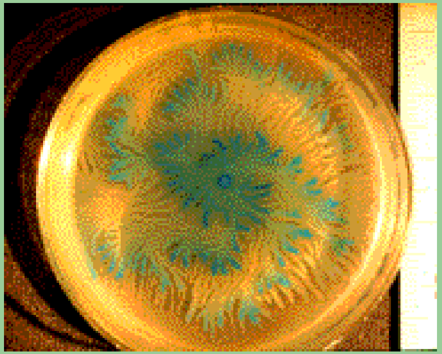
Dynamics and growth of bacterial colonies



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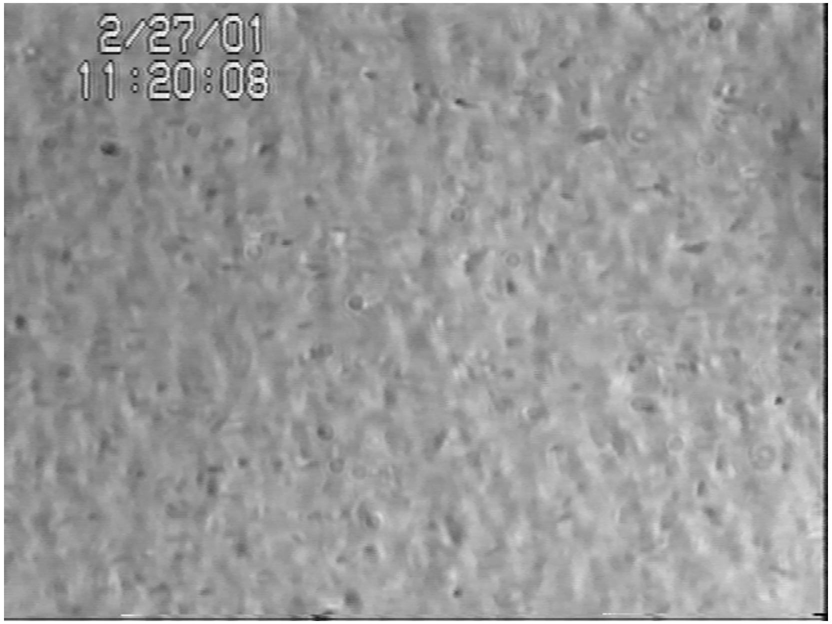
T. Passot
B. Salhi

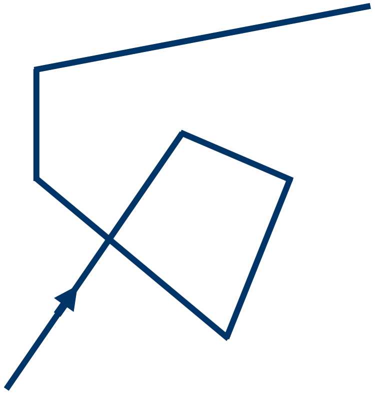
Movie by

Cathy Ott

Who is *Bacillus subtilis*?

- Rod-like bacterium
  - Length ≅ 2-3 μm
  - Diameter ≅ 0.7 μm
  - Swimming speed ≅ 10 times the cell length per second
- Swims with flagella (runs and tumbles)



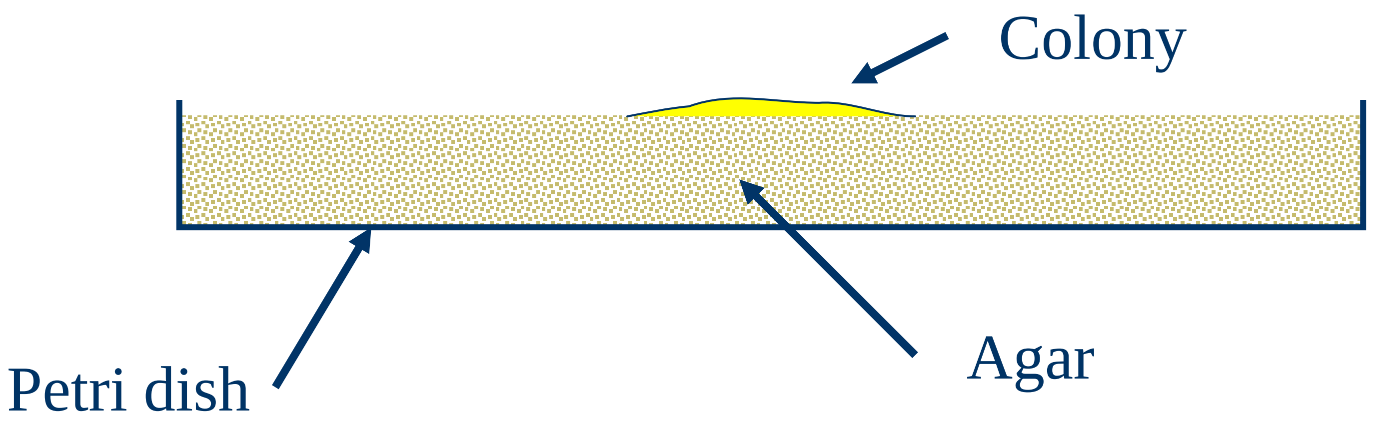


Examples of collective behaviors in bacterial systems

- Bioconvection: convection caused by the gathering of bacteria at the top of a fluid.
- Biofilms: communities of bacteria (more generally of microorganisms) attached to a surface.
- Bacterial colonies grown on agar plates: formed by motile or non-motile bacteria which multiply in a nutritive medium.

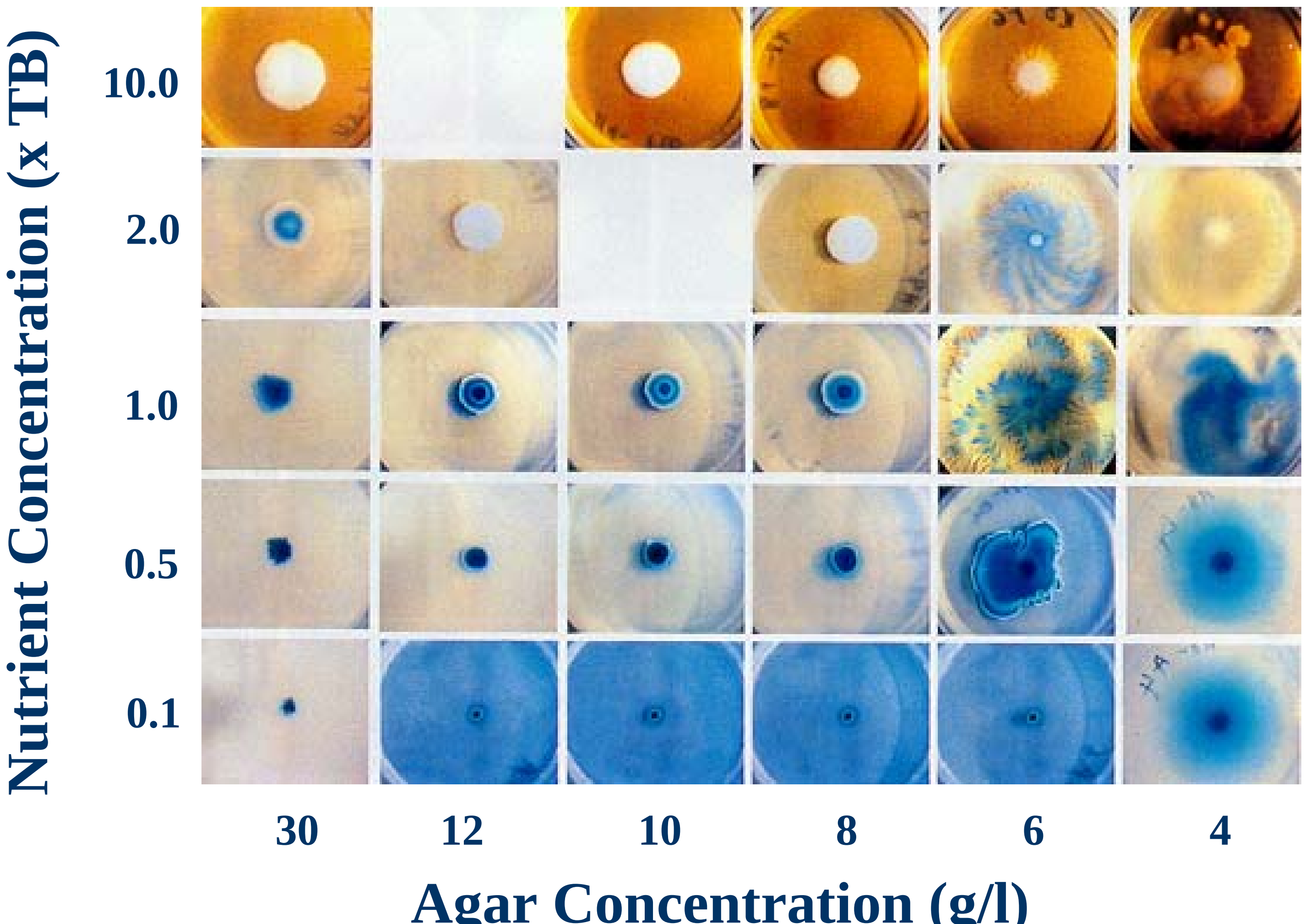
Colony growth on agar plates

- Colonies grow on agar, which is a gel containing water and nutrients.
- Colonies are inoculated at the center of the agar plate and are allowed to grow for weeks.



N. H. Mendelson & B. Salhi, J. Bacteriology **178**, 1980-1989 (1996)

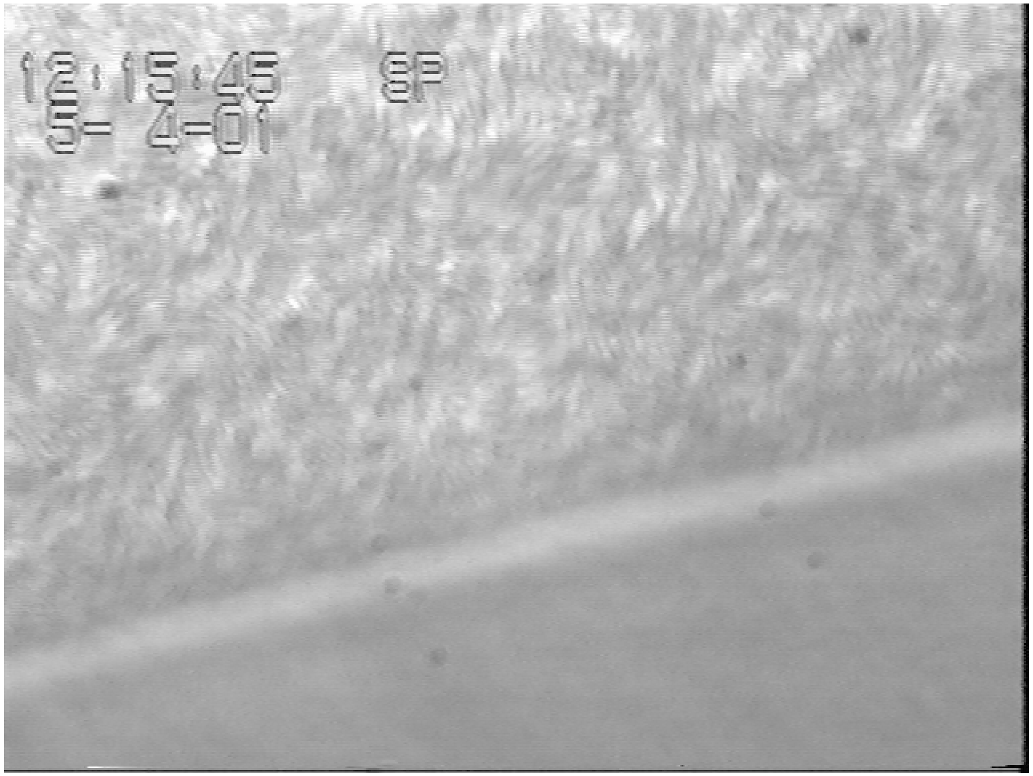
Different colony forms for *Bacillus subtilis*

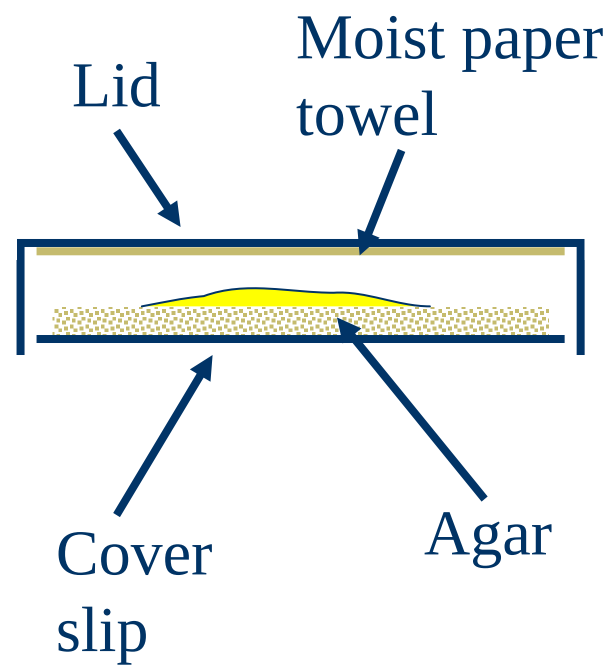


Experiments by

C. Ott & N. Mendelson

Large-scale motion in the colony



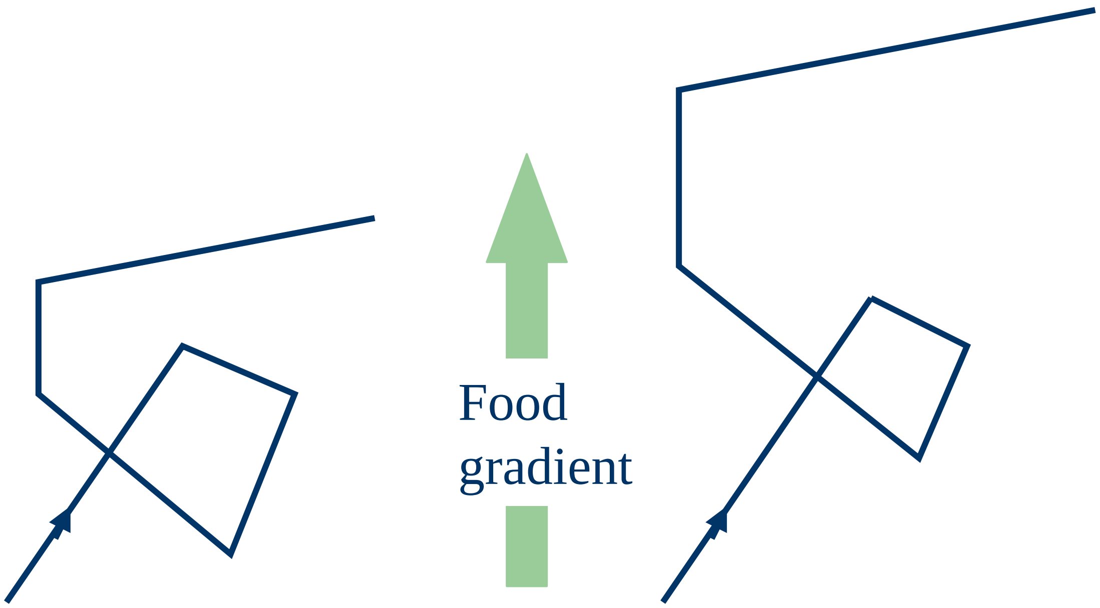


This movie illustrates the formation and dynamics of whirls and jets in the colony [N.H. Mendelson *et al.*, J. Bact. **181**, 600-609 (1999)]. When the cells are killed by formaldehyde vapors, all motions cease.

