajectories of swimming E. coli (Left: Berg and Brown; Right: Saragosti)

. . . to collective motion

Kinetic equation for the bacteria density $f(t,x,v)$:

$$\overbrace{\frac{\partial f}{\partial t}(t,x,v) + v\frac{\partial f}{\partial x}(t,x,v)}^{\text{free transport (run)}} = \underbrace{\int_{v'\in V} \mathbf{T}(t,x,v')f(t,x,v')\,dv' - \mathbf{T}(t,x,v)f(t,x,v)}_{\text{scattering (tumble)}}$$

Bacteria *E. coli* react positively to time variations of chemical signals (S, N,. . .)

runs are longer when concentration increases.

$$\mathbf{T} = \psi\left(\left.\frac{DS}{Dt}\right|_v\right) = 1 - \chi_S \operatorname{sign}\left(\frac{\partial S}{\partial t} + v\frac{\partial S}{\partial x}\right) \qquad \chi_S \in (0,1)$$

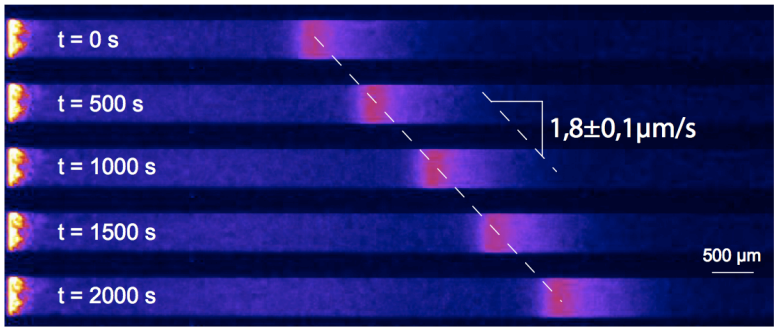
The full kinetic/reaction-diffusion coupled system

$$\begin{cases} \partial_t f + v \cdot \nabla_x f = \displaystyle\int_{v' \in V} \left(\mathbf{T}_S(v') + \mathbf{T}_C(v')\right) f(t,x,v')\, dv' \\ \qquad\qquad\qquad\qquad - \left(\mathbf{T}_S(v) + \mathbf{T}_C(v)\right) f(t,x,v) \\ \partial_t C = D_C \Delta C - \gamma \rho C \\ \partial_t S = D_S \Delta S - \alpha S + \beta \rho \end{cases}$$

$$\rho(t,x) = \int_V f(t,x,v)\, dv$$

$$\mathbf{T}_S = 1 - \chi_S \mathrm{sign}\left(\partial_t S + v \cdot \nabla_x S\right)$$

$$\mathbf{T}_C = 1 - \chi_C \mathrm{sign}\left(\partial_t C + v \cdot \nabla_x C\right)$$



Saragosti-C-Bournaveas-Perthame-Buguin-Silberzan (PNAS 2011), see also Xue-Hwang-Painter-Erban (Bull Math Biol 2010)

Analysis at the macro scale (the slow wave)

If biases are small ($\chi_S, \chi_C \ll 1$) then reduction to an advection-diffusion equation for the spatial density $\rho(t,x)$:

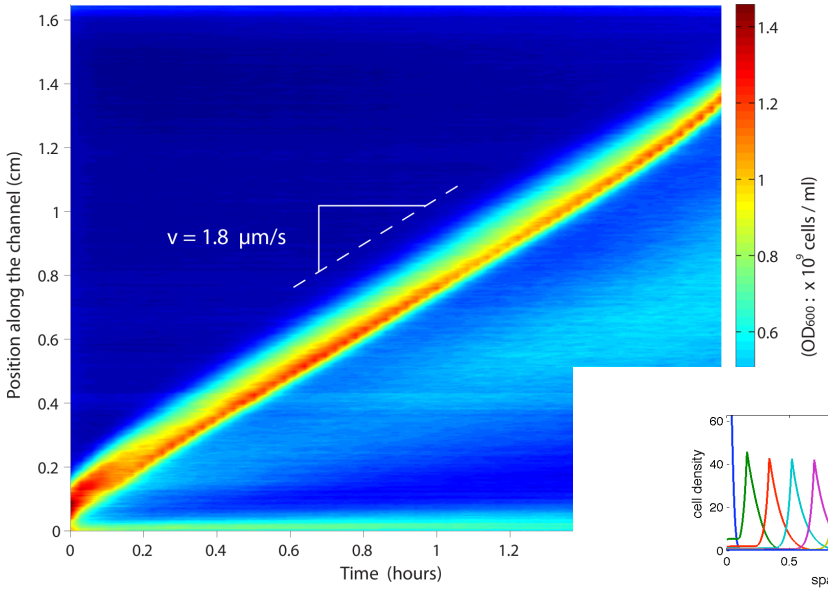
$$\begin{cases} \dfrac{\partial \rho}{\partial t} = D_\rho \dfrac{\partial^2 \rho}{\partial x^2} - \dfrac{\partial}{\partial x}(\rho u) \quad u = a_S \mathrm{sign}\left(\dfrac{\partial S}{\partial x}\right) + a_C \mathrm{sign}\left(\dfrac{\partial C}{\partial x}\right) \\ \dfrac{\partial C}{\partial t} = D_C \dfrac{\partial^2 C}{\partial x^2} - \gamma \rho C \\ \dfrac{\partial S}{\partial t} = D_S \dfrac{\partial^2 S}{\partial x^2} - \alpha S + \beta \rho \end{cases}$$

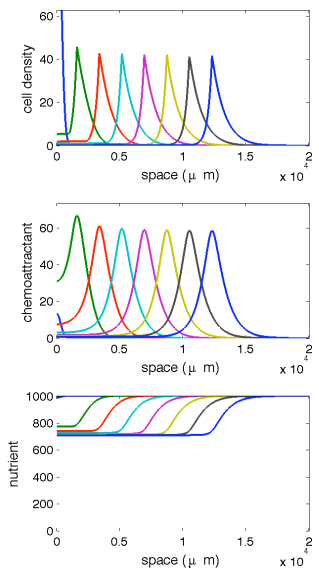
Theorem (Explicit computations)

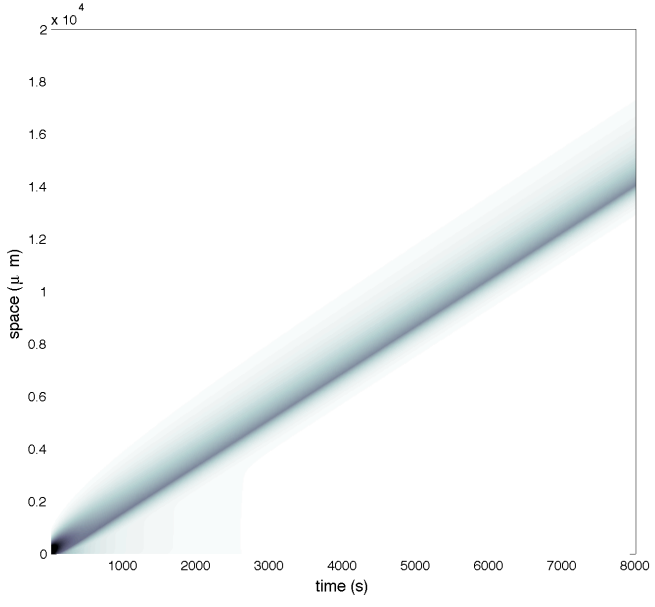
There exists a traveling wave $\boldsymbol{\rho}(x-ct), \mathbf{C}(x-ct), \mathbf{S}(x-ct)$. The wave speed is given by an implicit formula:

$$a_C - c = a_S \frac{c}{\sqrt{4 D_S \alpha + c^2}}$$

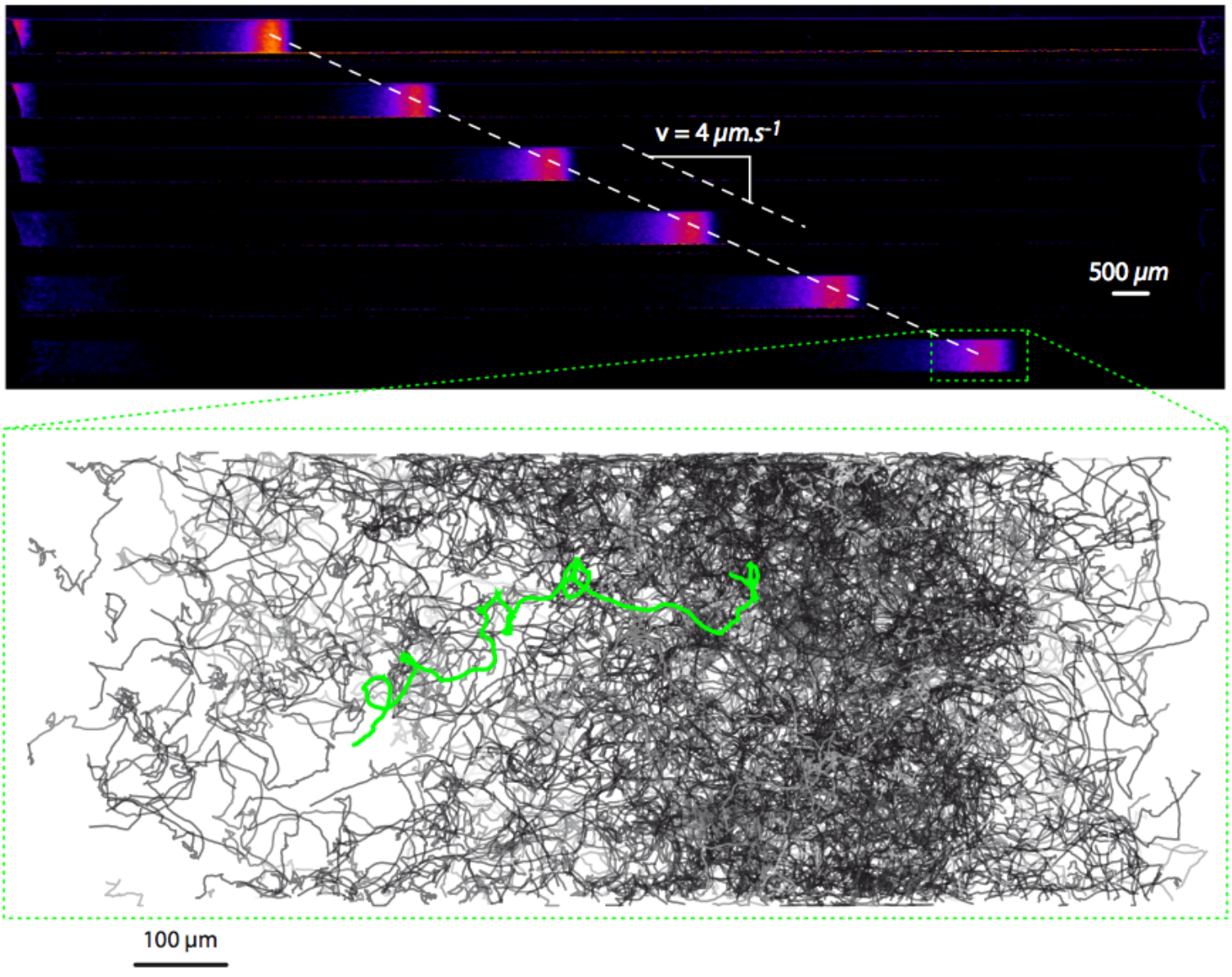
Validation on experimental data (I)







What about the fast wave?



