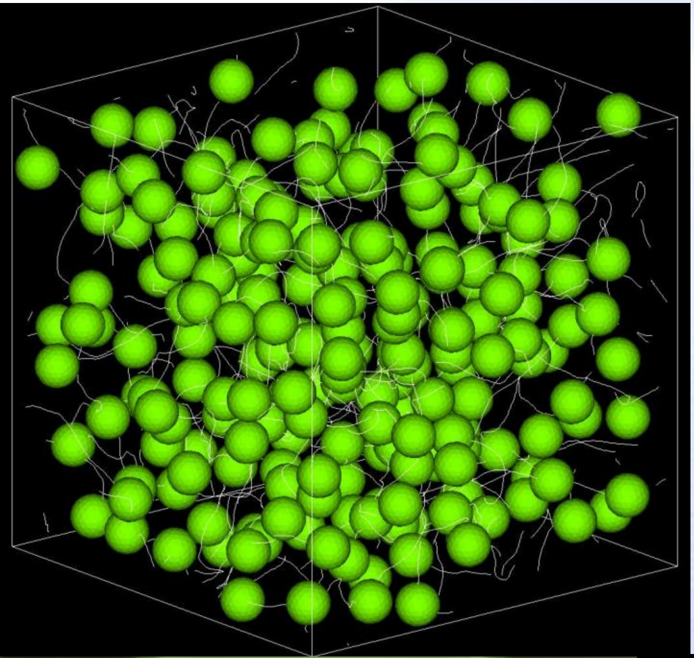
微生物の集団遊泳と懸濁液内の輸送現象



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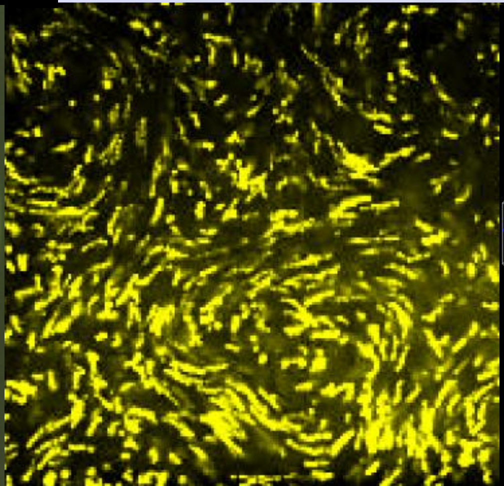
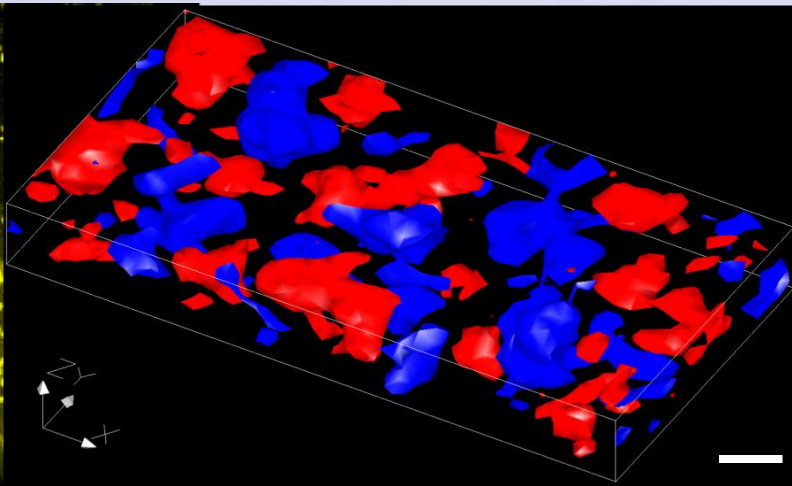




Introduction

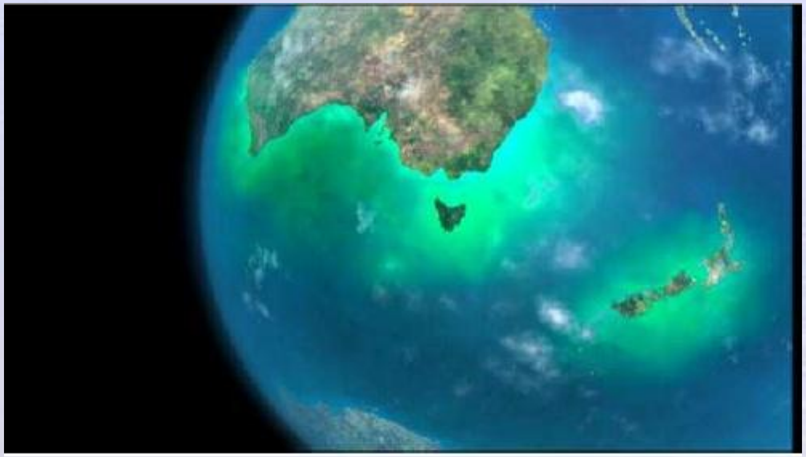
The role of the infinitely small in nature is infinitely large.