Who is *Bacillus subtilis* ?

- In these experiments, *B. subtilis* does not
  - form spores,
  - secrete a surfactant, or form a biofilm
- Shows chemotaxis to food: $j_N = \chi(S) N \nabla S$

From R. Macnab, *Motility and Chemotaxis*, in *E. coli and S. typhimurium: cellular and molecular biology*, pp. 732-759, Ed. by F.C. Neidhart *et al.*, ASM, Washington DC, 1987



Interesting aspects of this type of bacterial dynamics

- Hierarchy of scales:
  - <u>Microscopic level</u>: bacteria
  - <u>Mesoscopic level</u>: whirls and jets
  - <u>Macroscopic level</u>: colony shape
- Looks like two-dimensional turbulence
- Can such behaviors be explained in physical terms or is signaling between cells an important ingredient?

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    $\rightarrow$ **reaction-diffusion models**
- Looks like two-dimensional turbulence
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I. Golding *et al.*, Physica A **260**, 510-554 (1998)

Reaction-diffusion models

- It is well known that branched colony shapes can be captured by means of reaction-diffusion models

$$\frac{\partial S}{\partial t} = D^S \nabla^2 S - \eta\, N\, \mathrm{S}$$

S nutrient density

N bacterial density

  - Nonlinear diffusion

    [S. Kitsunezaki, J. Phys. Soc. Jpn. **66**, 1544-1550 (1997)]

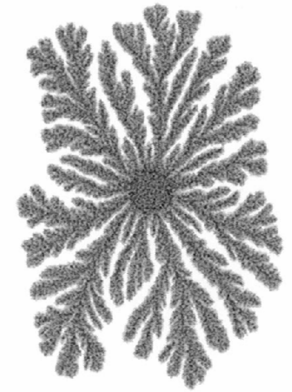
$$\frac{\partial N}{\partial t} = \nabla \cdot \left(D^N N^k \nabla N \right) + N\, S - \mu\, N$$

  - Nonlinear diffusion with stochastic diffusion coefficient

    [K. Kawasaki *et al.*, J. Theor. Biol. **188**, 177-185 (1997)]

$$\frac{\partial N}{\partial t} = \nabla \cdot \left(D^N (1+\sigma) N\, S\, \nabla N \right) + N\, S$$

where σ has a triangular distribution



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Interesting aspects of this type of bacterial dynamics

- Hierarchy of scales:
  - Microscopic level: bacteria
  - Mesoscopic level: whirls and jets $\rightarrow$ **hydrodynamic model**
  - Macroscopic level: colony shape
    $\rightarrow$ reaction-diffusion models
- Looks like two-dimensional turbulence
- Can such behaviors be explained in physical terms or is signaling between cells an important ingredient?

Why try a hydrodynamic approach?

- In wet conditions, bacterial motion is dominant in colony expansion and therefore needs to be modeled adequately. This dynamics <u>cannot</u> be described by existing reaction-diffusion models.
- Whirls and jets observed within the colony suggest a hydrodynamic approach.
- Bacterial density is too high to assume that the dynamics within the colony results from swimming of isolated bacteria: bacterium-bacterium interactions cannot be neglected.
- Joint work with T. Passot

  [J.L. & T. Passot, *Hydrodynamics of bacterial colonies: a model*, Phys. Rev. E **67**, 031906 (2003); *Hydrodynamics of bacterial colonies: phase diagrams*, Chaos **14**, 562-570 (2004)]

Hydrodynamic model

- Orders of magnitude
  - At the scale of a bacterium

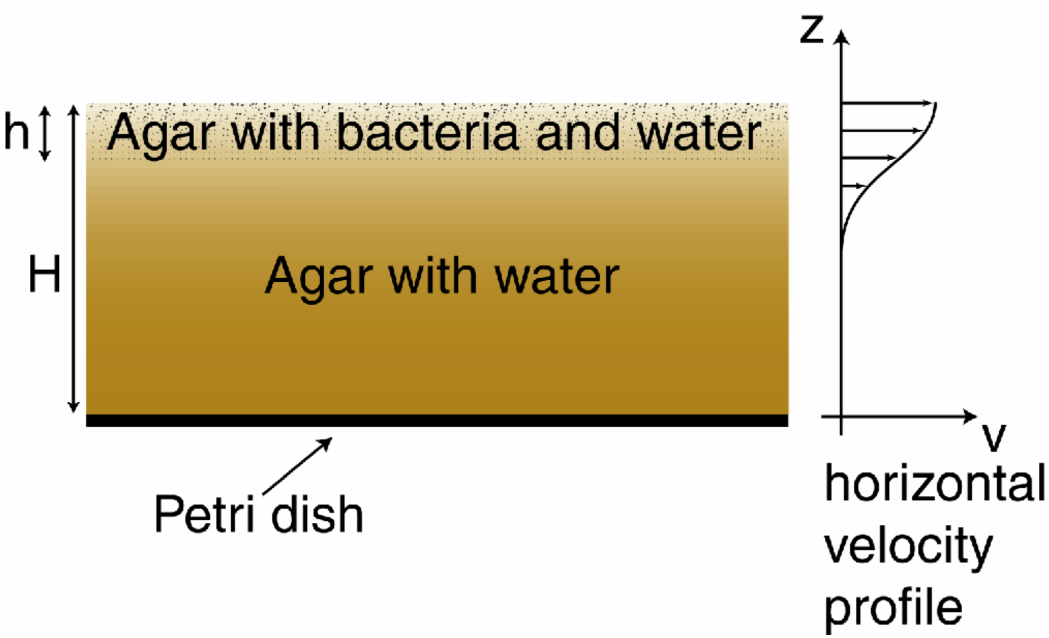
$$\mathrm{Re}^S = \frac{vL}{\upsilon} \cong \frac{30 \cdot 10^{-6} \cdot 3 \cdot 10^{-6}}{10^{-6}} \cong 10^{-4}$$

  - At the scale of a bacterium, in the presence of vortices and jets:

$$\mathrm{Re}^B \cong \frac{100 \cdot 10^{-6} \cdot 25 \cdot 10^{-6}}{10^{-6}} = 2.5 \cdot 10^{-3}$$

  - At the scale of the large-scale structures: $\mathrm{Re}^L \cong 1$
  - or $\mathrm{Re}^{WJ} = \dfrac{\tau_D}{\tau_C} \cong \dfrac{\text{time to reach characteristic size}}{\text{life - time of whirls and jets}} = \dfrac{5}{0.25} = 20$

Hydrodynamic model



- Model the agar as a porous medium.
- Brinkman's equations for porous media indicate that motion will occur in a thin layer near the surface of the agar.
- Model the mixture of bacteria and water as a two-phase fluid.

Hydrodynamic model

- Continuity equation for nutrients
  - S = nutrient concentration
  - Nutrients diffuse through the agar towards the mixture of bacteria and water
  - Nutrients are consumed by bacteria (R_S)
  - We assume that Fick's law is valid as a first approximation and neglect medium anisotropy for food diffusion
  - We assume that the fraction of nutrients advected by the fluid is negligible

$$\frac{\partial S}{\partial t} = R_S + D^S \nabla^2 S$$

Hydrodynamic model

- Continuity equation for bacteria
  - N = bacterial mass per unit volume
  - v^N = bacterial velocity field
  - Bacterial mass increases due to food consumption (R_N)
  - We assume there is no mass transfer at the interface between bacteria and water

$$\frac{\partial N}{\partial t} + \nabla \cdot (N v^N) = R_N$$

$$\frac{\partial N}{\partial t} + \nabla \cdot (N v) = \nabla \cdot \left(N (v - v^N) \right) + R_N = \nabla \cdot (-j^N) + R_N$$

$$j^N = N (v^N - v) \cong -D^N (N, W, S) \nabla N$$

Hydrodynamic model

- Continuity equation for water
  - W = mass of water per unit volume
  - v^W = water velocity field
  - Water "diffuses" through due to capillary dispersivity
  - Water may also evaporate (R_W)
  - Interfacial mass transfer is neglected

$$\frac{\partial W}{\partial t} + \nabla \cdot (W v^W) = R_W + \nabla \cdot \left(D^W \nabla W \right)$$

Hydrodynamic model

- Momentum equations for water
  - T^W = water stress tensor
  - $F^W = F_i^W + F_s^W + F_e^W$
  - F_i^W describes interactions between water and bacteria
  - F_s^W describes interactions with the substrate
  - F_e^W describes external forces (e.g. due to addition of water, …)

$$\frac{\partial}{\partial t}(Wv^W) + \nabla \cdot (Wv^W v^W) = \nabla T^W + F^W + R_W v^W + v^W \nabla \cdot \left(D^W \nabla W\right)$$

Hydrodynamic model

- Momentum equations for bacteria
  - T^N = bacteria stress tensor
  - $F^N = F_i^N + F_s^N + F_g^N$
  - F_i^N describes interactions between water and bacteria
  - F_s^N describes interactions with the substrate
  - F_g^N describes changes in linear momentum due to bacterial activity

$$\frac{\partial}{\partial t}(Nv^N) + \nabla \cdot (Nv^N v^N) = \nabla T^N + F^N + R_N v^N$$

Hydrodynamic model

- Interaction forces
  - We assume that $F_i^N + F_i^W = 0$, which is legitimate if one neglects surface tension effects at the interface between bacteria and water

- Stress tensors
  - $\nabla T^W = - \nabla p^W + \tau^W$; $\nabla T^N = - \nabla p^N + \tau^N$
  - $p^N = k\,T\,[N + B_2(T)\,N^2 + O(N^3)] = p_0^N + \gamma(S,N,W)\,N^2$ the second term describes pressure due to collisions between bacteria
  - For a newtonian fluid, $\tau^W = \mu^W \nabla^2 v^W$ and $\tau^N = \mu^N \nabla^2 v^N + \lambda^N \nabla (\nabla \cdot v^N)$

Hydrodynamic model

- Equations for global quantities

$$\rho = N + W \qquad v = \frac{1}{\rho}\left(Nv^N + Wv^W\right)$$

$$\frac{\partial \rho}{\partial t} + \nabla \cdot (\rho v) = R_N + R_W + \nabla \cdot \left(D^W \nabla W\right)$$

$$\rho \frac{\partial v}{\partial t} + \rho\left(v \cdot \nabla\right)v \cong -\nabla p - \nabla\left(\gamma(S, N, W)\rho^2(1-\delta)^2\right) + \nabla \cdot \left(\tau^W + \tau^N\right) + F$$

$$p = p^W + p_0^N \qquad F \cong -\eta\, v + F_e^W + F_g^N$$

$$v^W = v^N + \varepsilon\, m \qquad \|m\| = O\left(\|\, v^N \,\|\right) \qquad \varepsilon << 1$$

$$\delta = \frac{W}{N + W} = \text{wetness coefficient} \qquad \frac{\partial S}{\partial t} = R_S + D^S \nabla^2 S$$

Hydrodynamic model

- If δ is not constant, the following equations are used

$$\rho\frac{\partial v}{\partial t}+\rho\left(v\cdot\nabla\right)v\cong-\nabla p-\nabla\left(\gamma(S,N,W)N^{2}\right)+\nabla\cdot\left(\tau^{W}+\tau^{N}\right)+F$$

$$\frac{\partial N}{\partial t}+\nabla\cdot\left(Nv\right)=R_{N}+\nabla\cdot\left(D^{N}\nabla N\right)$$

$$\frac{\partial W}{\partial t}+\nabla\cdot\left(Wv\right)=R_{W}+\nabla\cdot\left(D^{W}\nabla W\right)-\nabla\cdot\left(D^{N}\nabla N\right)$$

$$\rho=N+W$$

$$\frac{\partial S}{\partial t}=R_{S}+D^{S}\nabla^{2}S$$

Hydrodynamic model

- Two-dimensional reduction
  - Assume that *W* and *S* do not depend on the vertical coordinate
  - Neglect vertical variations of *N* in the thin layer at the top of the agar
  - Neglect vertical dependence of velocity field and assume $v=f(z)\, u(x,y,t)$
  - Then average over the vertical coordinate in the thin layer near the top of the agar plate
- Separation between expansion-driven and hydrodynamic components of the flow
  - $p = p_0^{\,N} + p^W$ is such that the compressible part of the velocity field $v = v^{\,C} + v^{\,H}$ is due to chemotaxis-like behaviors

$$\nabla \cdot v^H = 0 \quad \text{and} \quad \frac{\partial v^C}{\partial t} = -\frac{1}{\rho}\nabla\left(\gamma\, N^2\right) + \frac{1}{\rho_m} D\ v^C - \frac{\eta_m}{\rho_m} v^C$$

where $D\,v = \mu\,\nabla^2 v + \lambda\,\nabla(\nabla\cdot v)$ and η_m, ρ_m are typical values of η, ρ.

