A hydrodynamic model for the growth of bacterial colonies

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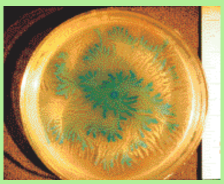


N. Mendelson
B. Salhi
C. Ott

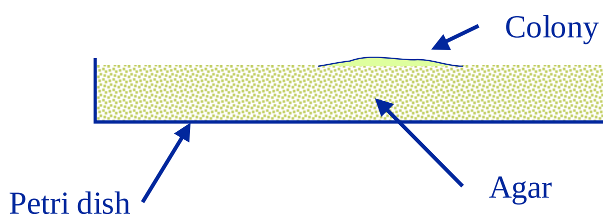
J.L. & T. Passot, *Hydrodynamics of bacterial colonies: a model*, Phys. Rev. E **67**, 031906 (2003)

Outline

- Brief overview of colony forms and colony dynamics for *Bacillus subtilis*
- Reaction-diffusion models
- Hydrodynamic model
- Chemotaxis-like behavior
- Numerical simulations
  - Chemotaxis-like behavior (advection-reaction-diffusion equations)
  - Full hydrodynamic model
  - Phase diagrams
- Conclusions

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.

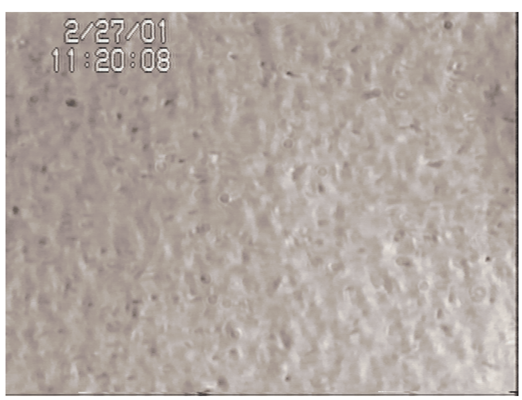


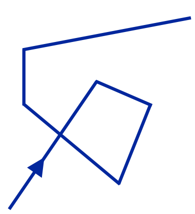
Movie by

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)

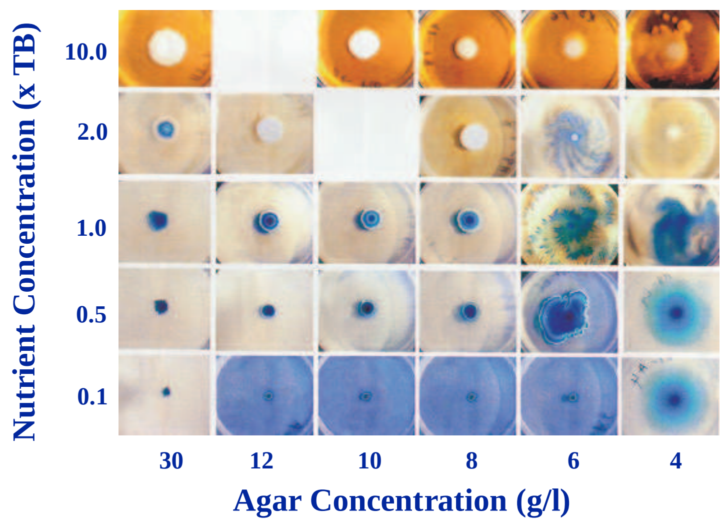




- In these experiments, *B. subtilis* does not
  - form spores,
  - secrete a surfactant, or form a biofilm.

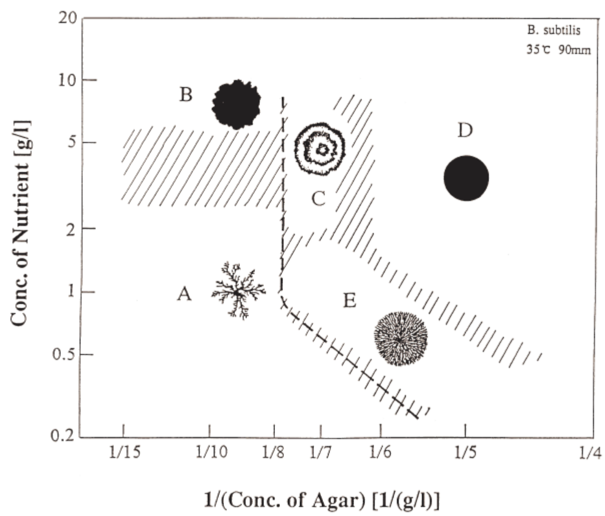
N. H. Mendelson & B. Salhi, J. Bacteriology **178**, 1980-1989 (1996)

Different colony forms for *Bacillus subtilis*



M. Matsushita *et al.*, Physica A **249**, 517-524 (1998)

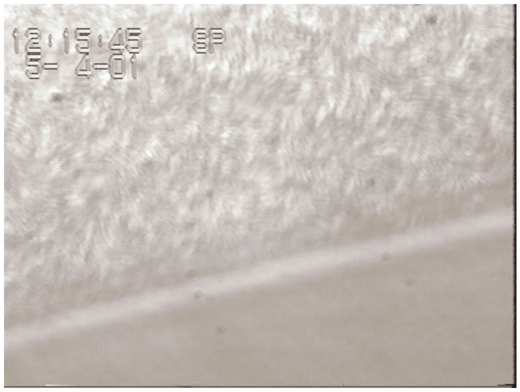
Different colony forms for *Bacillus subtilis* OG-01

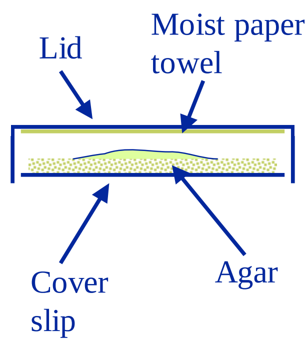


Experiments by

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.