Louis Pasteur (1822-1895)

Micro-organisms in the ocean

50% of biomass
Bottom of food chain
⇒ Oceanic ecosystem

Absorption of CO_2
Nitrogen cycle
⇒ Global environment



Plankton blooms around Australia and New Zealand
Picture from Byatt et al. (2001)

Introduction

Micro-organisms in bioreactors

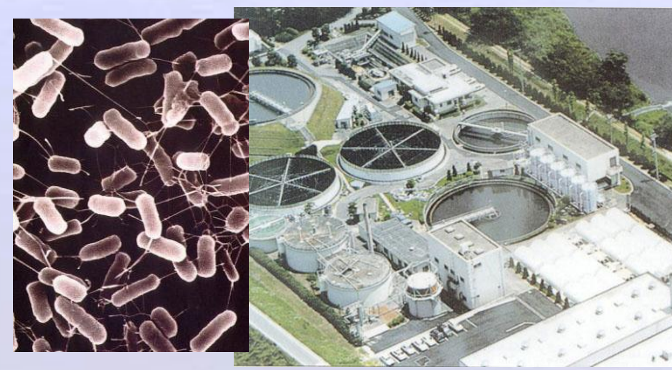
Making food

Yeast, Lactic acid bacterium

→ Food industry

Sewage treatment

→ Plant industry



Algae fuel

an alternative to fossil fuel

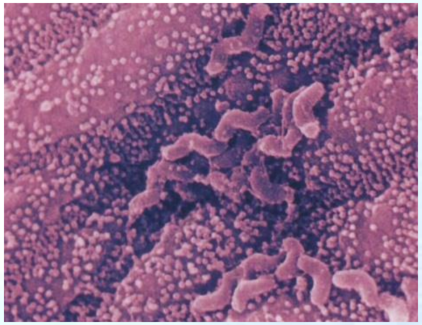
→ Energy revolution?

Introduction

Micro-organisms in human body

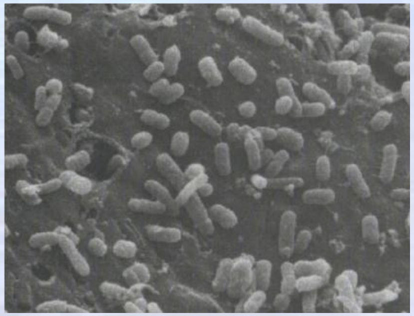
hundreds of species
about 10^{14} cells

Helicobacter pylori
in the stomach

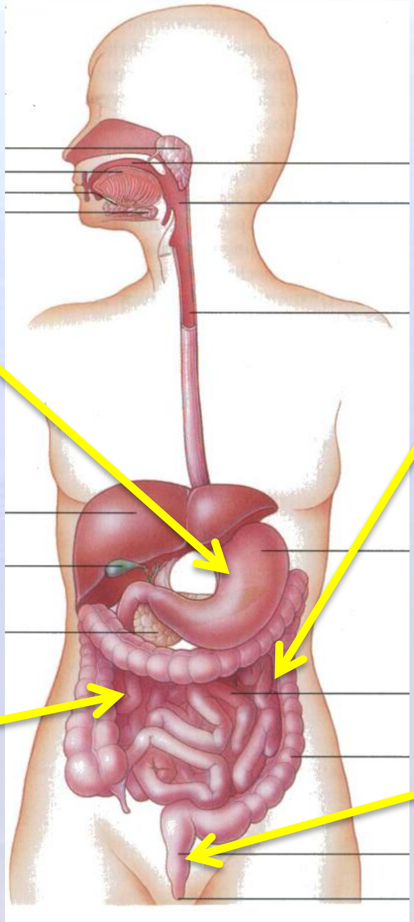


from Introduction to Microbiology

Infection by *salmonella*

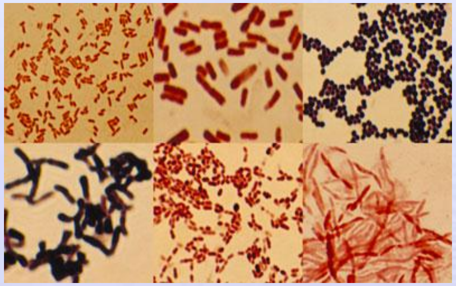


from Introduction to Microbiology



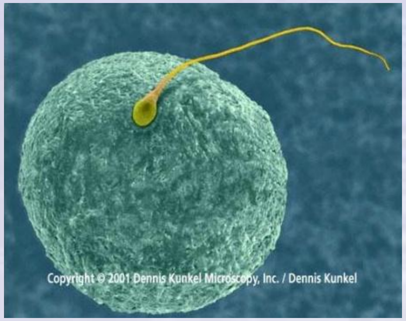
from Introduction to Microbiology

Digestion helped by enterobacteria
(vitamin K)