Hydrodynamic model

- Two-dimensional hydrodynamic model

$$\frac{\partial v}{\partial t} = \mathrm{P}\left[-(v \cdot \nabla)v + \left(\frac{1}{\rho} - \frac{1}{\rho_m} \right) \mathrm{D}\ v - \left(\frac{\eta}{\rho} - \frac{\eta_m}{\rho_m} \right) v + \frac{F}{\rho} \right]$$

$$- \frac{1}{\rho} \nabla \left(\gamma\ N^2 \right) + \frac{\mathrm{D}\ v}{\rho_m} - \frac{\eta_m}{\rho_m} v$$

$$\frac{\partial N}{\partial t} + \nabla \cdot (Nv) = R_N + \nabla \cdot \left(D^N \nabla N \right)$$

$$\frac{\partial W}{\partial t} + \nabla \cdot (Wv) = R_W + \nabla \cdot \left(D^W \nabla W \right) - \nabla \cdot \left(D^N\ \nabla N \right)$$

$$\frac{\partial S}{\partial t} = R_S + D^S \nabla^2 S$$

Gradients are now horizontal gradients and $v = u <f>$ is the averaged velocity field.

Chemotaxis-like behavior

- Neglect inertial and viscous terms, as well as the incompressible part of the pressure term
- Assume N/ρ and $\gamma(S)$ are constant
- Then if the consumption term dominates the nutrient dynamics, we have

$$N = -\frac{1}{k_0}\frac{\partial G(S)}{\partial t} \quad \text{if} \quad R_S = -k_0 N\, f(S) \quad \text{and} \quad \frac{dG}{dS} = \frac{1}{f(S)}$$

$$\frac{\partial v}{\partial t} = -2\gamma \frac{N}{\rho}\nabla\left(\frac{1}{k_0}\frac{\partial G(S)}{\partial t}\right)$$

$$v \cong \frac{2\gamma}{k_0}\frac{N}{\rho}\frac{\nabla S}{f(S)} = \chi(S)\nabla S \qquad \chi(S) = \text{"chemotactic" coefficient}$$

Chemotaxis-like behavior

- $f(S) = S$ gives the Keller-Segel model for chemotaxis [E.F. Keller and L.A. Segel, J. Theor. Biol. **30**, 225-234 (1971)].
- $f(S) = (1+S)^2$ gives the "receptor law" for chemotaxis.
- We then obtain the following reaction-diffusion model

$$v \cong \frac{2\gamma}{k_0}\frac{N}{\rho}\frac{\nabla S}{f(S)} = \chi(S)\nabla S \qquad \chi(S) = \text{"chemotactic" coefficient}$$

$$\frac{\partial N}{\partial t} + \nabla\cdot\left(Nv\right) = R_N + \nabla\cdot\left(D^N\nabla N\right)$$

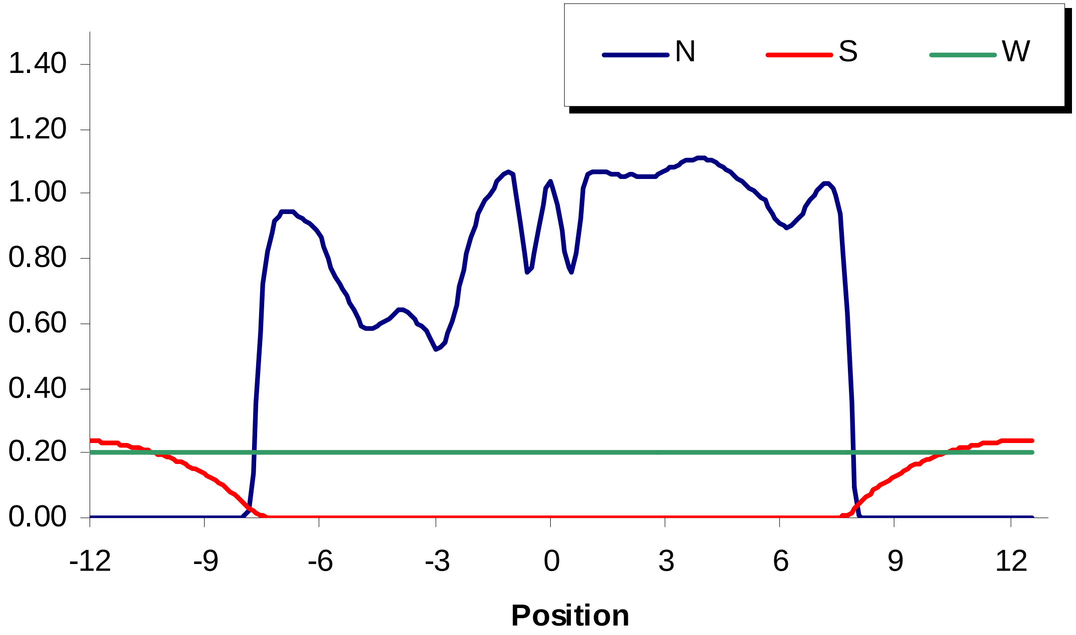
$$\frac{\partial W}{\partial t} + \nabla\cdot\left(Wv\right) = R_W + \nabla\cdot\left(D^W\nabla W\right) - \nabla\cdot\left(D^N\nabla N\right)$$

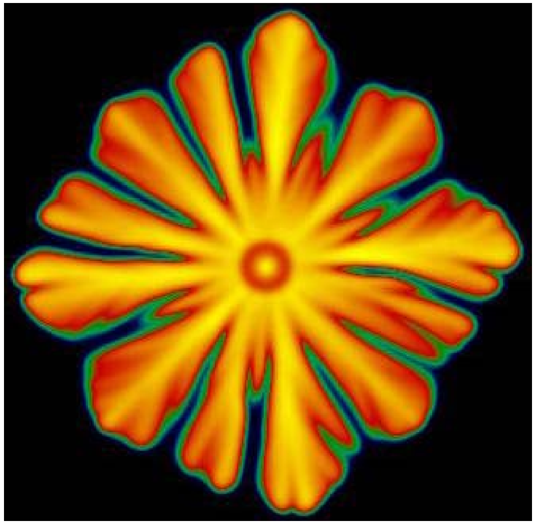
$$\frac{\partial S}{\partial t} = -k_0 N\ f(S) + D^S\nabla^2 S$$

Numerical simulations

- New reaction-diffusion equations without chemotaxis

$t = 2700$; $D^N(N,W,S) = 5.\ 10^{-3}\,(1+\sigma)\,N\,S$; $D^S = 10^{-2}$; $D^W = 5.\ 10^{-3}$; $k_0 = 1$;
$\gamma = 0$; $R_S = -\,N\,S$; $L = 8\,\pi$; $W_0 = 0.20$; $S_0 = 0.35$; $N_0 = 0.71\ \exp(-\,20\,r^2)$



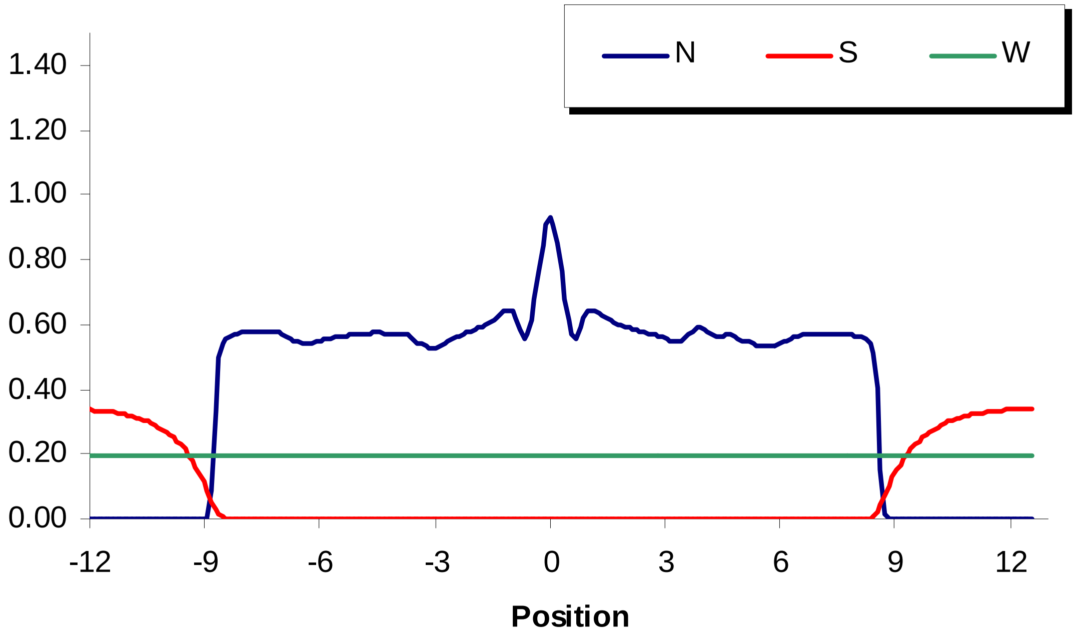


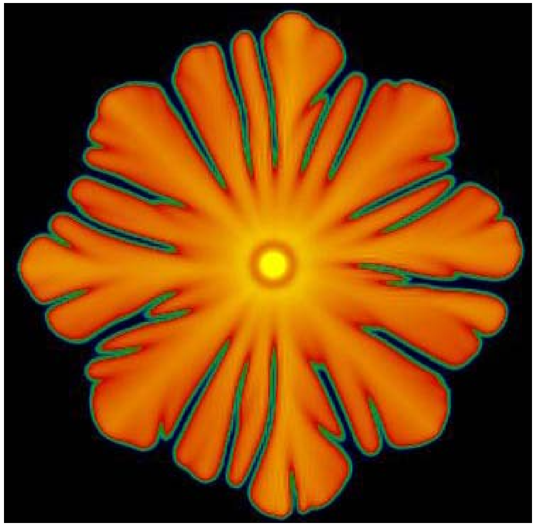
Numerical simulations

- New reaction-diffusion equations with chemotaxis

$t = 1700$; $D^N(N,W,S) = 5.\ 10^{-3}\ (1+\sigma)\ N\ S$; $D^S = 5.\ 10^{-3}$; $D^W = 10^{-1}$; $k_0 = 1$;

$\gamma = 2.5\ 10^{-4}$; $R_S = -\ N\ S$; $L = 8\ \pi$; $W_0 = 0.20$; $S_0 = 0.35$; $N_0 = 0.71\ \exp(-\ 20\ r^2)$



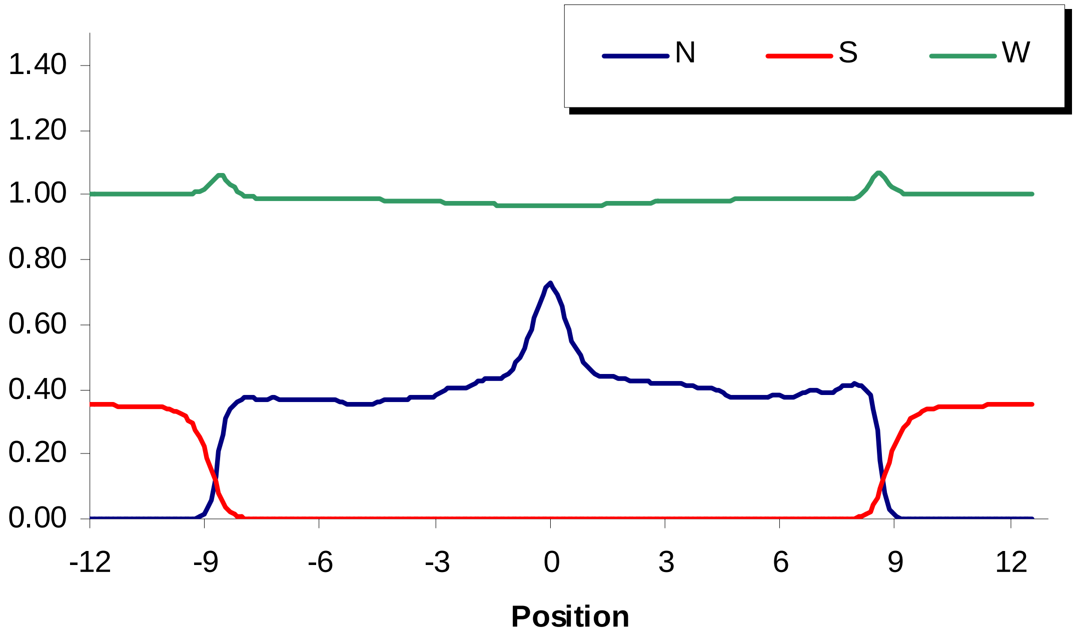


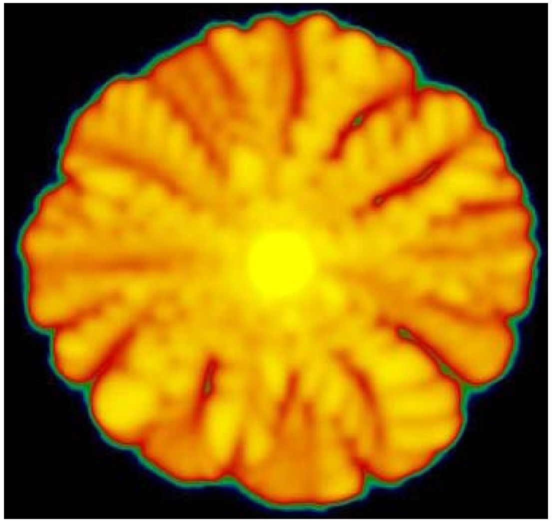
Numerical simulations

- New reaction-diffusion equations with chemotaxis

t = 300; $D^N(N,W,S) = 5.\ 10^{-2}\ (1+\sigma)\ N\ S$; $D^S = 10^{-2}$; $D^W = 5.\ 10^{-3}$; $k_0 = 1$;