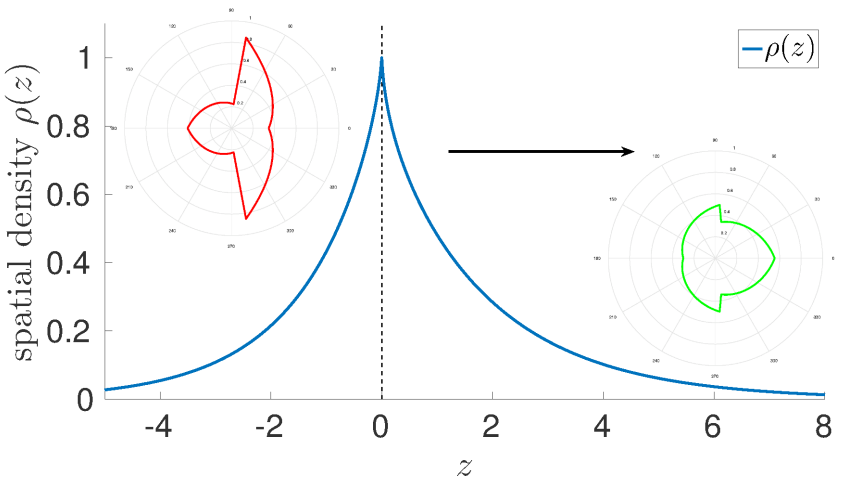
Experiments and pictures by J. Saragosti

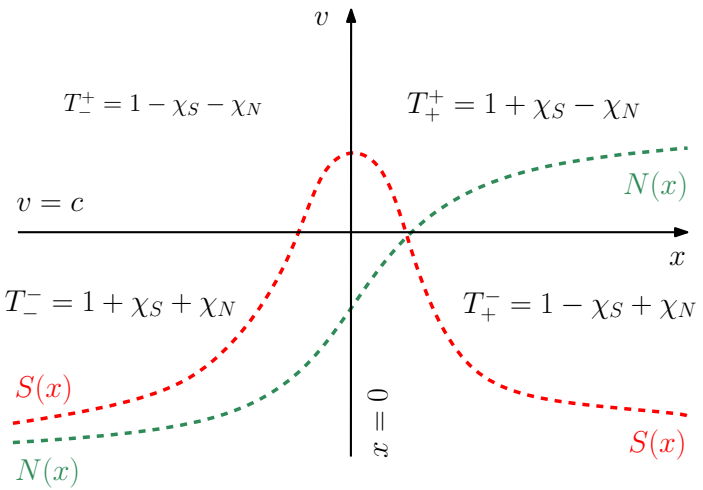
Analysis at the meso scale (the fast wave)

The diffusive limit is not always valid on experimental data (biases can be relatively large).

Theorem

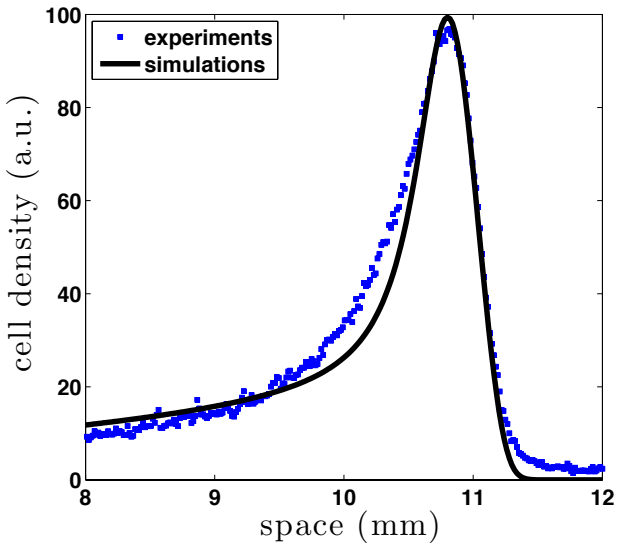
Under extra conditions on the parameters, there exists a traveling wave $\mathbf{F}(x-ct,v), \mathbf{C}(x-ct), \mathbf{S}(x-ct)$ *moving at some speed* c.