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I. Golding *et al.*, Physica A **260**, 510-554 (1998)

Reaction-diffusion models

Such models describe the evolution of bacterial density and nutrient concentration. The dynamics of these quantities is sometime coupled to that of other variables, such as the concentrations of non-motile bacteria or of a lubricant.

- The “Diffusive Fisher-Kolmogorov” equations

$$\frac{\partial N}{\partial t} = D^N \nabla^2 N + F(N,S)$$

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

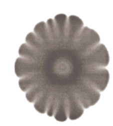
$$F(N,S) = N\,S$$

[R.A. Fisher, Annu. Eugenics **7**, 255-369 (1937).
A.I. Kolmogorov, I. Petrovsky and N. Piscounov, Moscow Univ. Bull. Math. **1**, 1-25 (1937).]

I. Golding *et al.*, Physica A **260**, 510-554 (1998)

Reaction-diffusion models

- Cut-off in reaction term (Kessler-Levine)



$$F(N,S) = N\,S\,\Theta(N - N_0)$$

[D.A. Kessler and H. Levine, Nature **394**, 556-558 (1998)]

- Add bacterial death term

$$F(N,S) = N\,S\,\Theta(N - N_0) - \mu\, N$$

in equation for N (Kitsunezaki, Golding *et al.*)

- Nonlinear diffusion (Kitsunezaki)

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

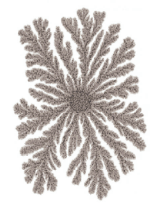
[S. Kitsunezaki, J. Phys. Soc. Jpn. **66**, 1544-1550 (1997)]

But branched patterns are seen *only if* randomness is introduced in the model.

I. Golding *et al.*, Physica A **260**, 510-554 (1998)

Reaction-diffusion models

- Nonlinear diffusion with stochastic diffusion coefficient (Kawasaki *et al.*)

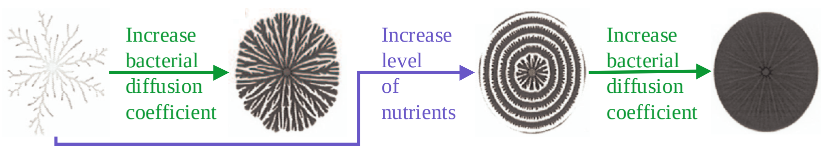


$$\frac{\partial N}{\partial t} = \nabla \cdot \left(D^N (1+\sigma) N\, S\, \nabla N \right) + N\, S$$

where σ has a triangular distribution

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

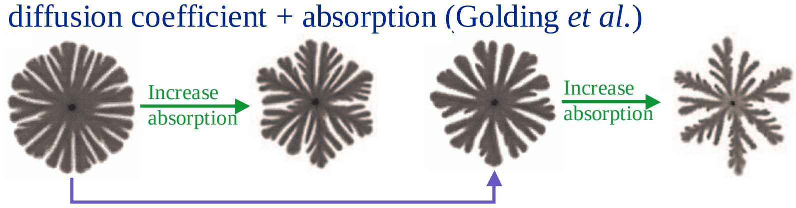
- Active and inactive bacteria + nonlinear diffusion + different functional forms for nonlinear diffusion and bacterial "death" term (Mimura *et al.*) [M.Mimura, H. Sakaguchi, and M. Matsushita, Physica A **282**, 283-303 (2000)]



I. Golding *et al.*, Physica A **260**, 510-554 (1998)

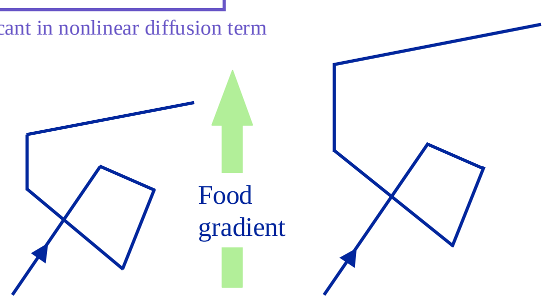
Reaction-diffusion models

- Active and "dead" bacteria + lubricant + lubricant-dependent diffusion coefficient + absorption (Golding *et al.*)



- Chemotaxis is often included in these models by adding a term of the form $\nabla\cdot(N\,\chi(S)\,\nabla S)$ to the left hand side of the equation for N.

From R. Macnab, 1987.



Why try a hydrodynamic approach?

- In wet conditions, bacterial motion is dominant in colony expansion and therefore needs to be modeled adequately. This dynamics cannot 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.