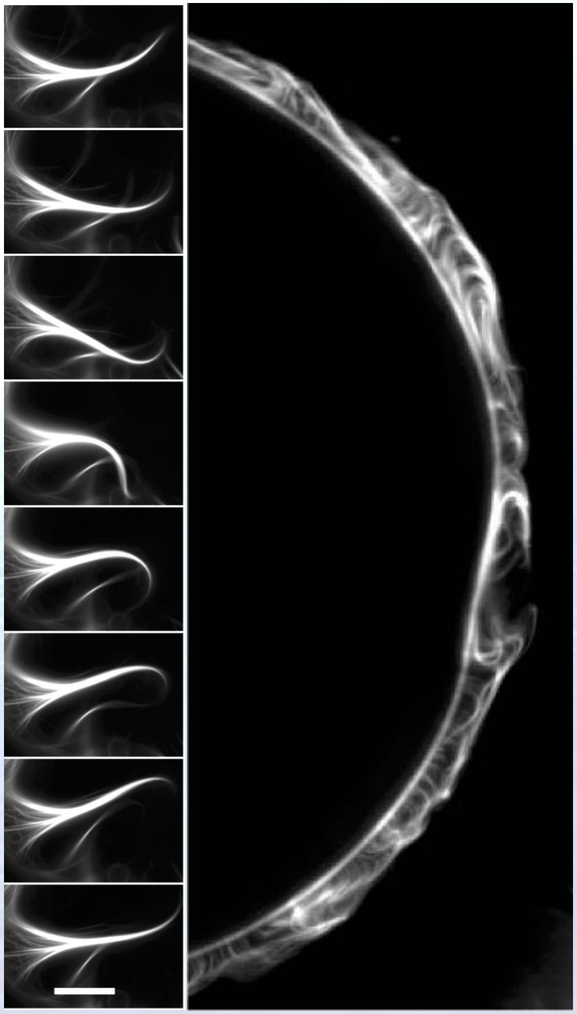
http://www.riken.go.jp/

Reproduction owed to sperm swimming

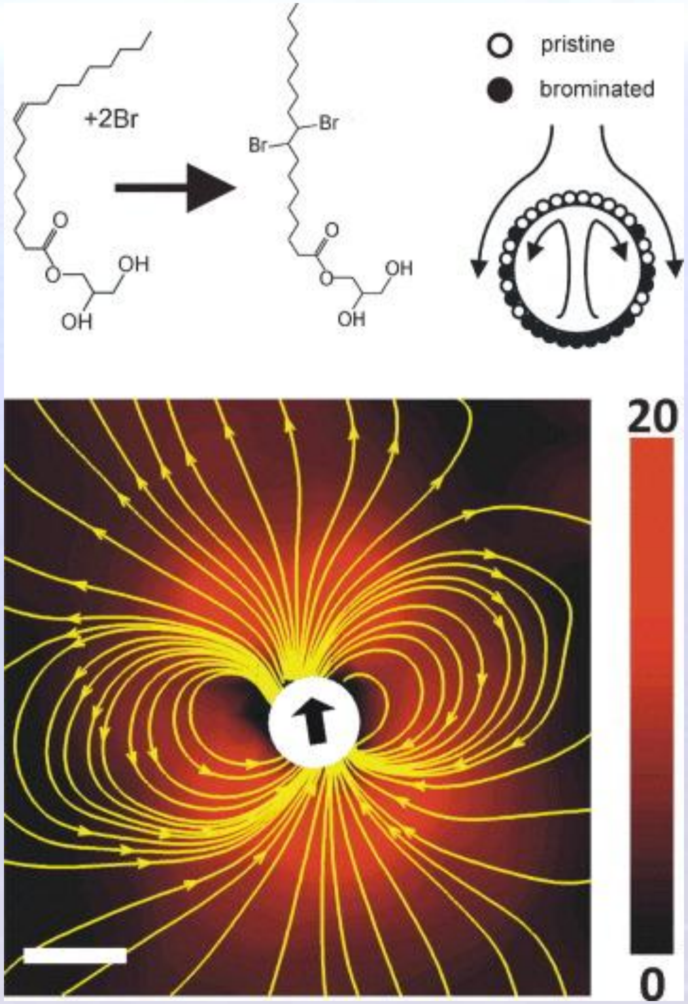


Introduction

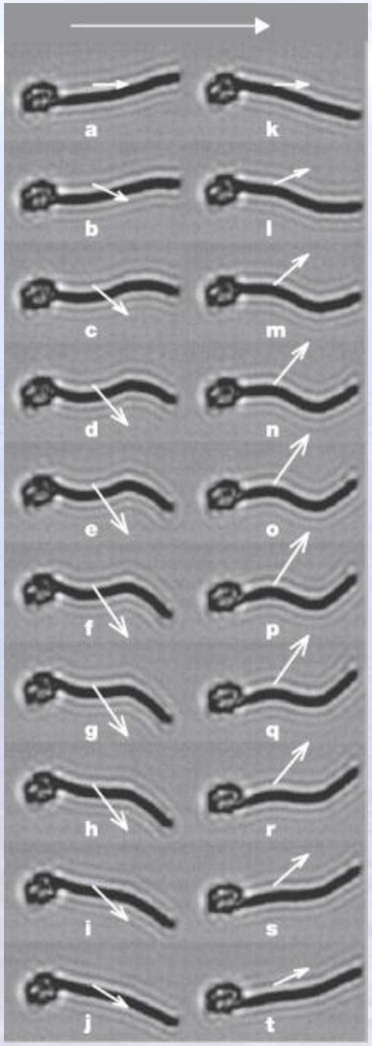
Artificial Micro-swimmers



Sanchez, et al. (2011)



Thutupalli, et al. (2011)



Dreyfus et al. (2005)