$\gamma = 2.5\ 10^{-3}$; $R_S = -\ N\ S$; $L = 8\ \pi$; $W_0 = 1.0$; $S_0 = 0.35$; $N_0 = 0.71\ \exp(-\ 20\ r^2)$



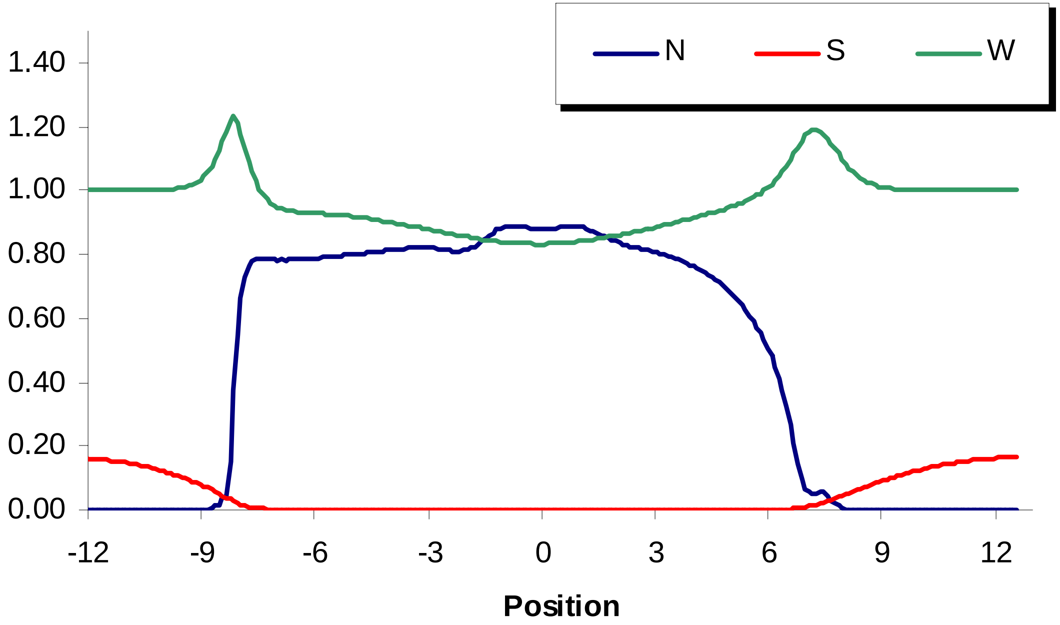


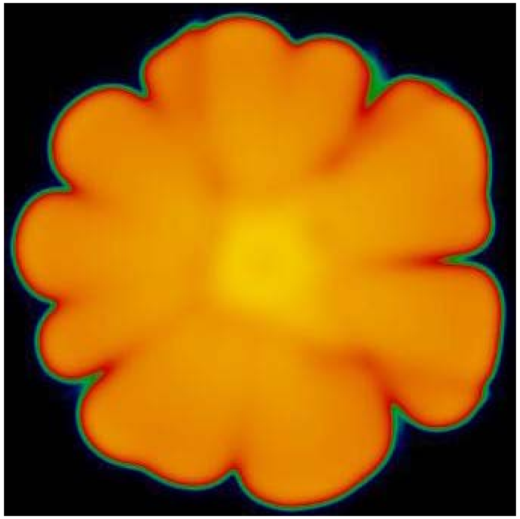
Numerical simulations

- New reaction-diffusion equations with chemotaxis

t = 400; $D^N(N,W,S)$ = 5. 10^{-2} $(1+\sigma)\, N\, S$; $D^S = 10^{-1}$; D^W = 5. 10^{-3} ; $k_0 = 1$;

γ = 1. 10^{-2}; $R_S = -\,N\,S$; $L = 8\,\pi$; $W_0 = 1.0$; $S_0 = 0.35$; $N_0 = 0.71 \exp(-\,20\, r^2)$



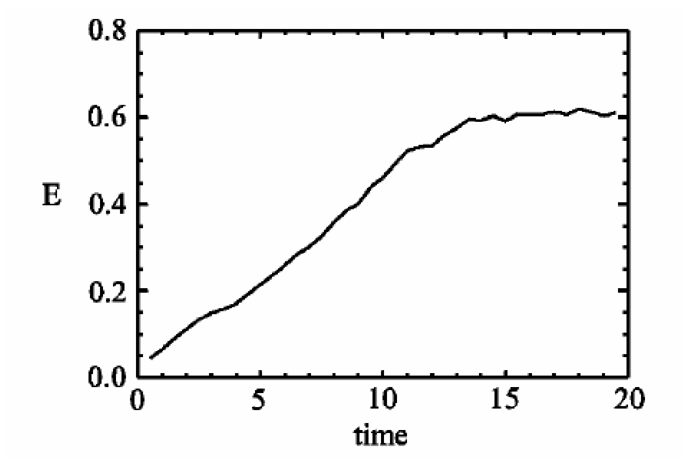


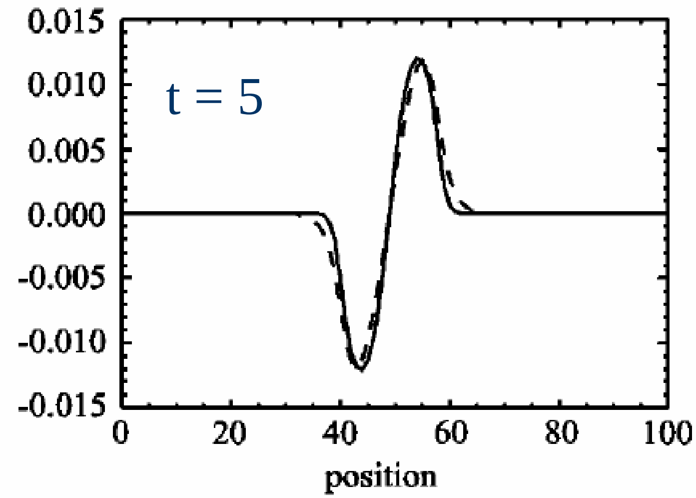
Numerical simulations

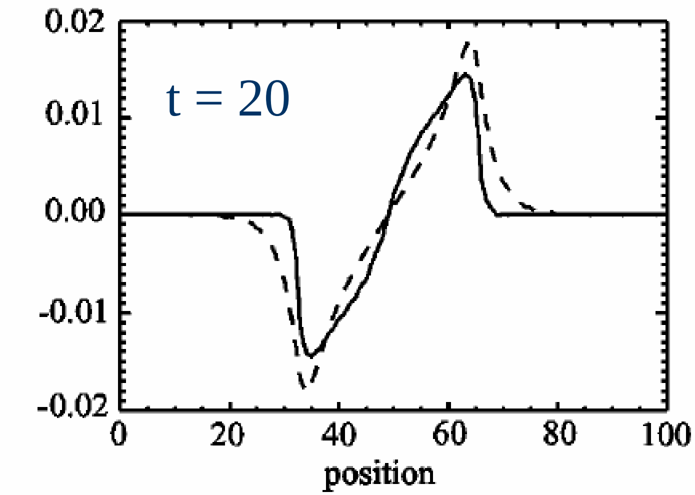
- The chemotaxis-like model is a singular limit of the full hydro-dynamic model

$D^N(N,W,S) = 5.\ 10^{-2}\ (1+\sigma)\ N\ S$;
$D^S = 0.005$; $D^W = 0.1$; $k_0 = 1$;
$\gamma = 1/900$; $\mu = 0.0002$; $W_0 = 0.02$;

$E = \max(\|v - v^{chem}\|)/\max(\|v\|)$.
Solid line: x component of v^{chem}
Dashed line: x component of v







Hydrodynamic model

- Two-dimensional hydrodynamic model

$$\frac{\partial v}{\partial t} = \mathrm{P}\left[-\left(v \cdot \nabla\right)v + \left(\frac{1}{\rho} - \frac{1}{\rho_m}\right)\mathrm{D}\ v - \left(\frac{\eta}{\rho} - \frac{\eta_m}{\rho_m}\right)v + \frac{F}{\rho} \right]$$

$$-\frac{1}{\rho}\nabla\left(\gamma\ N^2\right) + \frac{\mathrm{D}\ v}{\rho_m} - \frac{\eta_m}{\rho_m}v$$

$$\frac{\partial N}{\partial t} + \nabla \cdot \left(Nv\right) = R_N + \nabla \cdot \left(D^N \nabla N\right)$$

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$$\frac{\partial S}{\partial t} = R_S + D^S \nabla^2 S$$

Gradients are now horizontal gradients and $v = u < f >$ is the averaged velocity field.

Numerical simulations

- Full hydrodynamic model (newtonian fluid)

$t = 2000$

$D^N{}_0 = D^S = 5.\ 10^{-3}$; $D^W = 10^{-1}$

$D^N(N,W,S) = D^N{}_0\ (1+\sigma)\ N\ S$

$R_S = -\ N\ S = -\ R_N$; $R_W = 0$

$k_0 = 1$; $\gamma = 0.44\ 10^{-\ 4}$

$\mu = 0.01$; $\lambda = \mu/3$; $\eta = 0$

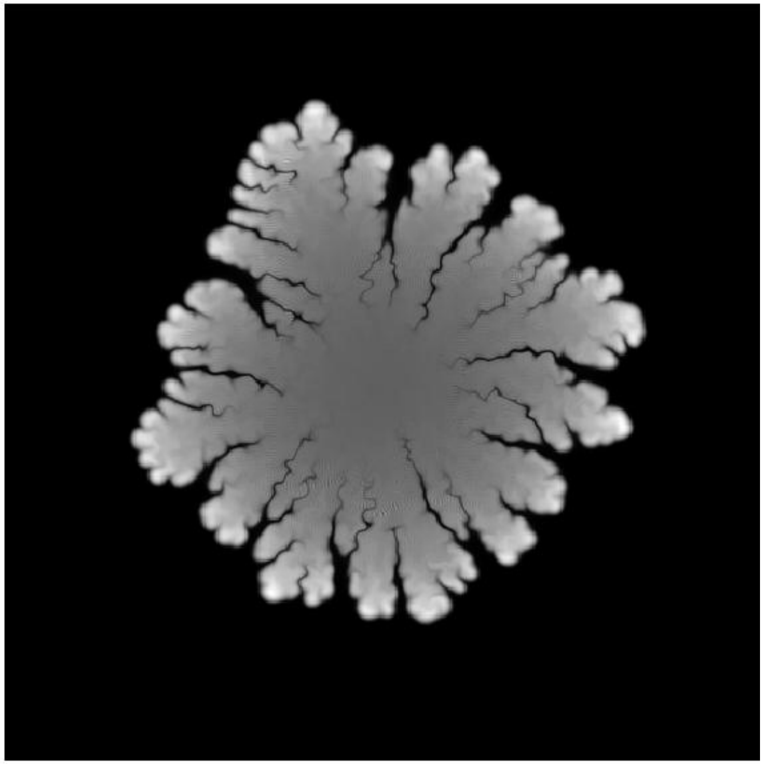
$F_g = N\ \rho\ f$

f = solenoidal white noise

$L = 8\ \pi$

$W_0 = 0.25$; $S_0 = 0.35$

$N_0 = 0.71\ \exp(-\ 20\ r^2)$



Numerical simulations

- Full hydrodynamic model (newtonian fluid)

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$D^N(N,W,S) = D^N_0\ (1+\sigma)\ N\ S$