Hydrodynamic model

- Orders of magnitude
  - At the scale of a bacterium

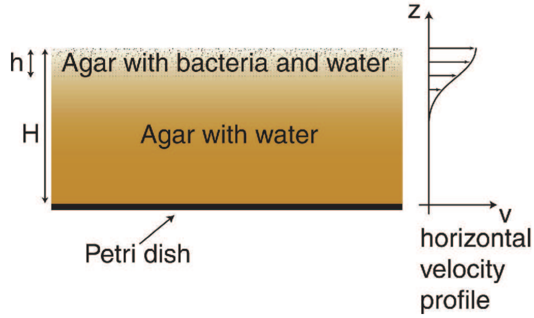
$$\mathrm{Re}^S = \frac{vL}{\upsilon} \cong \frac{30\cdot 10^{-6}\cdot 3\cdot 10^{-6}}{10^{-6}} \cong 10^{-4}$$

  - 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 $\mathrm{Re}^{WJ} = \frac{\tau_D}{\tau_C} \cong \frac{\text{time to reach characteristic size}}{\text{life-time of whirls and jets}} = \frac{5}{0.25} = 20$

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

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

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

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

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

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

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

Hydrodynamic model

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

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

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

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

$$\rho = N + W$$

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

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

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

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

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

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

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

Gradients are now horizontal gradients and $v = u \langle f \rangle$ is the averaged velocity field.

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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

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

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

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

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

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

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

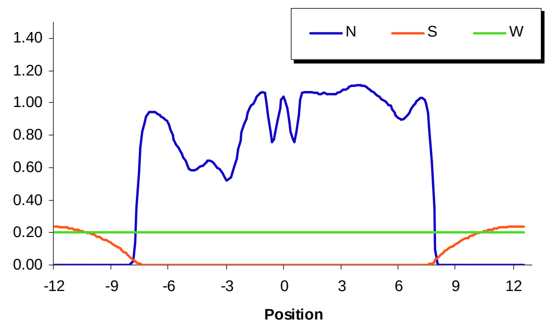
$$\frac{\partial W}{\partial t} + \nabla\cdot(Wv) = R_W + \nabla\cdot\left(D^W \nabla W\right) - \nabla\cdot\left(D^N \nabla N\right)$$

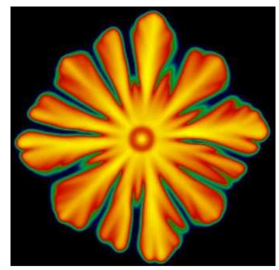
$$\frac{\partial S}{\partial t} = -k_0 N\, f(S) + D^S \nabla^2 S$$

Numerical simulations

- New reaction-diffusion equations without chemotaxis

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

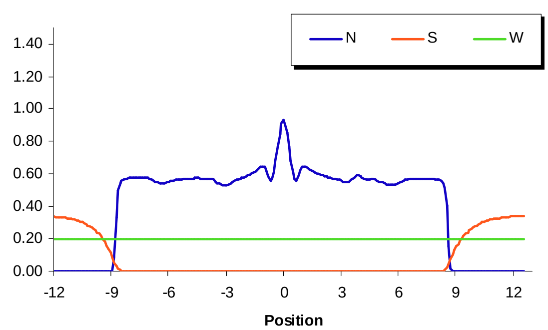


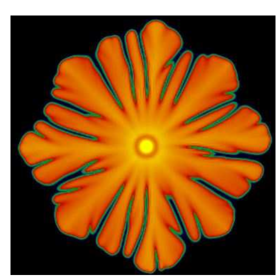


Numerical simulations

- New reaction-diffusion equations with chemotaxis

$t = 1700$; $D^N(N,W,S) = 5.\ 10^{-3}\ (1+\sigma)\ N\ S$; $D^S = 5.\ 10^{-3}$; $D^W = 10^{-1}$; $k_0 = 1$;
$\gamma = 2.5\ 10^{-4}$; $R_S = -\ N\ S$; $L = 8\ \pi$; $W_0 = 0.20$; $S_0 = 0.35$; $N_0 = 0.71\ \exp(-\ 20\ r^2)$

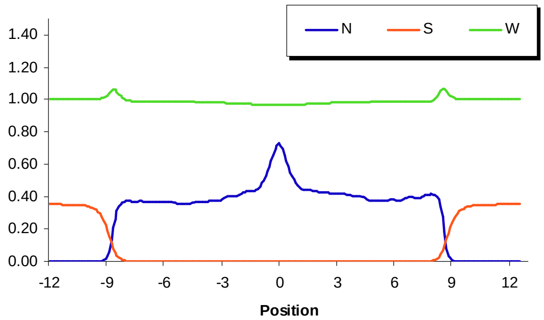


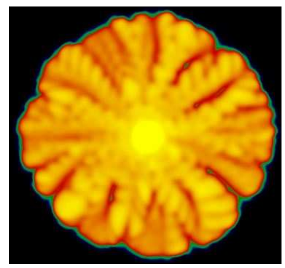


Numerical simulations

- New reaction-diffusion equations with chemotaxis

$t = 300$; $D^N(N,W,S) = 5.\ 10^{-2}\ (1+\sigma)\ N\ S$; $D^S = 10^{-2}$; $D^W = 5.\ 10^{-3}$; $k_0 = 1$;
$\gamma = 2.5\ 10^{-3}$; $R_S = -\ N\ S$; $L = 8\ \pi$; $W_0 = 1.0$; $S_0 = 0.35$; $N_0 = 0.71\ \exp(-\ 20\ r^2)$