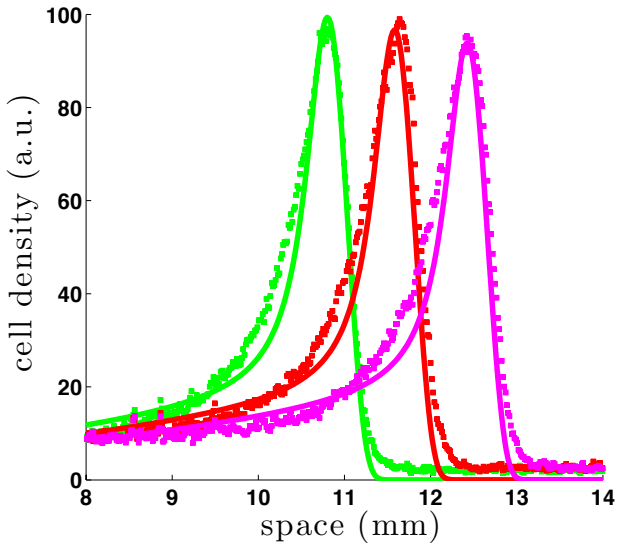


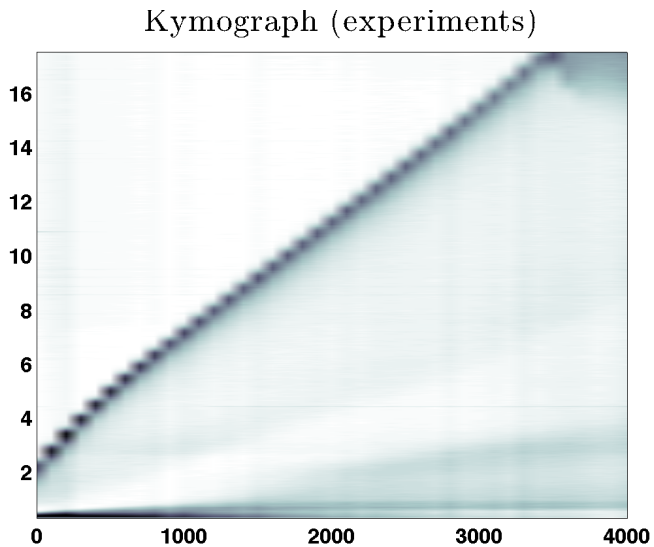


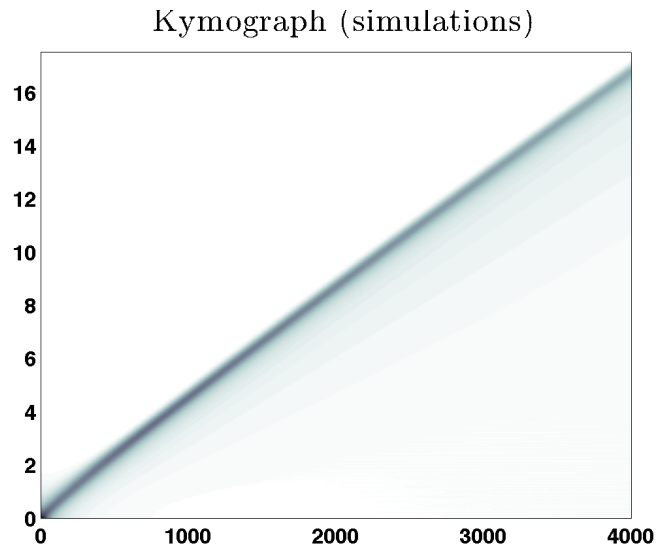
C (J. Europ. Math. Soc. 2019)