$R_S = -\ N\ S = -\ R_N$; $R_W = 0$

$k_0 = 1$; $\gamma = 0.44\ 10^{-4}$

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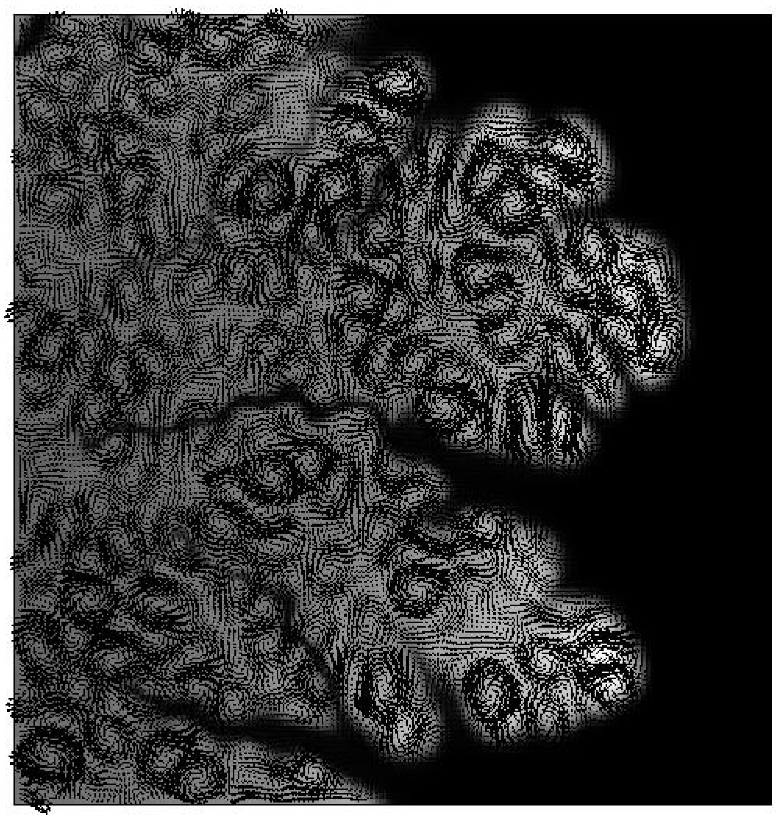
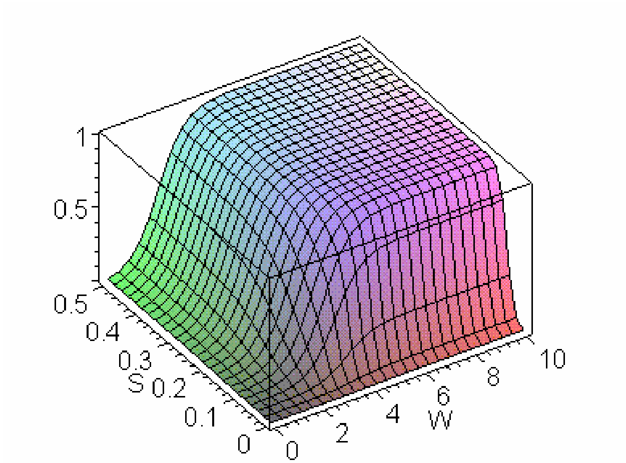
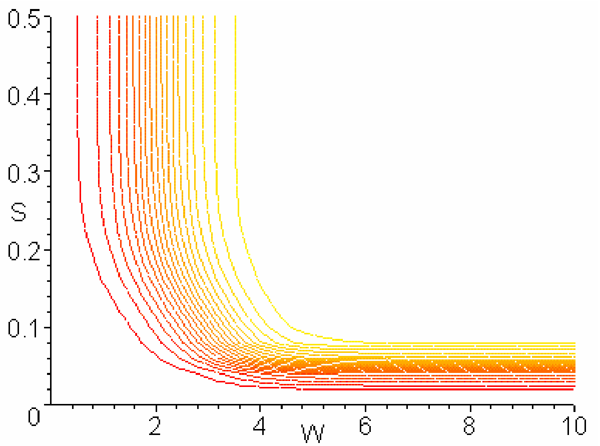


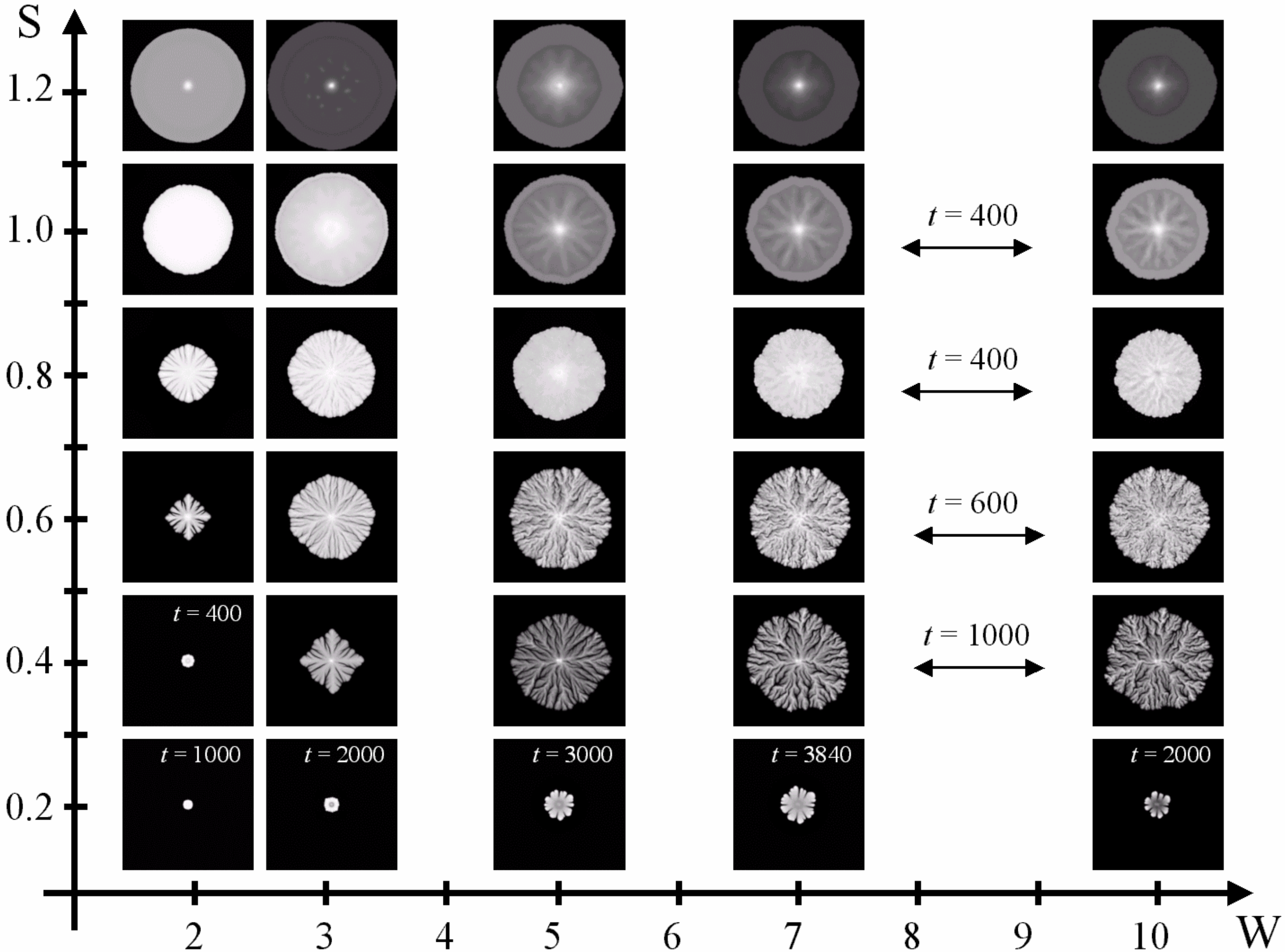
Functional Forms

- Diffusion coefficient of *N*: $D^N = D^0 f(N,W,S)$.
- Small-scale forcing: $F_g = \rho\, f_0\, f(N,W,S)$.
- "Chemotaxis": $\gamma = \gamma_0\, f(N,W,S)$.
- $f(N,W,S) = \frac{1}{2}\tanh^2(4N)\left(1+\tanh\left(W-2\left(1+\frac{1}{2}\left(1-\tanh\left(\frac{S-0.1}{0.1}\right)\right)\right)\right)\right)\frac{1}{2}\left(1+\tanh\left(\frac{S-0.05}{0.02}\right)\right)$

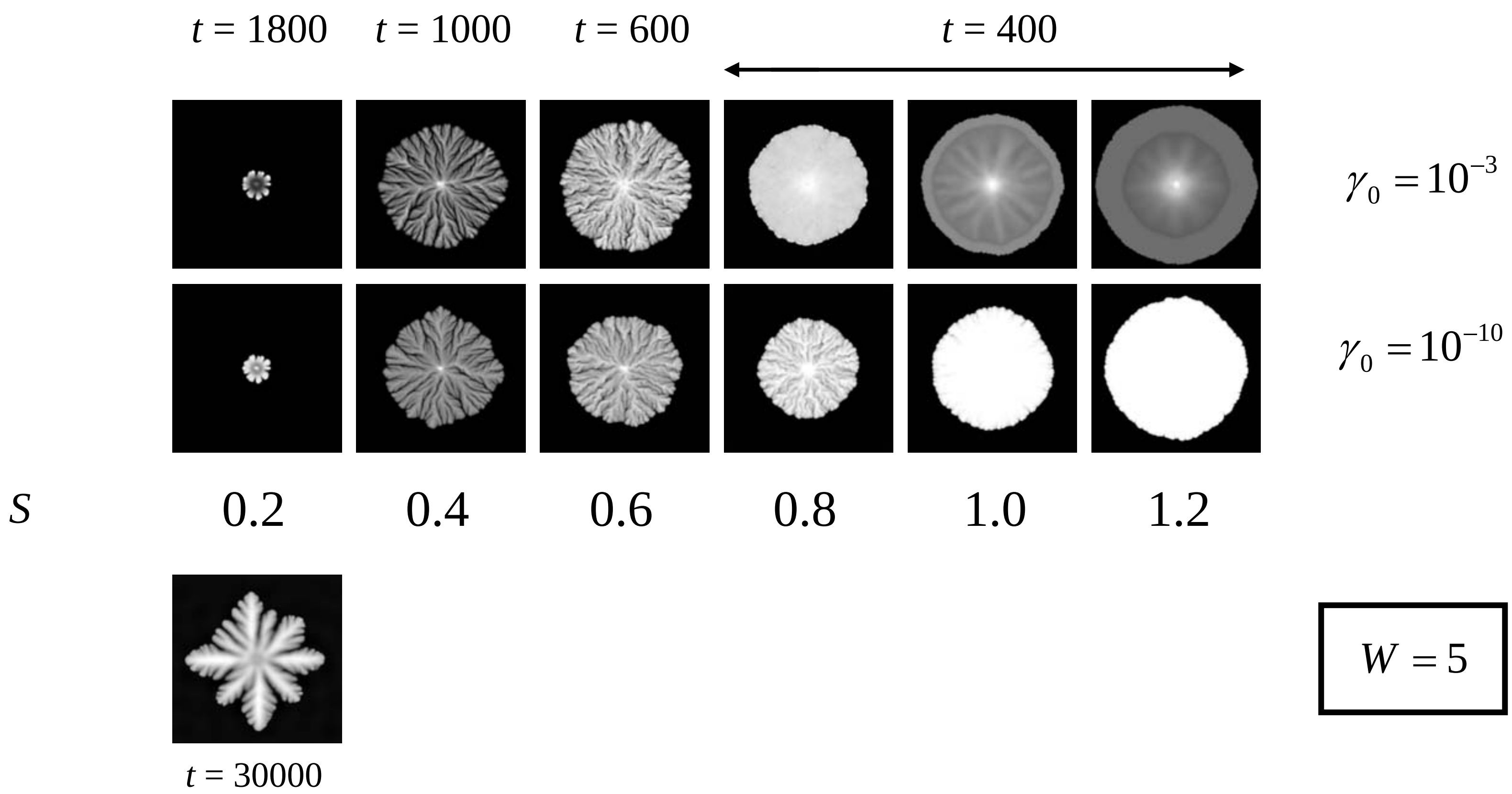




Full Hydrodynamic Model
Example of Phase Diagram



Role of pressure coefficient



Interesting aspects of this type of bacterial dynamics

- Hierarchy of scales:
  - Microscopic level: bacteria
  - Mesoscopic level: whirls and jets → hydrodynamic model
  - Macroscopic level: colony shape
    → reaction-diffusion models
- Looks like two-dimensional turbulence
- Can such behaviors be explained in physical terms or is signaling between cells an important ingredient?

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  - Yes!

Open questions

- What are the rheological properties of a bacterial fluid? What role would non-Newtonian effects have if they were included in the model?
- Understand, at a microscopic level, the nature of the small-scale forcing due to bacterial activity.
- Can one find microscopic models whose averaged properties are described by the hydrodynamic model described here?

Interesting mathematical issues

- Absence of blow-up in finite time
- Role of nonlinear diffusion in reaction-diffusion equations
  - Kawasaki et al. underscored the importance of nonlinear diffusion
  - Satnoianu et al. [Disc. Cont. Dyn. Sys. **B 1**, 339-362 (2001)] proved the existence of traveling wave solutions (fronts) in the absence of noise
- Effect of whirls and jets on the stability of fronts
  - A first step would be to understand how fronts become unstable in the presence of noise

Interesting biophysical issues

- Understand and model the signaling pathways involved in the random walk done by bacteria in the absence and presence of chemotaxis.
  [R. Erban & H.G. Othmer, SIAM J. Appl. Math. **65**, 361-391 (2004); Multiscale Model. Simul. **3**, 362-394 (2005)]

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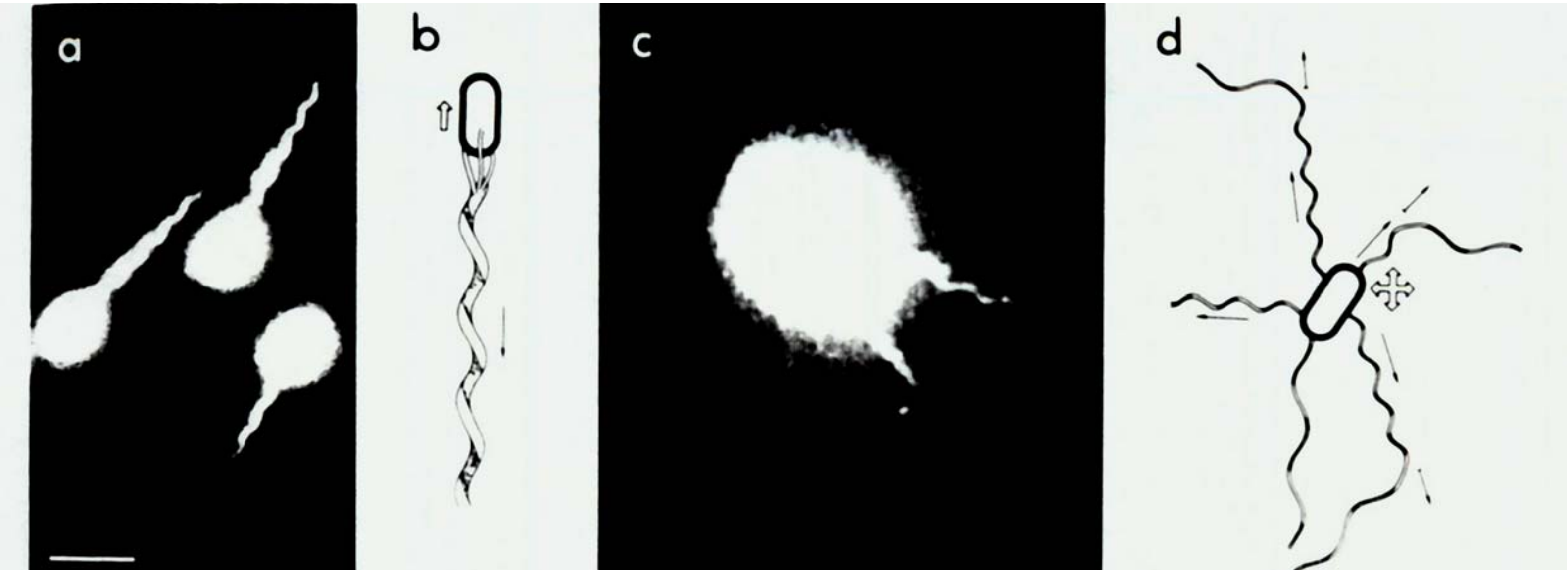
R.Macnab,
Motility and chemotaxis,
1987