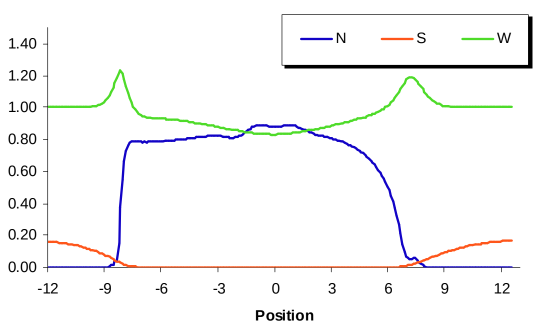


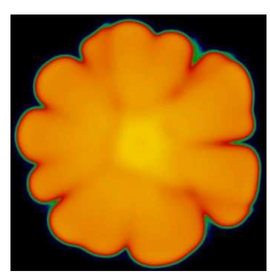


Numerical simulations

- New reaction-diffusion equations with chemotaxis

$t = 400$; $D^N(N,W,S) = 5.\ 10^{-2}\ (1+\sigma)\ N\ S$; $D^S = 10^{-1}$; $D^W = 5.\ 10^{-3}$; $k_0 = 1$;
$\gamma = 1.\ 10^{-2}$; $R_S = -\ N\ S$; $L = 8\ \pi$; $W_0 = 1.0$; $S_0 = 0.35$; $N_0 = 0.71\ \exp(-\ 20\ r^2)$



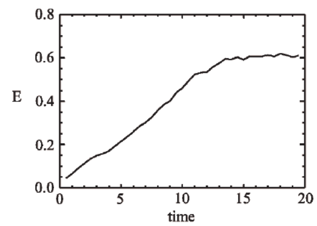


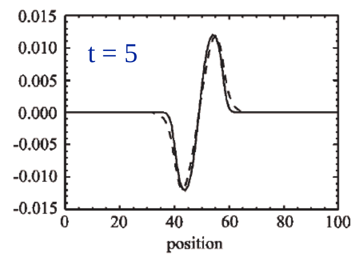
Numerical simulations

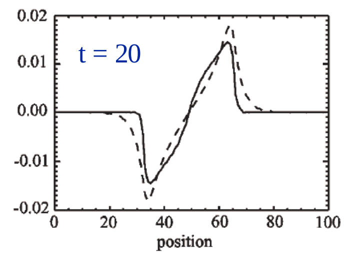
- The chemotaxis-like model is a singular limit of the full hydro-dynamic model

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

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

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

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

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

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

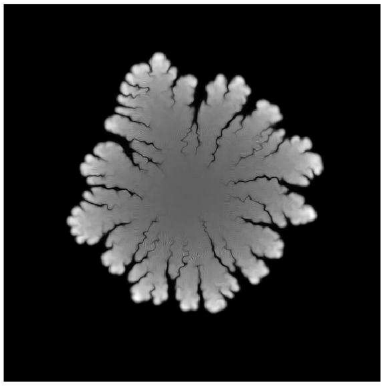
$$\frac{\partial S}{\partial t} = R_S + D^S \nabla^2 S$$

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

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)

$t = 2000$
$D^N_0 = D^S = 5.\ 10^{-3}$; $D^W = 10^{-1}$
$D^N(N,W,S) = D^N_0\ (1+\sigma)\ N\ S$
$R_S = -\ N\ S = -\ R_N$; $R_W = 0$
$k_0 = 1$; $\gamma = 0.44\ 10^{-4}$
$\mu = 0.01$; $\lambda = \mu/3$; $\eta = 0$
$F_g = N\ \rho\ f$
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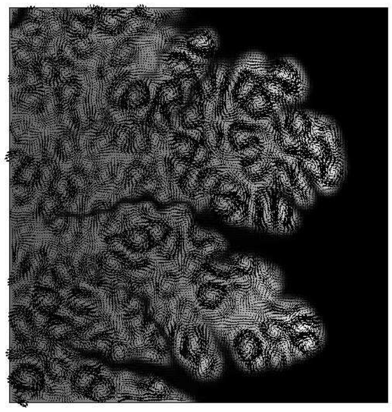
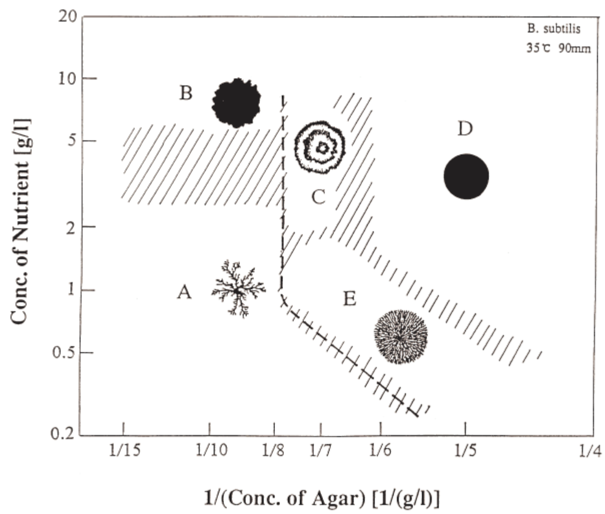