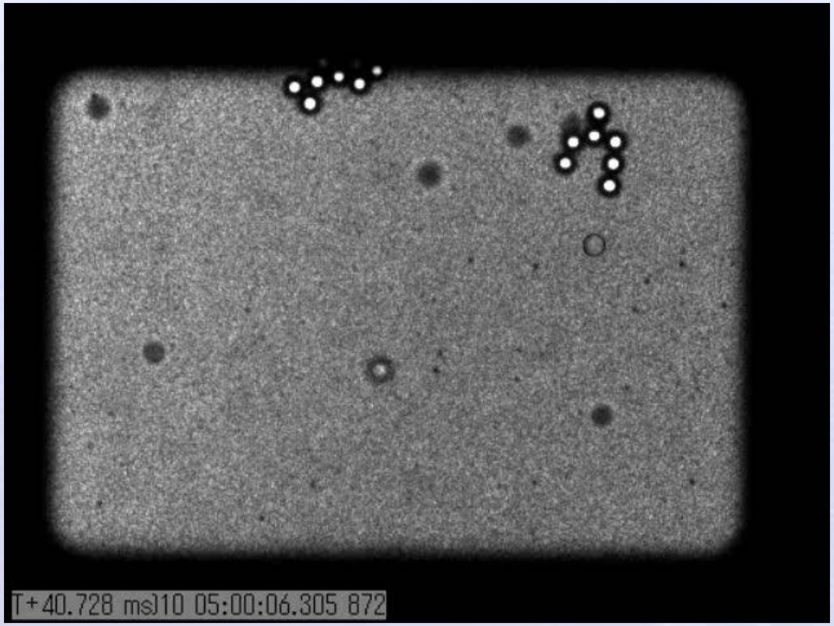
Introduction

In order to understand variety of micro-organisms' phenomena Ecology, Biology & Chemistry have been used.

One example of bacterial phenomena

In this suspension, chemical substances spread 10^3 times more than the Brownian diffusion.

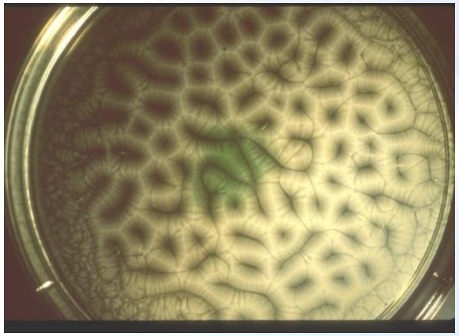
Can we explain this by ecology, biology or chemistry?



A suspension of *Escherichia coli*

Biophysics & biomechanics can contribute more in this field

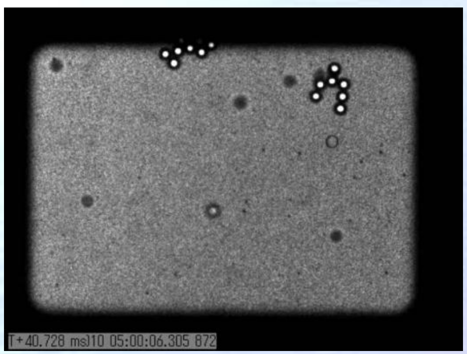
Bottom-up Strategy



Macroscopic level

Rheological and Diffusion properties

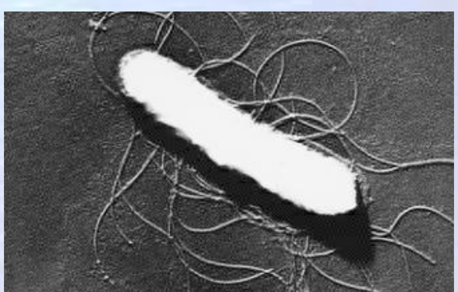
Strong influence



Mesoscale level

Collective motions, Coherent structures

Strong influence



Cellular level

Cell-cell interactions

Bottom-up Strategy

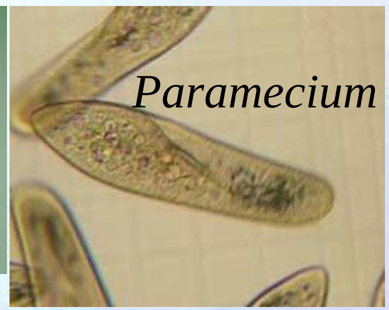
Outline of the talk

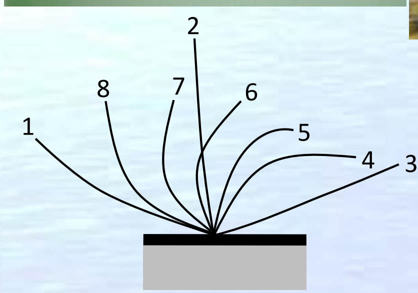
- Introduction
- Biomechanics of an **individual** and a **pair** of micro-organisms
- **Collective swimming** in meso-scale
- **Macroscopic properties** of a suspension of micro-organisms
- Conclusions