Runs and tumbles



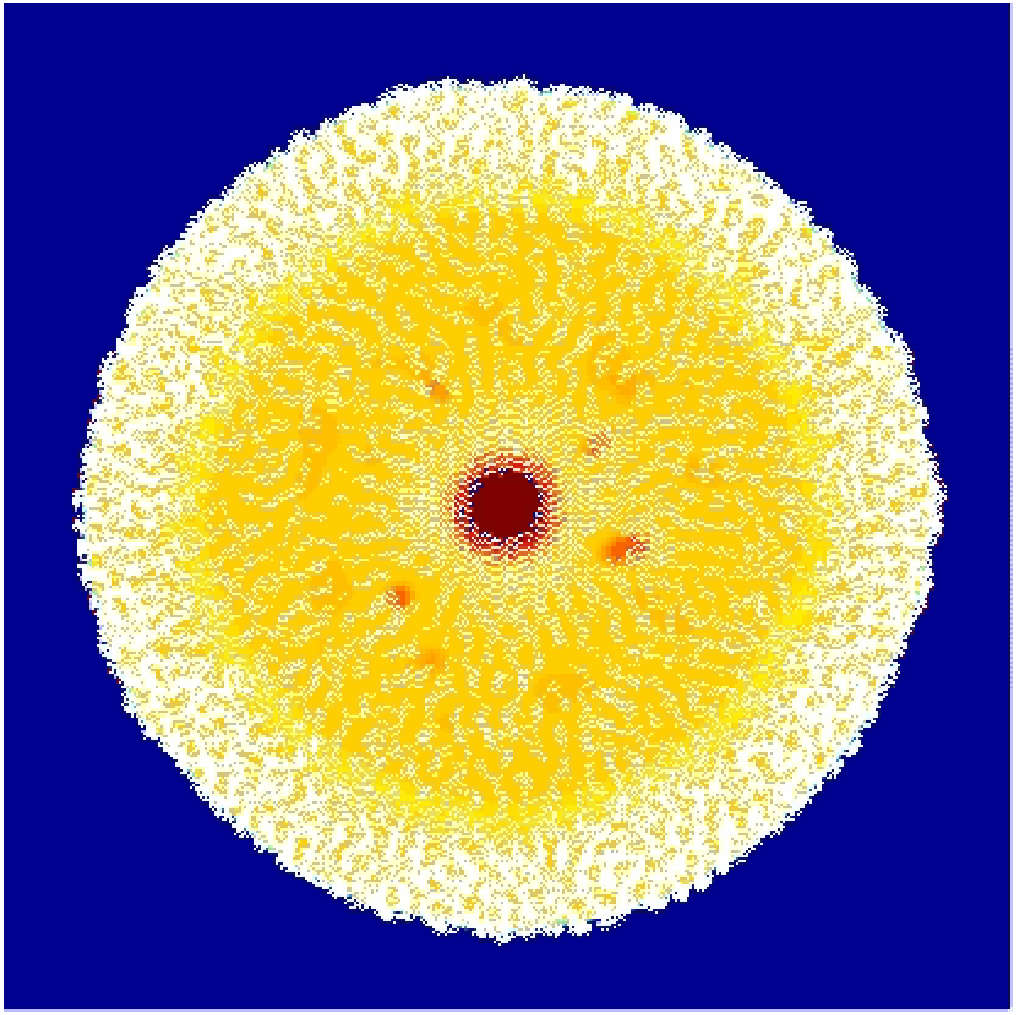
Swimming: CCW rotation

Tumbling: CW rotation

Bar: 5 µm (*E. coli* or *S. typhimurium*)

R. Macnab, *Motility and Chemotaxis*, in *E. coli and S. typhimurium: cellular and molecular biology*, pp. 732-759, Ed. by F.C. Neidhart *et al.*, ASM, Washington DC, 1987