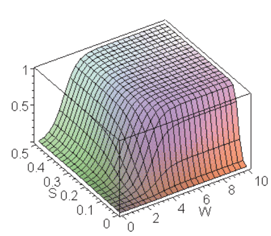
M. Matsushita *et al.*, Physica A **249**, 517-524 (1998)

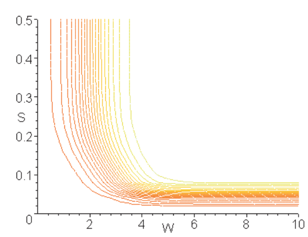
Different colony forms for *Bacillus subtilis* OG-01

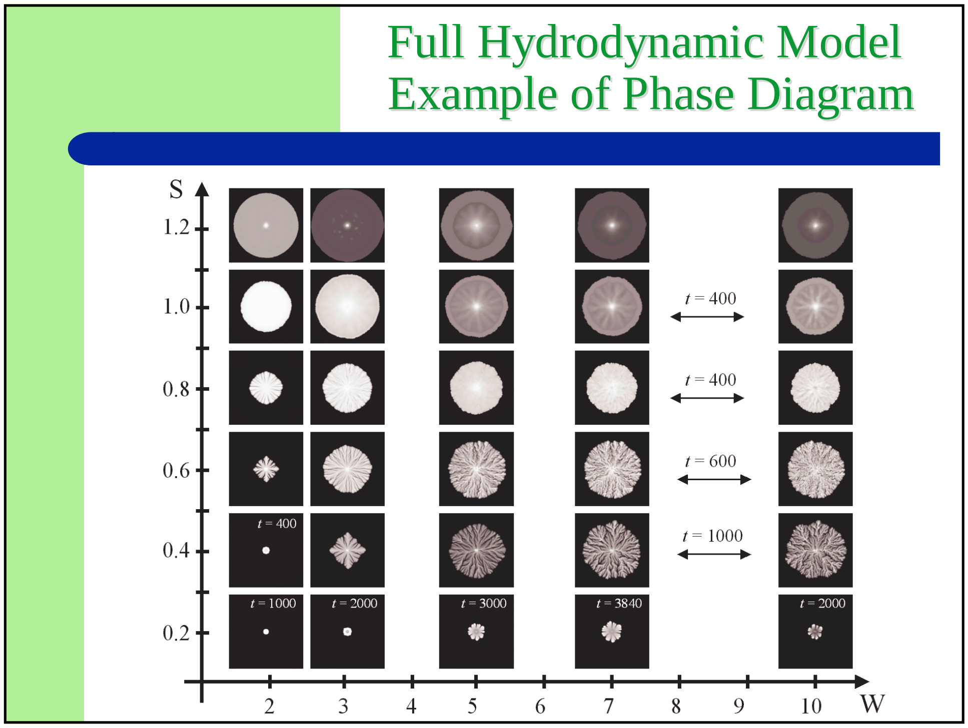


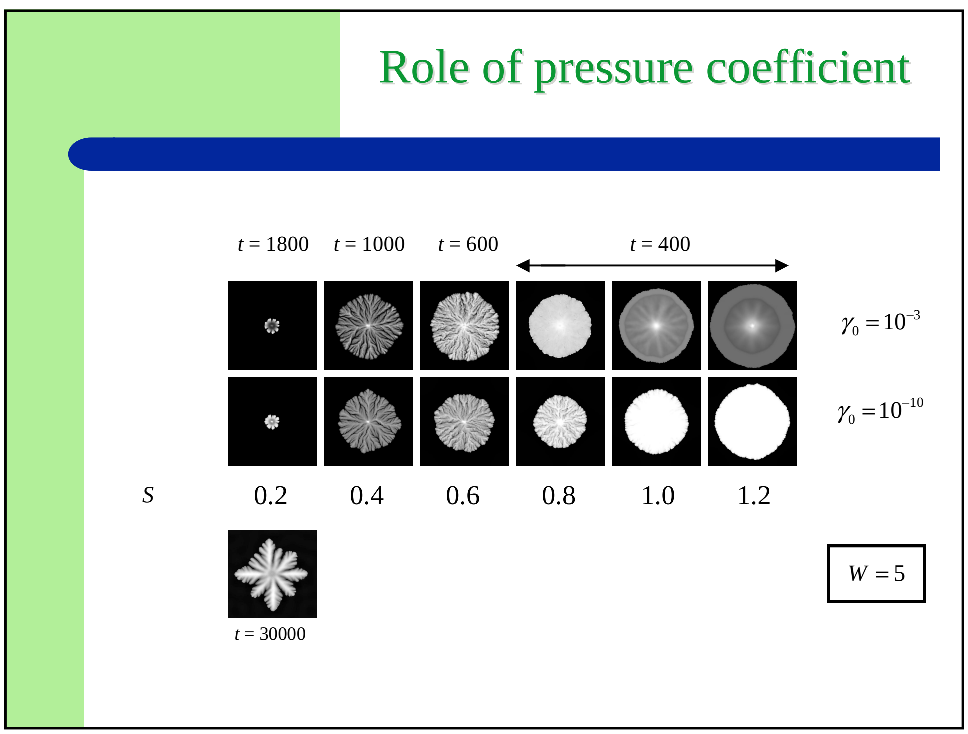
Functional Forms

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






Full Hydrodynamic Model
Example of Phase Diagram
S
1.2
1.0
0.8
0.6
0.4
0.2
t = 400
t = 400
t = 600
t = 1000
t = 400
t = 1000
t = 2000
t = 3000
t = 3840
t = 2000
2
3
4
5
6
7
8
9
10
W