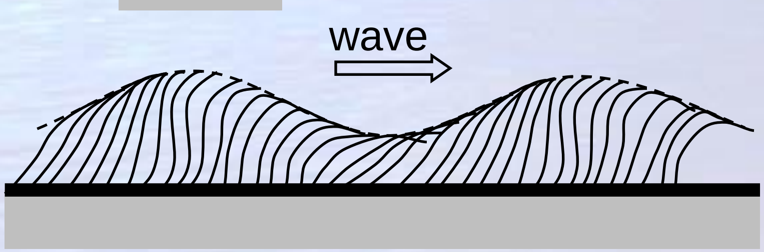
Classification of micro-organisms

In terms of swimming motion

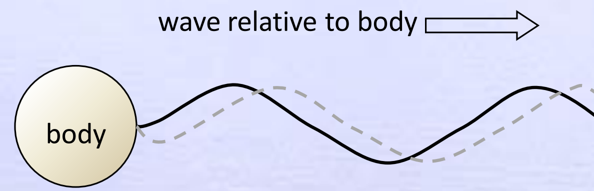
Ciliate



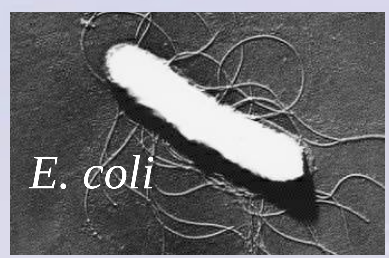


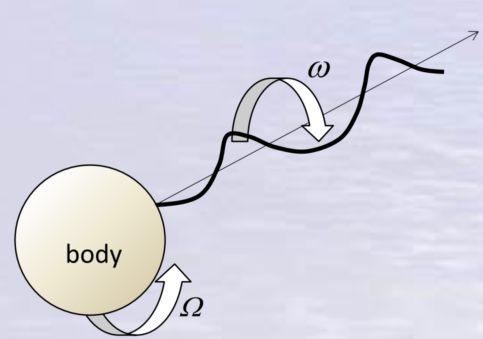


Flagellate (eukaryote)



Bacteria





Hydrodynamics of a single cell

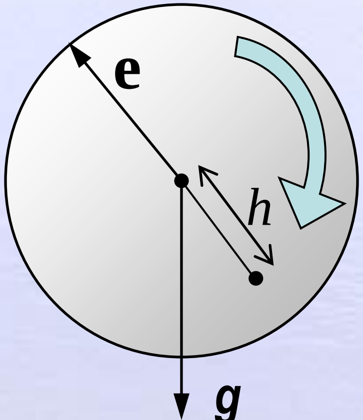
Flow field

Size of a single cell: 1-100μm

Swimming speed: 1-10 body length / sec

⇨ Re = 10^{-6} – 10^{-3}

Stokes flow (Inertia-free)



Force-Torque condition of a cell

Force is almost free

Torque may not be free (bottom-heaviness)

Review paper

Brennen & Winet, *Ann. Rev. Fluid Mech*. (1977)

Lauga & Powers, *Rep. Prog. Phys*. (2009)

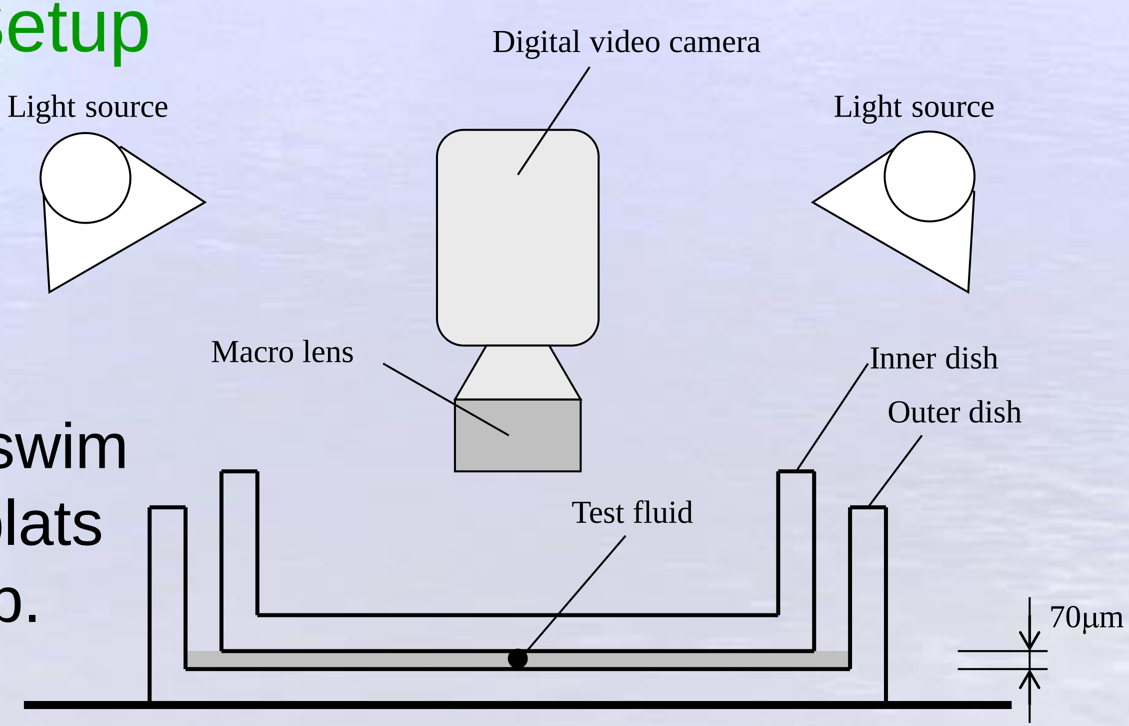
<u>When two cells come close, what happens?</u>