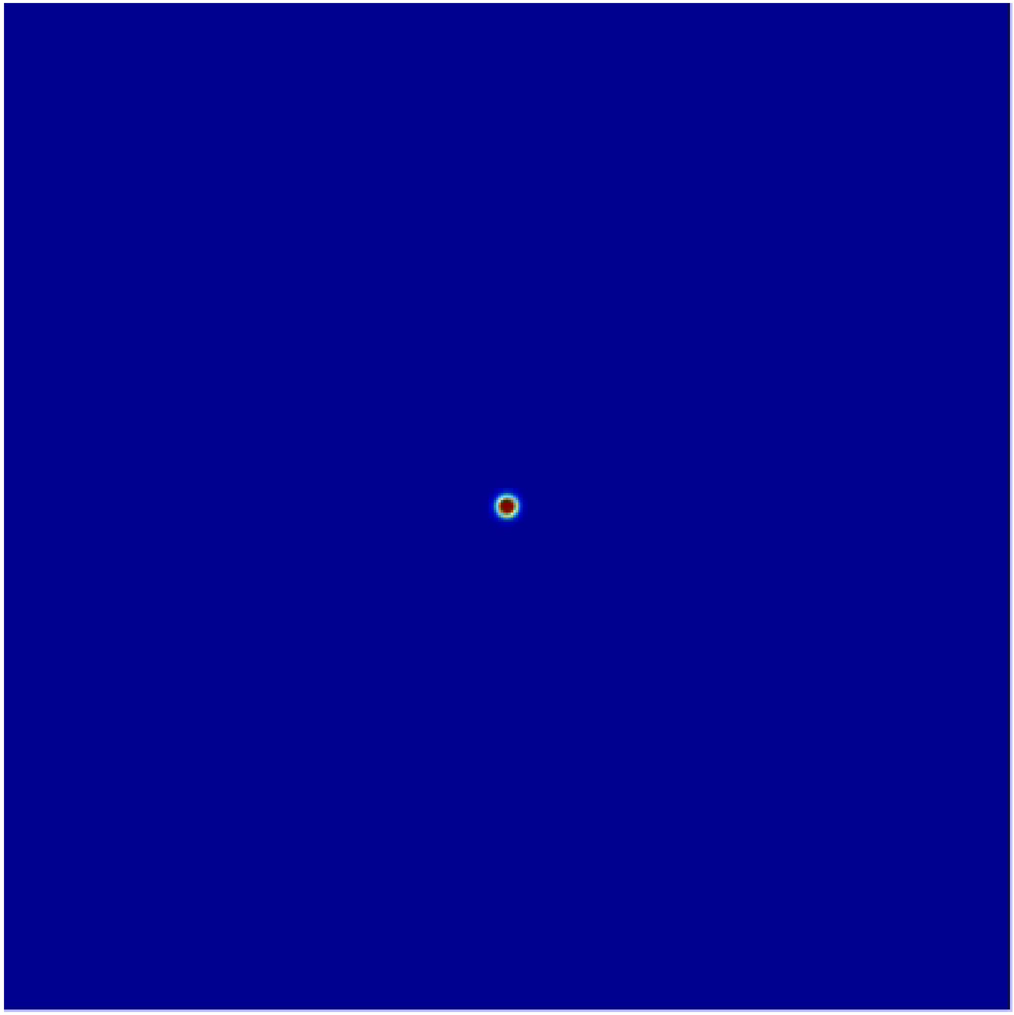
$S = 1.2 – W = 3 – \lambda = 0$



Movie from t = 340 to t = 400

One frame every unit of time

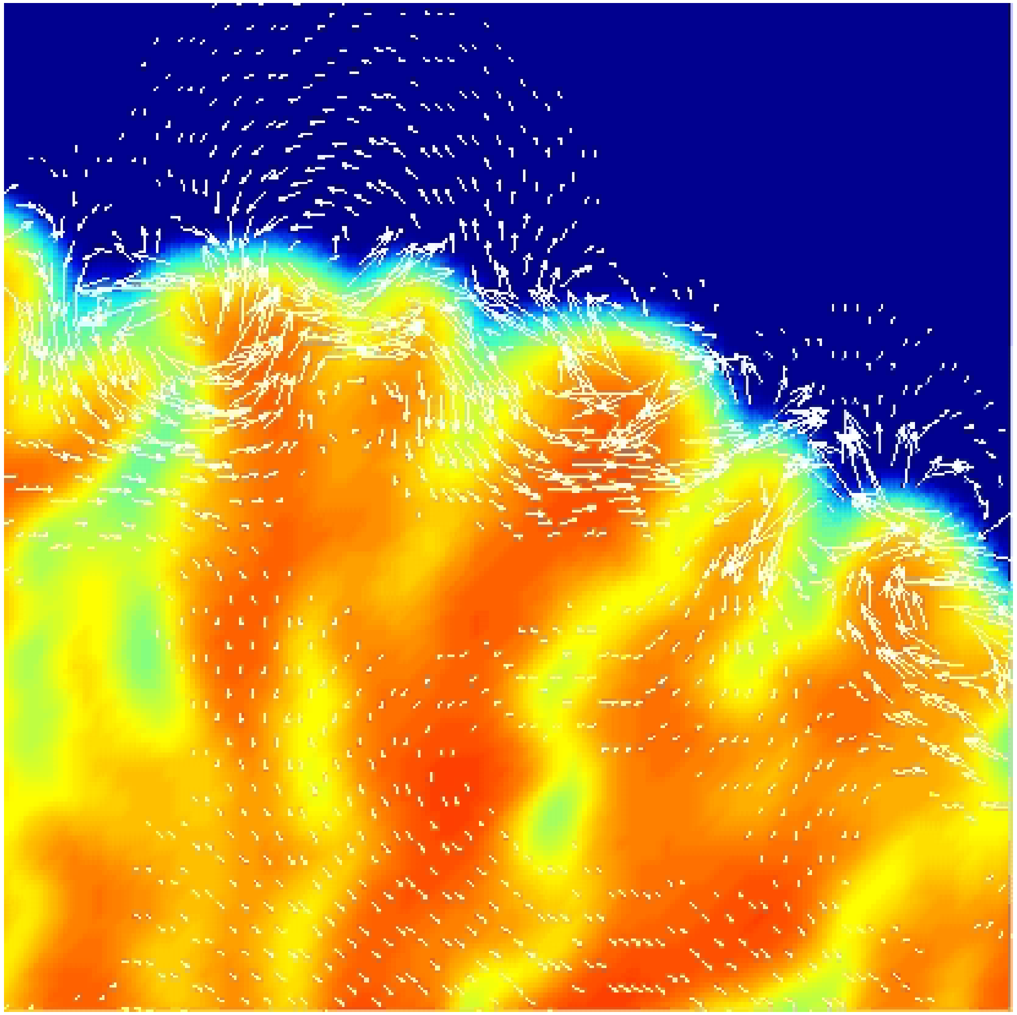
S = 0.4 – W = 7 – λ = 0



Movie from t = 0 to t = 1000

One frame every 20 units of time

$S = 0.8 – W = 5 – \lambda = 0$



Movie from t = 400 to t = 410

One frame every 0.1 unit of time

E. Banin, M.L. Vasil & E.P. Greenberg, PNAS **102**, 11076-11081 (2005)

P. aeruginosa biofilms

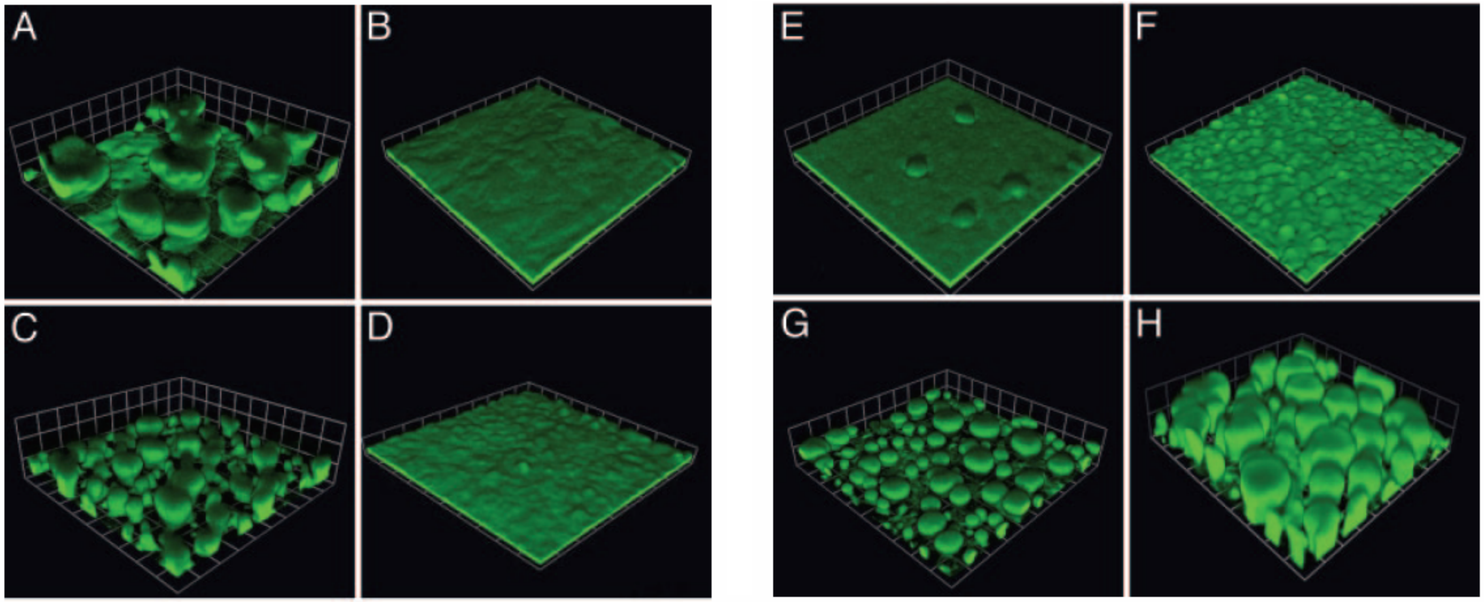
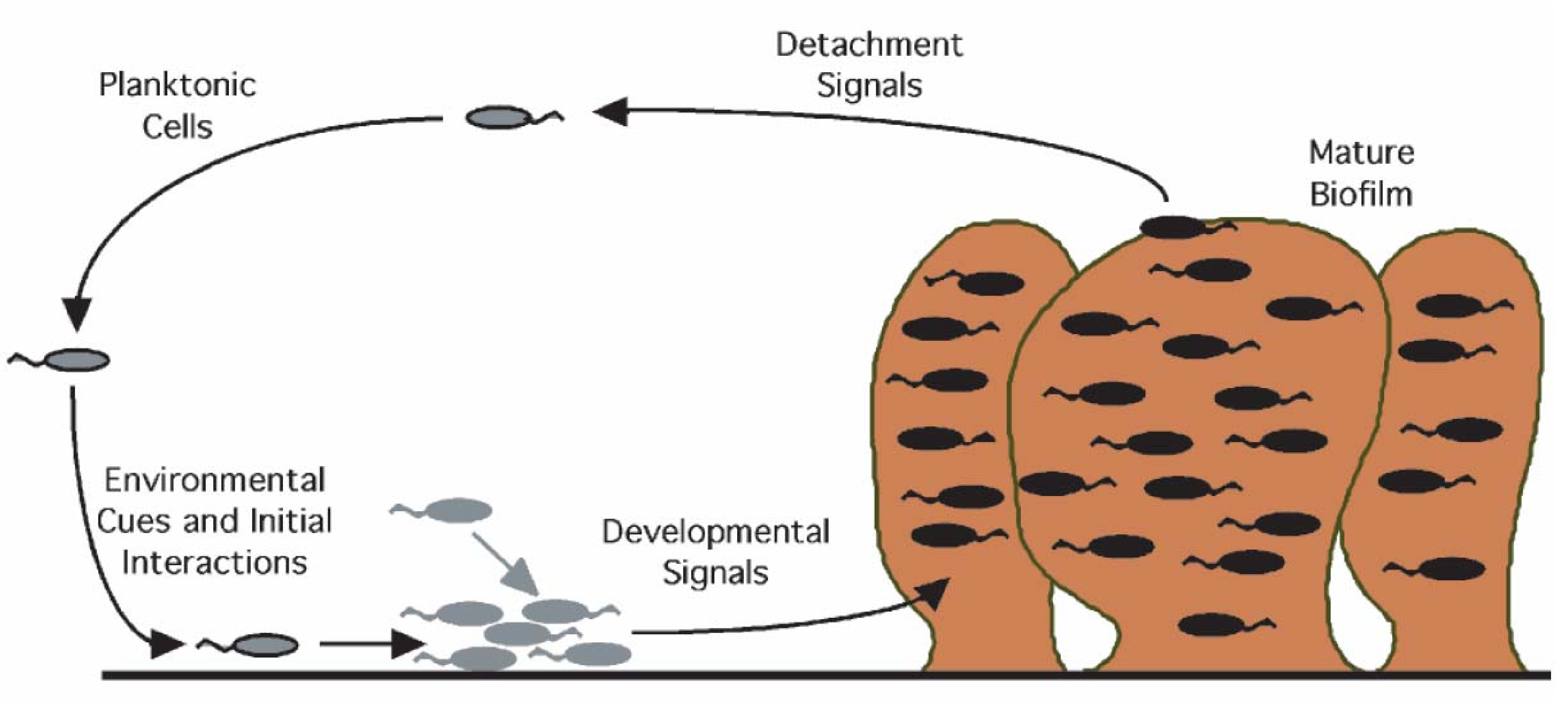


Fig. 1. Biofilm formation of *P. aeruginosa* pyoverdine and pyochelin mutants. The parent without (*A*) and with (*B*) lactoferrin (20 μg/ml), the pyochelin mutant PAO1*pchA*::Tc^R without (*C*) and with (*D*) lactoferrin (20 μg/ml), the pyoverdine synthesis mutant PAO1Δ*pvdA* (*E*), the pyoverdine ECF σ-factor PvdS mutant PAOΔ*pvdS* without lactoferrin (*F*), the pyoverdine mutant carrying the *pvdA* expression vector pEB4 without lactoferrin (*G*), and the pyoverdine mutant grown in pyoverdine-conditioned medium without lactoferrin (*H*). The *P. aeruginosa* cells contained the *gfp* plasmid pMRP9-1. Images are from 6-day biofilms (the squares are 61 μm on a side).

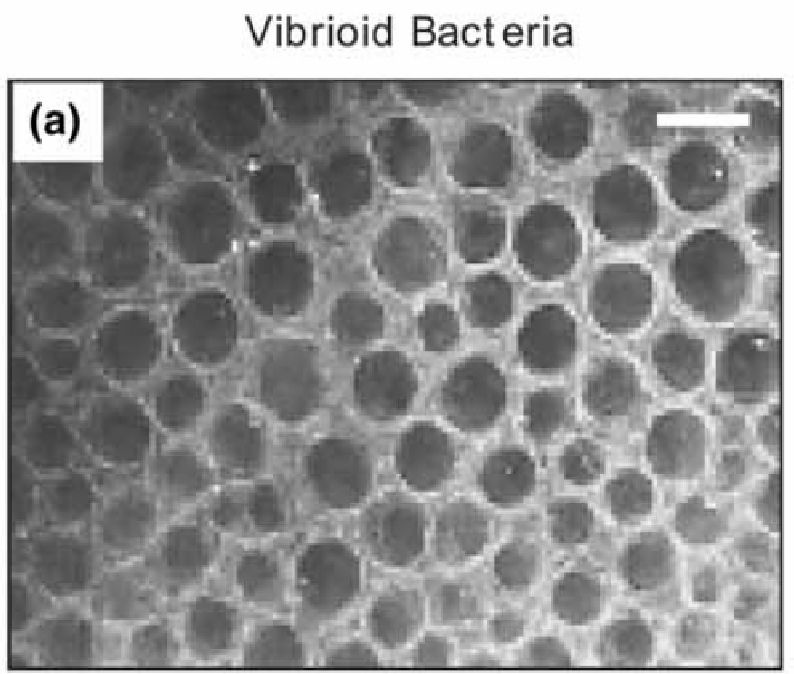
G. O'Toole, H.B. Kaplan & R. Kolter, Ann. Rev. Microbiol. **54**, 49-79 (2000)

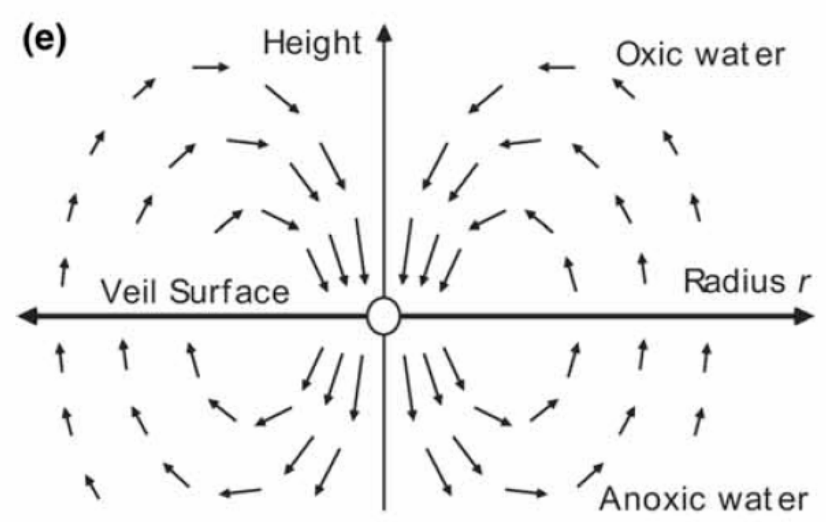
Model of biofilm development



R. Thar & M. Kühl, FEMS Microbiology Letters **246**, 75-79 (2005)

Model of biofilm development

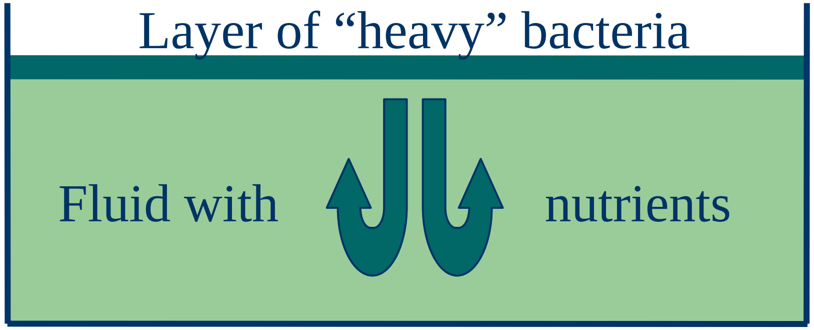


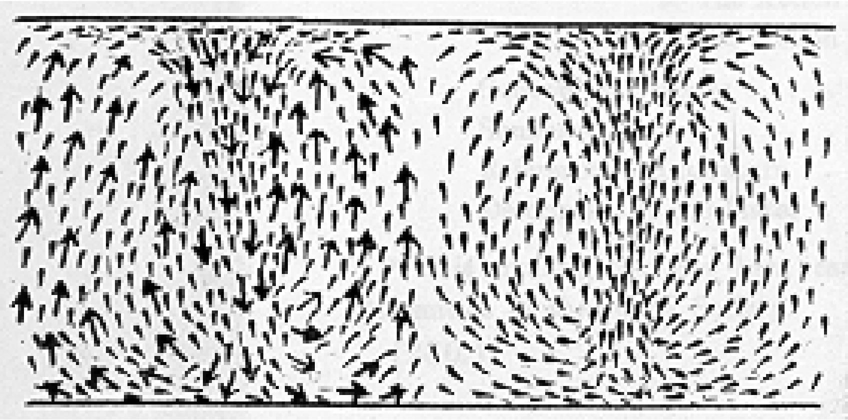


(a) Top-view of honeycomb patterns formed by veil-forming vibroid bacteria. Bright areas are colonized by bacteria, scale bar is 0.5 mm.

(e) Schematic drawing of the flow field around an attached bacterium (white circle); arrows denote the velocity vector of the water.

Bioconvection





• H. Wager, *On the effect of gravity upon the movements and aggregation of Euglena viridis, Ehrb., and other micro-organisms*, Philos. Trans. R. Soc. London Ser. **B 201**, 333 (1911)

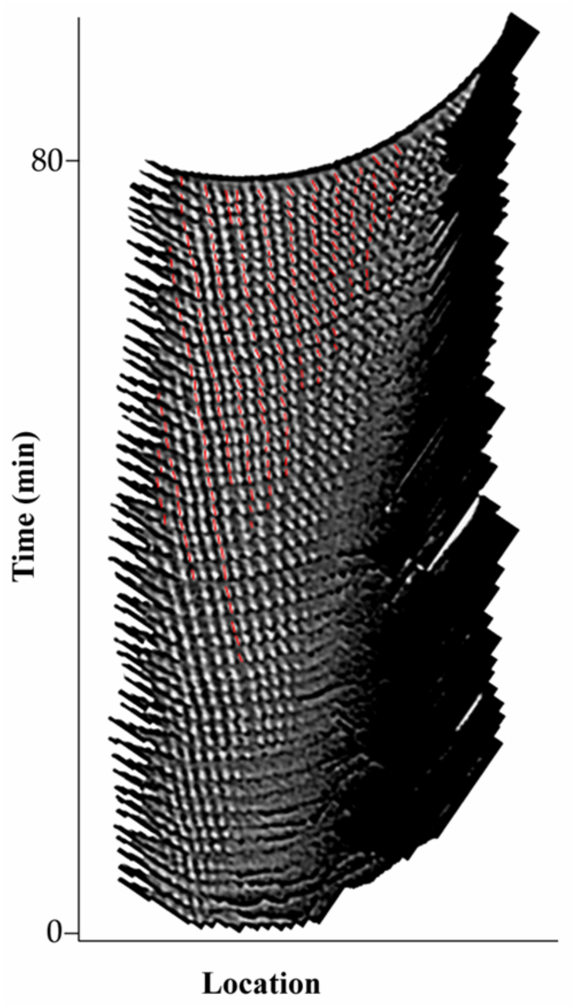
• J.R. Platt, *Bioconvection patterns in cultures of free-swimming organisms*, Science **133**, 1766 (1961)