Role of pressure coefficient
t = 1800
t = 1000
t = 600
t = 400
$\gamma_0 = 10^{-3}$
$\gamma_0 = 10^{-10}$
s
0.2
0.4
0.6
0.8
1.0
1.2
t = 30000
W = 5

Conclusions

- Hydrodynamic model
  - Describes bacterial dynamics *within* (c.f. vortices and jets) and *at the boundary of* (c.f. branched structures) the colony.
  - Proposes *general framework* for the use of advection-reaction-diffusion equations in modeling bacterial colonies.
  - Identifies a *mechanism for collective motion* towards fresh nutrients, which, in its modeling aspects is similar to classical chemotaxis.

Conclusions

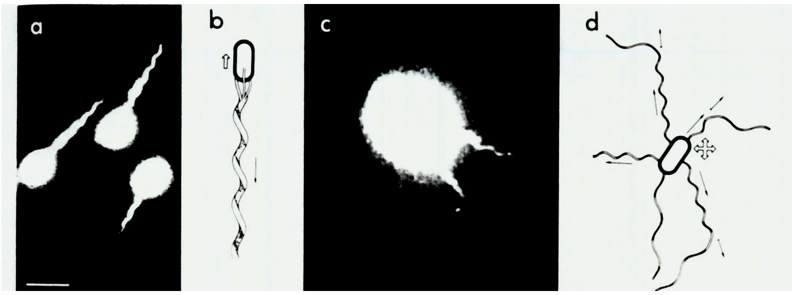
- Hydrodynamic model
  - Qualitatively *reproduces phase diagrams* describing colony shapes in terms of initial concentrations of nutrients and water.
  - Can be adapted to describe bacterial strains other than *B. subtilis*.
  - Can be made more precise by modeling water and bacterial dynamics separately or by introducing a more elaborate closure relation between the water and bacterial velocity fields.

Conclusions

- Open questions
  - What are the rheological properties of a bacterial fluid? What role would non-Newtonian effects have if included in the model?
  - Understand, at a microscopic level, the nature of the small-scale forcing due to bacterial activity.
  - Analyze the coupling between hydrodynamics and reaction-diffusion equations and understand how the complex dynamics within the colony destabilizes the colony boundary.

R.Macnab,
Motility and chemotaxis,
1987

Runs and tumbles



Swimming: CCW rotation

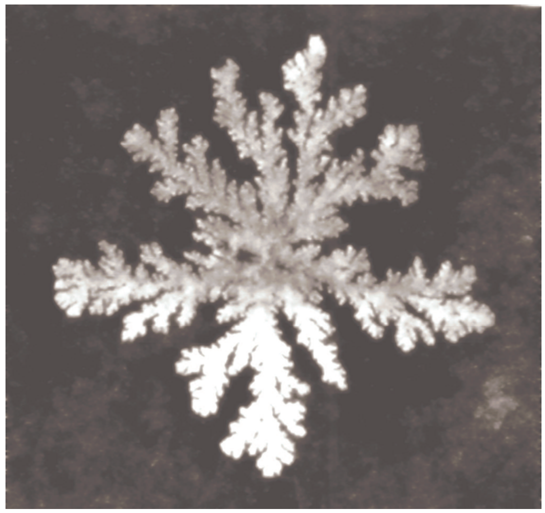
Tumbling: CW rotation

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

M. Ohgiwari *et al.*,
J. Phys. Soc. Jpn. **61**,
816-822 (1992)

DLA-like colonies



M. Matsushita *et al.*,
Physica A **249**, 517-524
(1998)

Colonies with "rough contour"

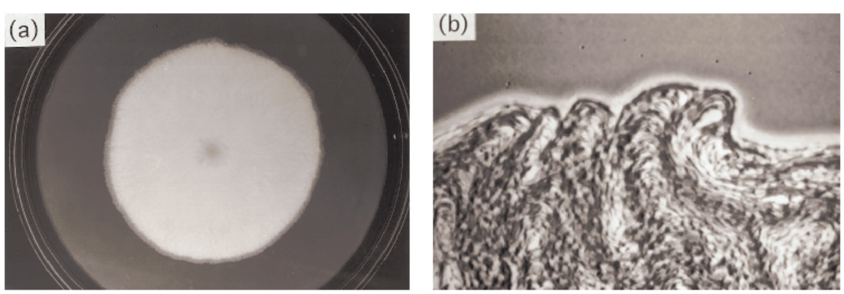


Fig. 2. Photographs of a bacterial colony in region B. Here we used wild-type bacteria. $C_a = 10$ g/l, $C_n = 20$ g/l: (a) A macroscopic snapshot of the whole colony. It was taken 3 days after inoculation. The diameter of the plastic petri dish is 88 mm; (b) A microscopic snapshot of the colony interface. The scale of the figure is 0.4 mm in width.