Experiment of *Paramecia*

Paramecium caudatum

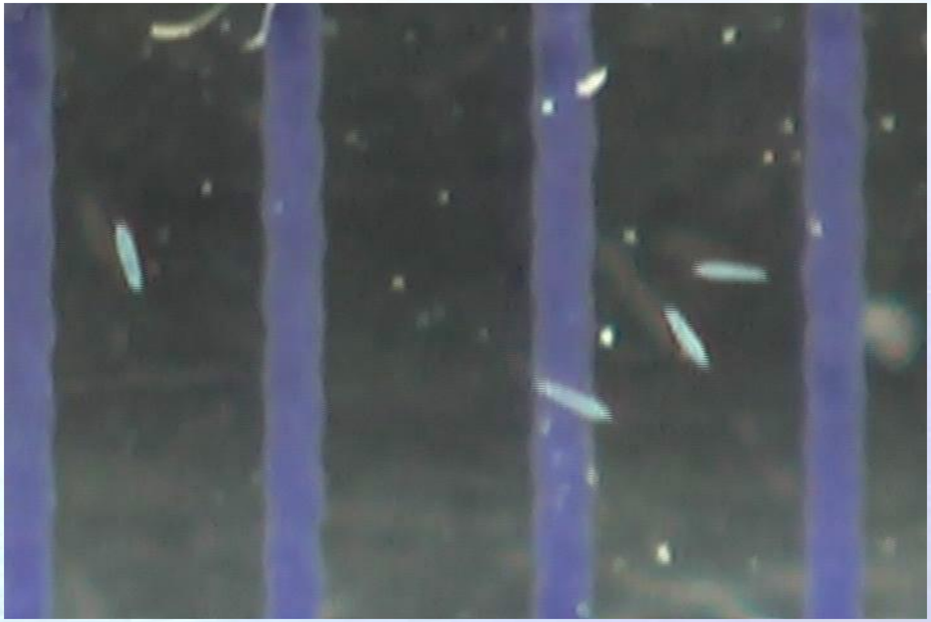
Approximately
250μm in length
50μm in width

Experimental Setup

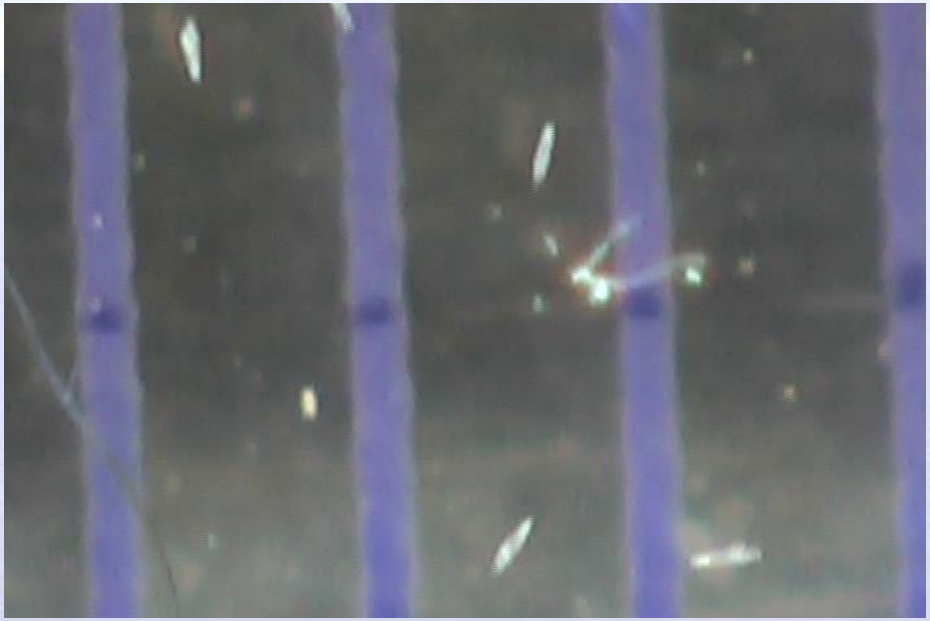


Paramesium swim between flat plats with 70μm gap.