Validation on experimental data









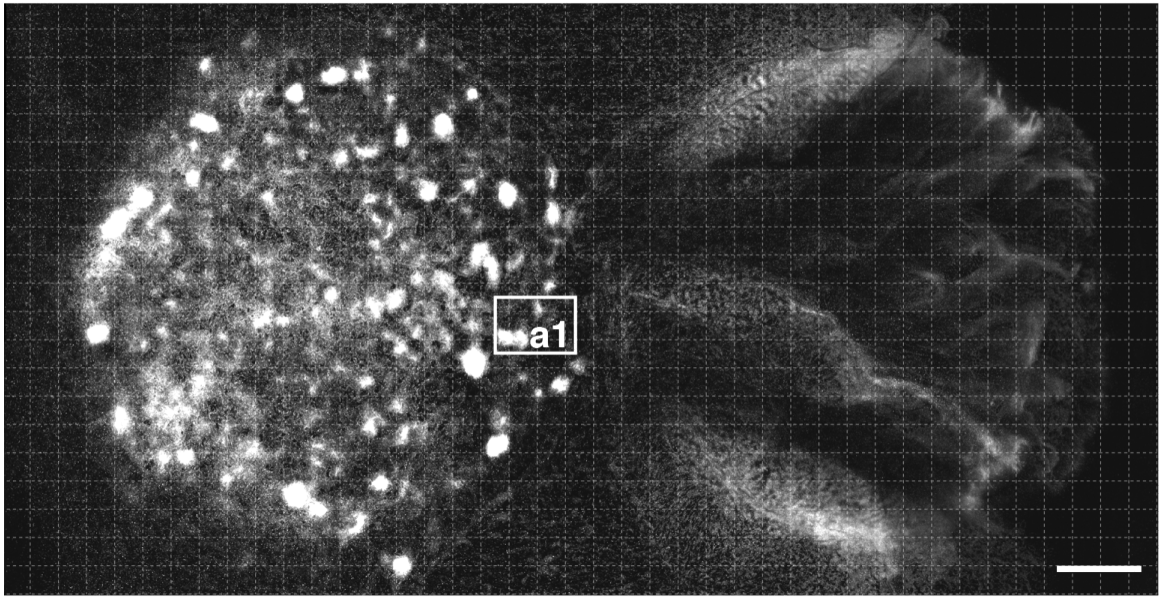
Conclusions

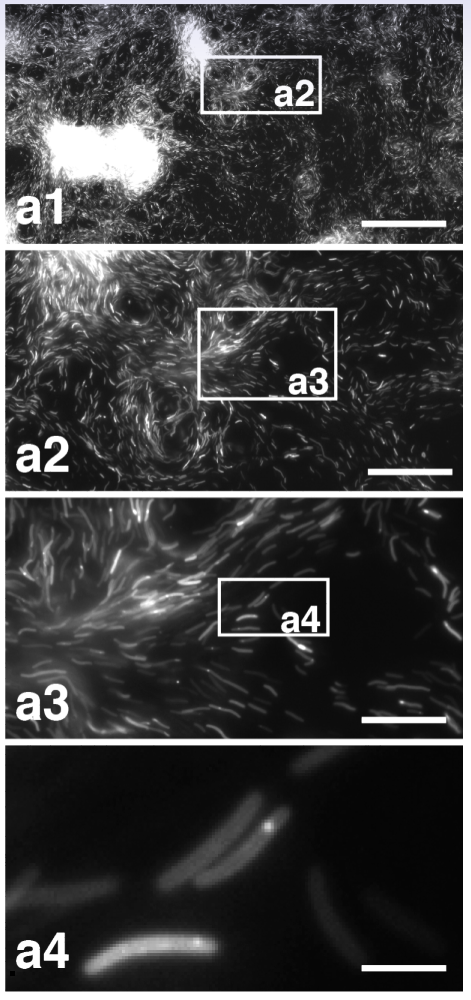
- Generic models were turned into piecewise constant models to get formula for the wave speed
- Mesoscopic (kinetic) traveling waves can be more relevant, but there is a significant mathematical step in the analysis
- The two case studies exhibit waves of different nature: (1) growth+migration; (2) migration with two signals

Open problems

- Stability of the traveling waves
- Design of non-oscillating numerical schemes for the case of discontinuous advection
- Heterogeneity in the chemotactic response within the wave (spatial sorting: see Fu et al, Nature Comm 2018)

Perspectives





Picture acquisition in the Mignot Lab (Marseille)

Dynamics of myxobacteria following the predation stage:
multiscale picture $\rightarrow$ refined model:

$$\frac{\partial g}{\partial t}(t,x,v,a)+v\frac{\partial g}{\partial x}(t,x,v,a)+\frac{\partial g}{\partial a}(t,x,v,a)+T(\rho)\mathbf{H}(a-a^*(\rho))g = \ldots$$

Thank you!

European Research Council

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