I. Golding *et al.*, Physica A **260**, 510-554 (1998)

Colonies with concentric rings

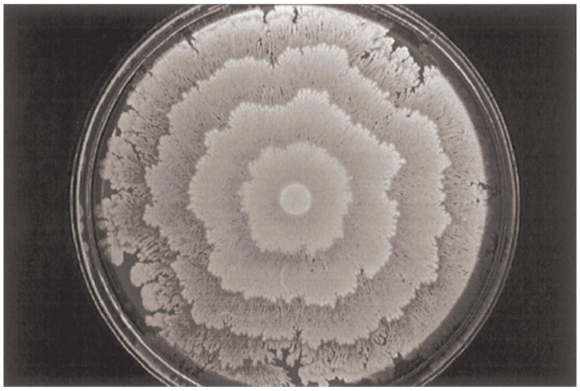


Fig. 7. Colony of *B. subtilis.* Pattern of concentric rings superimposed on a branched colony. Taken with permission from [60].

I. Rafols, *Formation of concentric rings in bacterial colonies*, MSc thesis, Chuo University, Japan (1998).

M. Matsushita *et al.*, Physica A **249**, 517-524 (1998)

Round colonies

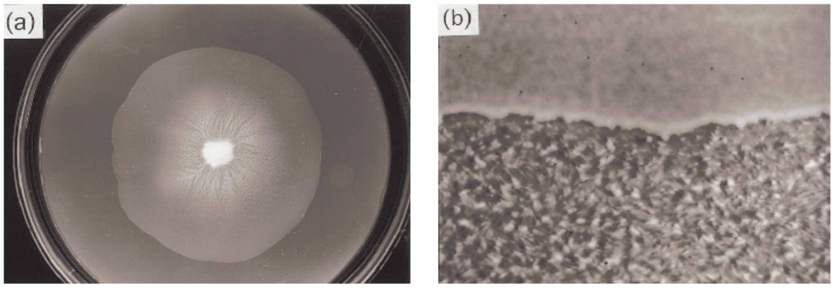


Fig. 3. Photographs of a bacterial colony in region D. Here we used mutant bacteria which do not secrete surfactant. $C_a = 5$ g/l, $C_n = 10$ g/l: (a) A macroscopic snapshot of the whole colony. It was taken 19 h after inoculation. The diameter of the petri dish is 88 mm; (b) A microscopic snapshot of the colony interface. The scale of the figure is 0.4 mm in width.

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

Colonies with DBM

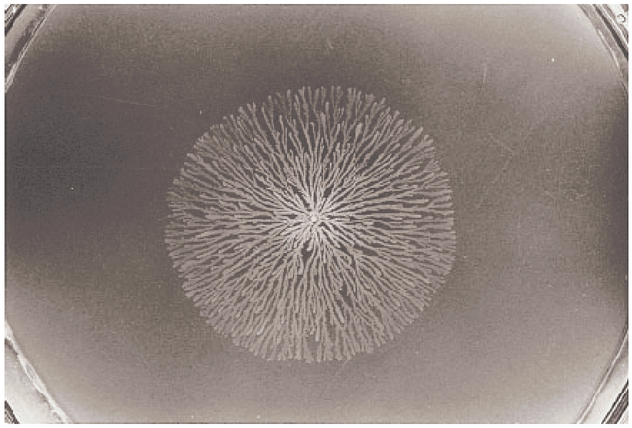
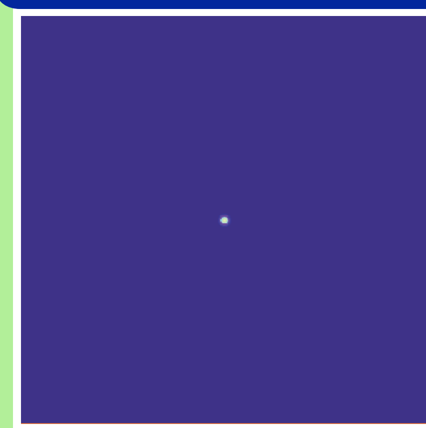


FIG. 2. A typical DBM-like colony pattern. The agar plate contains 0.5 g l^{-1} of peptone and 5 g l^{-1} of agar. The colony is photographed 2 days after inoculation.