Biological reaction



Avoiding Reaction (AR)



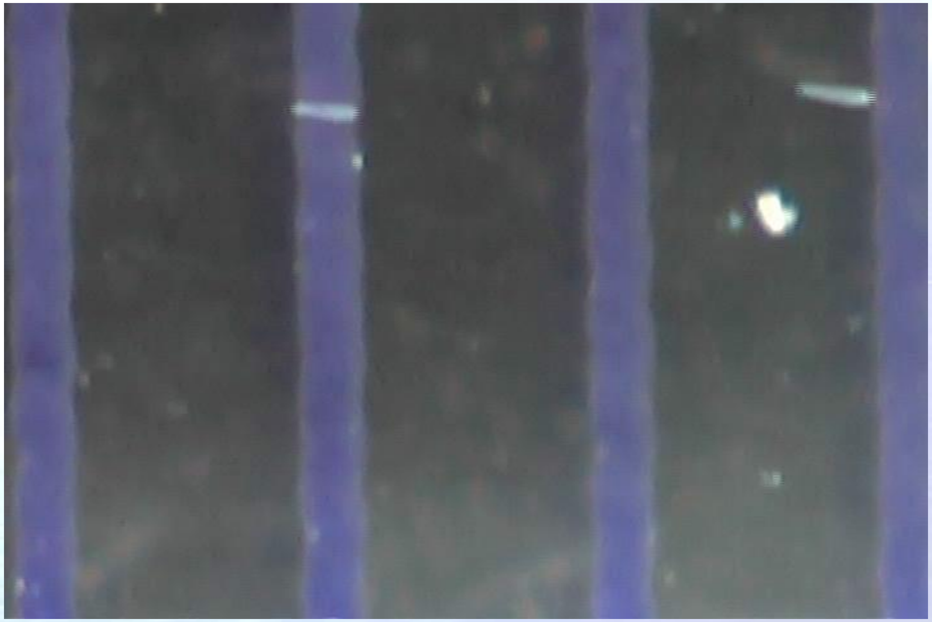
Escape Reaction (ER)

Anterior end: Ca^{2+} channel

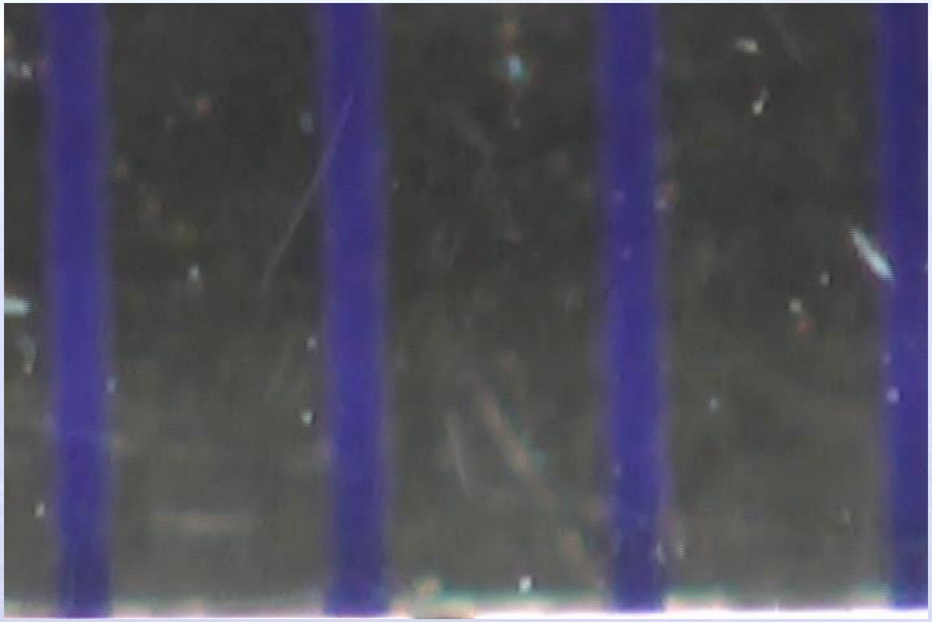
Posterior end: K^{+} channel

Ishikawa and Hota, *J. Exp. Biol.* (2006)

Hydrodynamic interaction



Initially facing each other



Two orientation vectors initially have a large angle

Ishikawa and Hota, *J. Exp. Biol.* (2006)

Experimental results

Ratio of three kinds of interaction

The total number of experimental cases recorded in this study is 301, and the total number of cells is 602.

Kinds of interaction	Number of cells	Percent [%]
Hydrodynamic Interaction (HI)	510	84.7
Avoiding Reaction (AR)	29	4.8
Escape Reaction (ER)	63	10.5

Ishikawa and Hota, *J. Exp. Biol.* (2006)

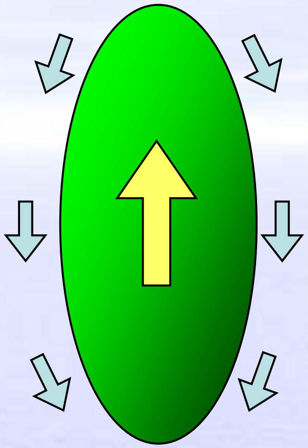
Mainly hydrodynamic interaction

How to model *Paramecium*?