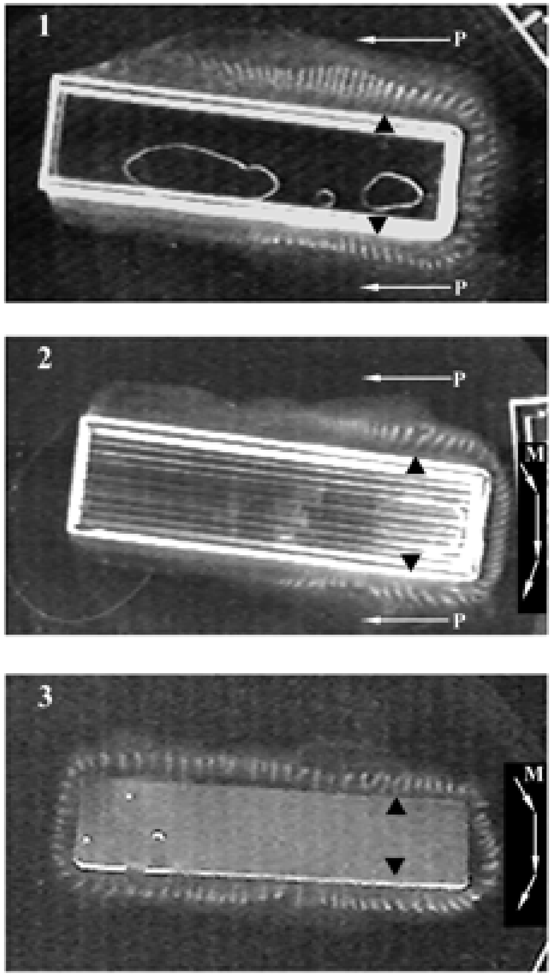
• T. Pedley & J. Kessler, *Hydrodynamic phenomena in suspensions of swimming micro-organisms*, Ann. Rev. Fluid Mech. **24**, 313-358 (1992)

• N.A. Hill & T.J. Pedley, *Bioconvection*, Fluid Dynamics Research **37**, 1-20 (2005)

N. Mendelson & J.L., J. Bacteriology **180**, 3285-3294 (1998)

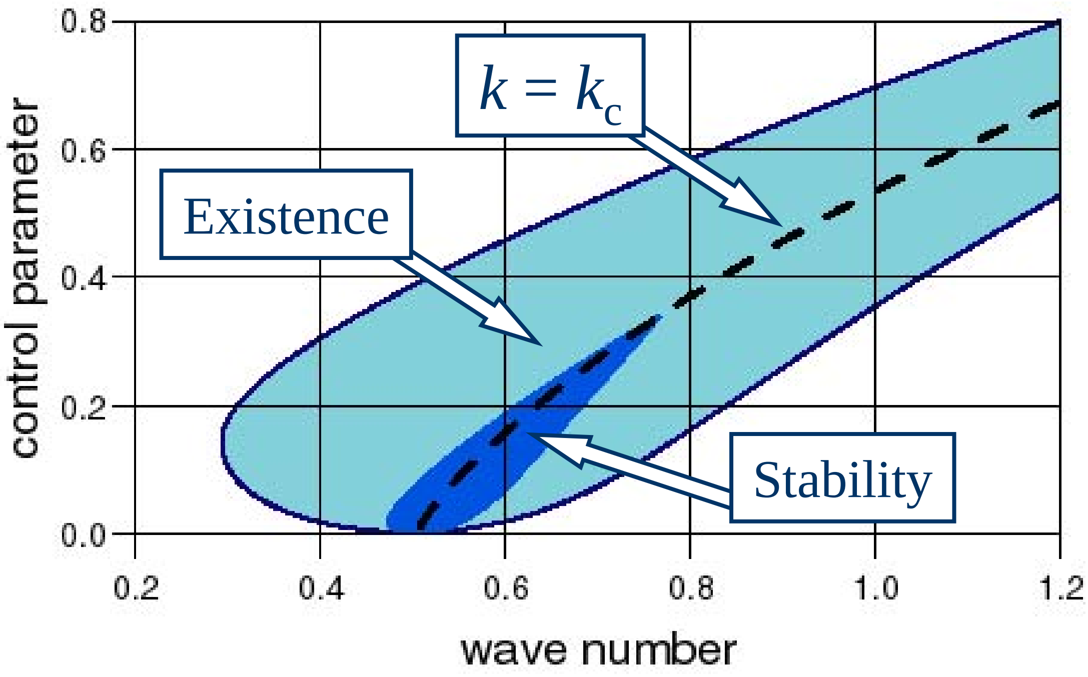
Wave patterns in bioconvection





J.L. & N. Mendelson, Phys. Rev. E 59, 6267-6274 (1999)

Complex Swift-Hohenberg model



When μ is constant, the complex Swift-Hohenberg equation has traveling wave solutions of the form given below. Their stability is summarized by the "Busse balloon" on the left.

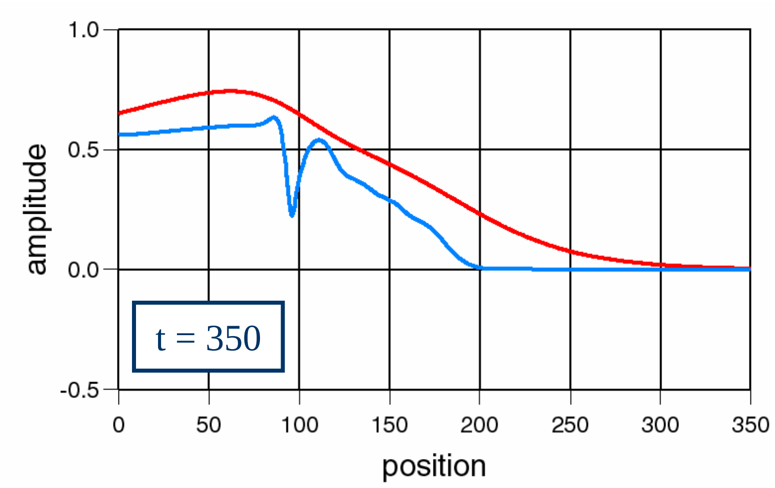
$$\frac{\partial \psi}{\partial t} = (\mu + i\nu)\psi - (\alpha_r + i\alpha_i)\left(k_c^2 + \nabla^2\right)^2 \psi$$
$$+ i\gamma\, \nabla^2 \psi - (\beta_r + i\beta_i)\,|\,\psi\,|^2\,\psi$$
$$-(\zeta_r + i\zeta_i)\,|\,\psi\,|^4\,\psi$$

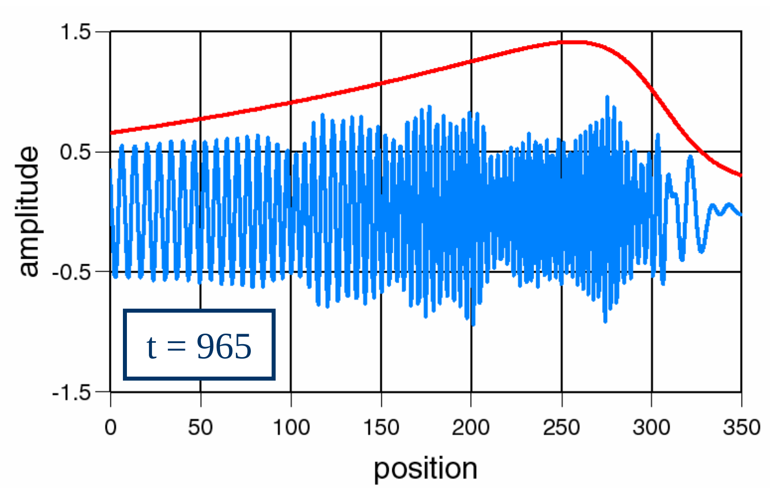
Traveling wave solution

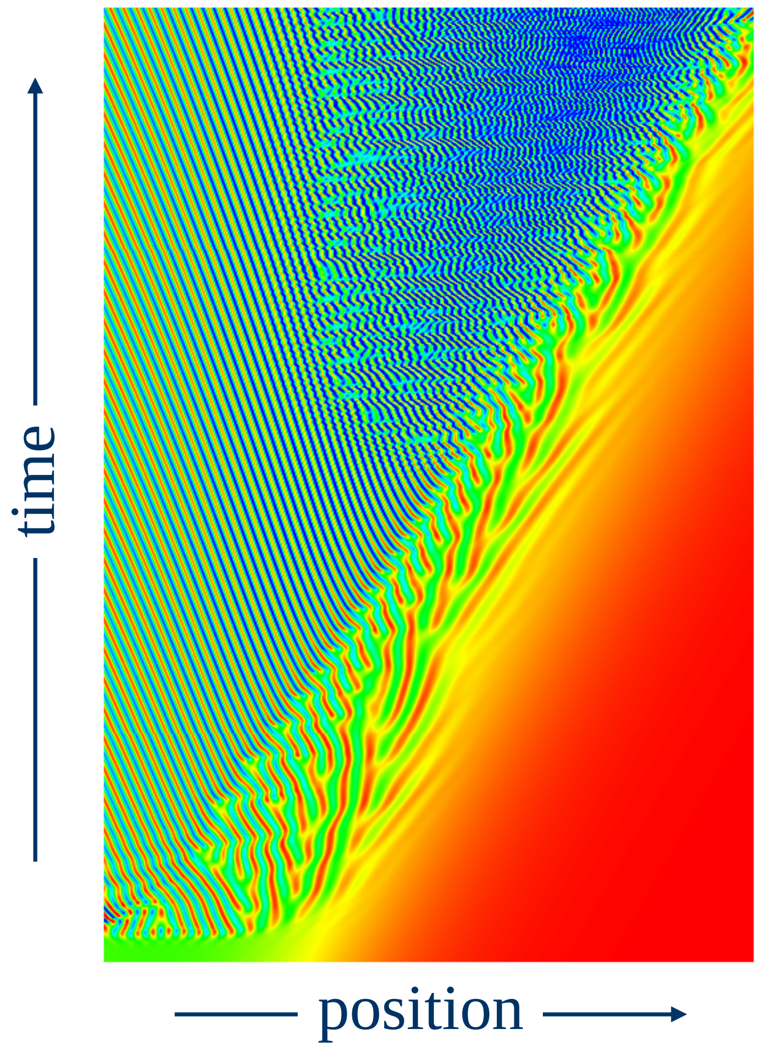
$$\psi = R_0 \exp(i\,[kx + \omega t]\,)$$
$$\zeta_r R_0^4 + \beta_r R_0^2 + \alpha_r (k - k_c)^2 - \mu = 0$$
$$\omega = \upsilon - \alpha_i (k - k_c)^2 - \beta_i R_0^2 - \zeta_i R_0^4 - \gamma\, k^2$$

J.L. & N. Mendelson,
Phys. Rev. E 59, 6267-6274
(1999)

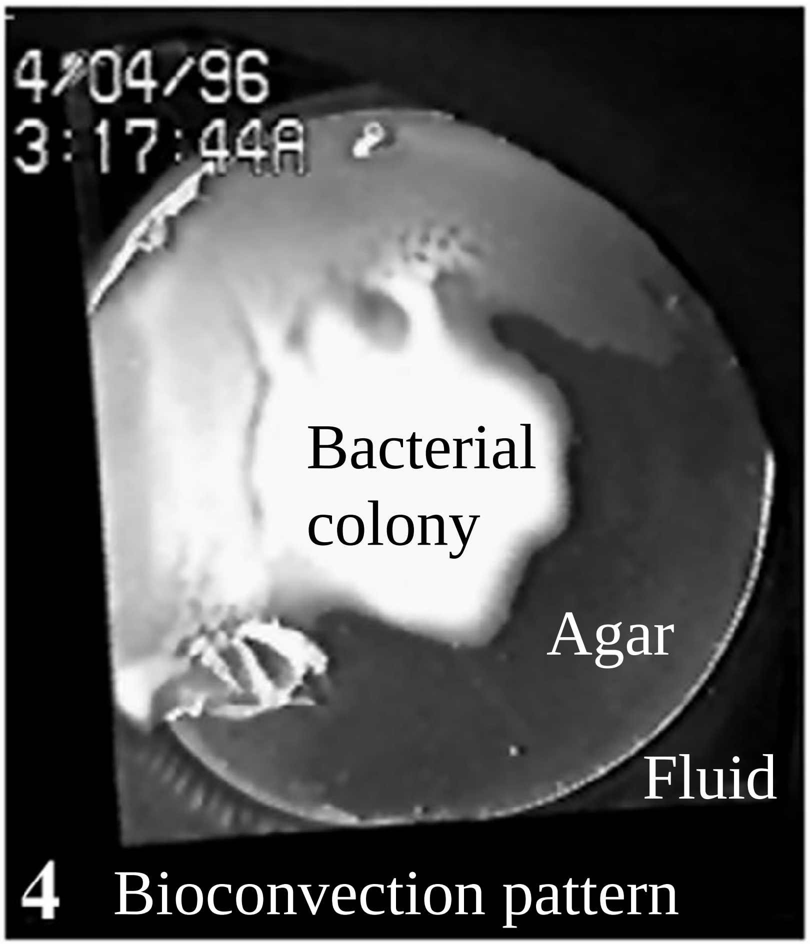
Numerical simulations

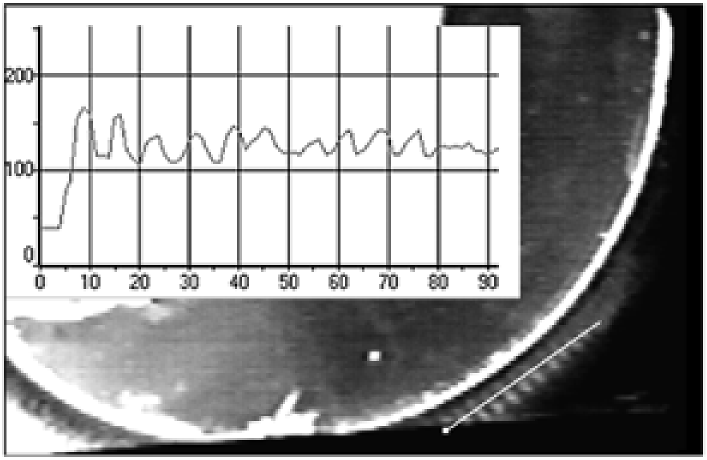






Wave patterns in bioconvection





B. Subtilis OI2836

N.H. Mendelson & J.L., *A complex pattern of traveling stripes is produced by swimming cells of Bacillus subtilis*, J. Bacteriology **180**, 3285-3294 (1998)

N. Mendelson & J.L., J. Bacteriology **180**, 3285-3294 (1998)

One-dimensional traveling wave bioconvection pattern