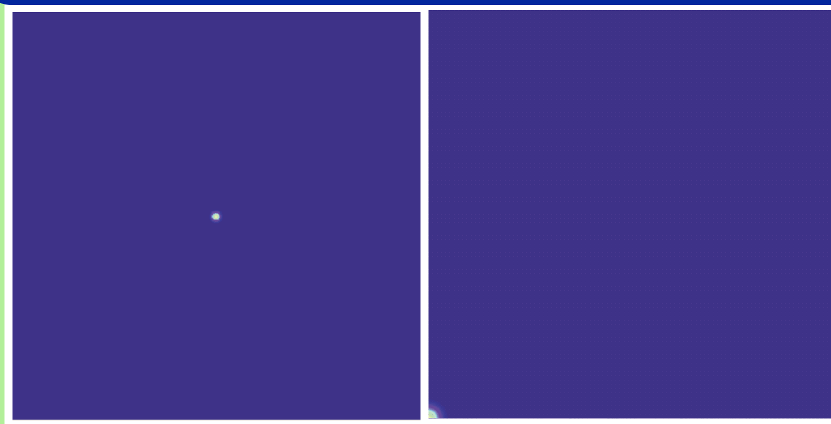
$S = 1 - W = 7 - \lambda = 0$



Left: animation showing the growth of the colony until t = 400

Right: animation showing a quarter of the colony together with the corresponding velocity fied

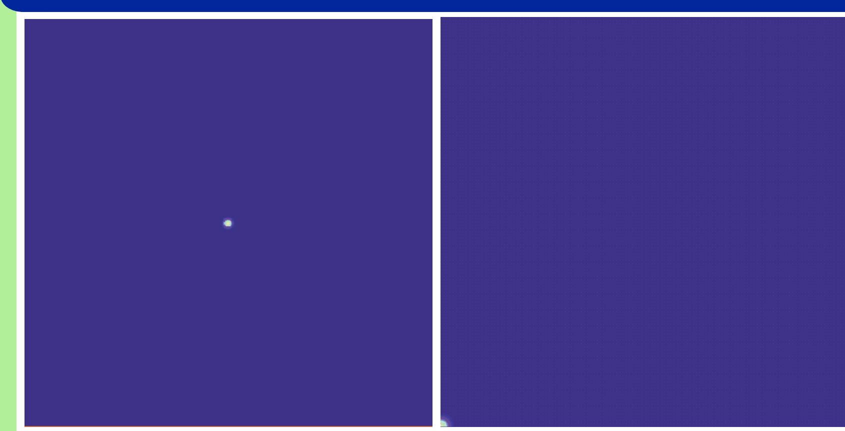
$S = 1 - W = 2 - \lambda = 0$



Left: animation showing the growth of the colony until t = 400

Right: animation showing a quarter of the colony together with the corresponding velocity fied

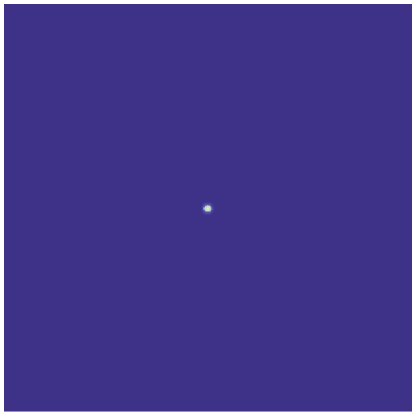
$S = 1.2 - W = 3 - \lambda = 0$



Left: animation showing the growth of the colony until t = 400

Right: animation showing a quarter of the colony together with the corresponding velocity fied

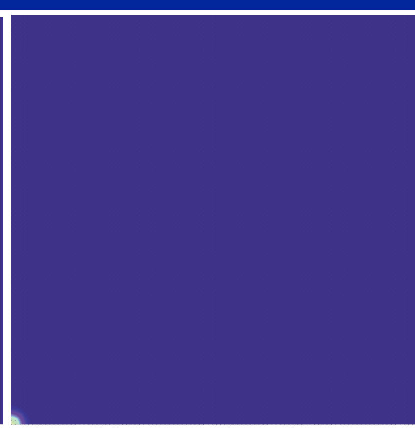
$S = 0.8 – W = 5 – \lambda = 0$



Left: animation showing the growth of the colony until t = 400

Right: animation showing a quarter of the colony together with the corresponding velocity fied

$S = 0.8 – W = 7 – \lambda = 0$



Left: animation showing the growth of the colony until t = 400

Right: animation showing a quarter of the colony together with the corresponding velocity fied

Parameters

- Reaction-diffusion equations
  - Diffusion coefficient of S: 0.002
  - Diffusion coefficient of W: 0.002
  - Diffusion coefficient of N: $D^0 = 0.0004$
  - Logistic growth coefficient for N: $\alpha = 1.0$
  - Carrying capacity: $N_0 = 1.0$
  - Nutrient consumption coefficient: $k_0 = 1.0$
  - Cut-off value: 0.015
  - Noise on D^N of amplitude: 0
  - Evaporation: $\lambda = 0.00$
- Initial conditions
  - Maximum amplitude of initial condition for N: 1.00
  - Initial condition for W: 2.00, 3.00, 5.00, 7.00, or 10.00
  - Initial condition for S: 0.2, 0.4, …, 1.2
- Hydrodynamic equation
  - Friction: $\eta = 0.01$
  - Viscosity: $\nu = 0.01$
  - Bulk viscosity: $\zeta = 0$
  - Small-scale forcing: $f_0 = 0.04$
  - Support of forcing in Fourier space: $35 < k < 55$
  - Forcing is maximum at $k = 45$
  - Pressure coefficient γ_0: 0.001
- Simulations
  - Time step: 0.1
  - Number of points: 512 x 512