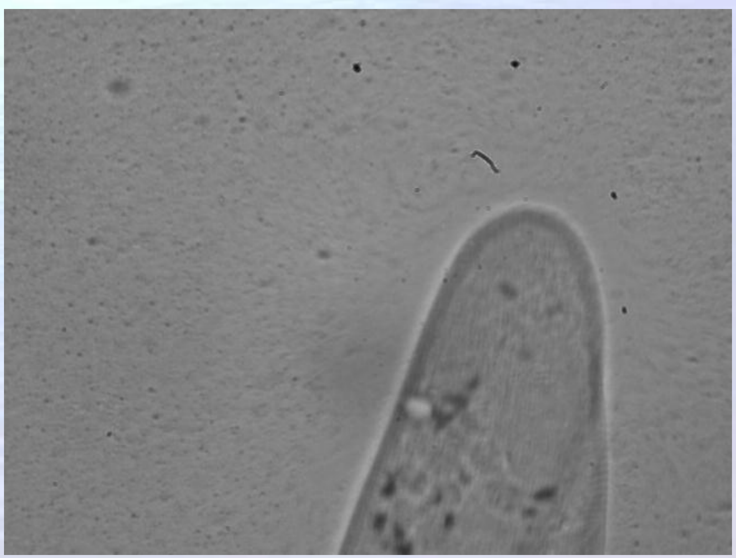
Squirmer model

assumed to propel itself by generating tangential velocities on its surface.

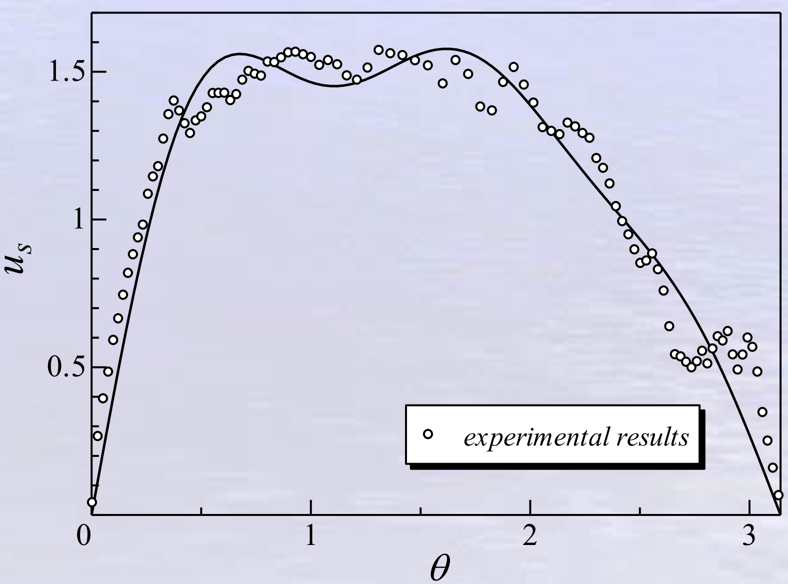
Surface velocity is given as a B.C.



Velocity field around *Paramecium*



PIV



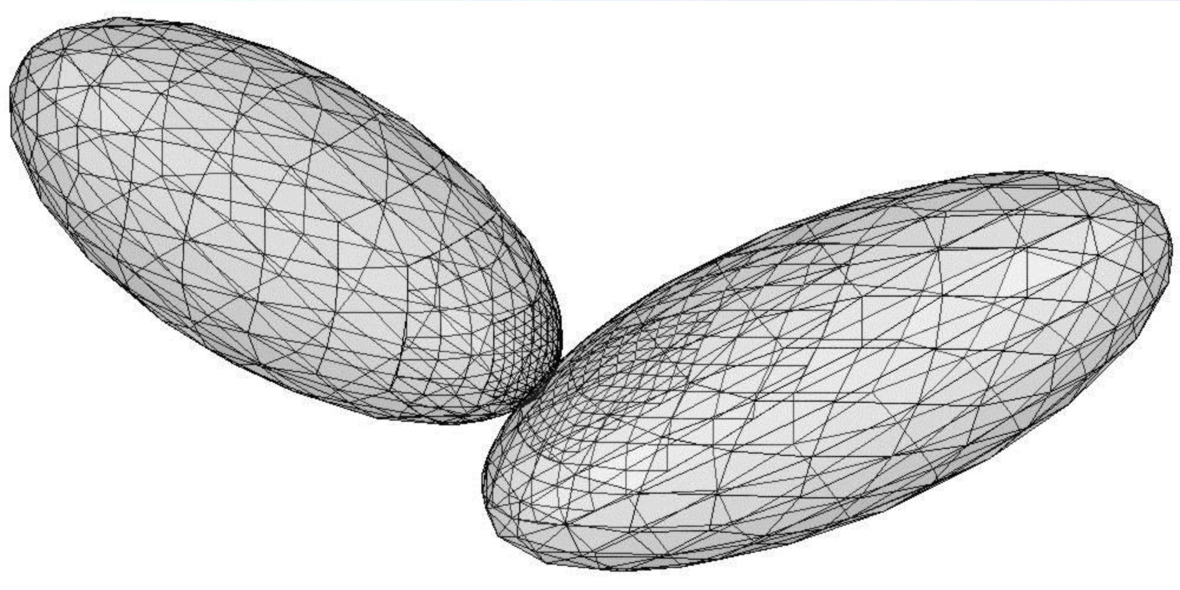
Numerical Methods

Paramecium: Force-free, Torque-free

Flow Field: Boundary Element Method

Ishikawa *et al.*, *J. Fluid Mech.* (2006)

$$u_i(\mathbf{x}) - \langle u_i(\mathbf{x}) \rangle = -\frac{1}{8\pi\mu} \sum_{\alpha=1}^{N} \int_{A_\alpha} J_{ij}(\mathbf{x}-\mathbf{y}) q_j(\mathbf{y}) dA_y$$



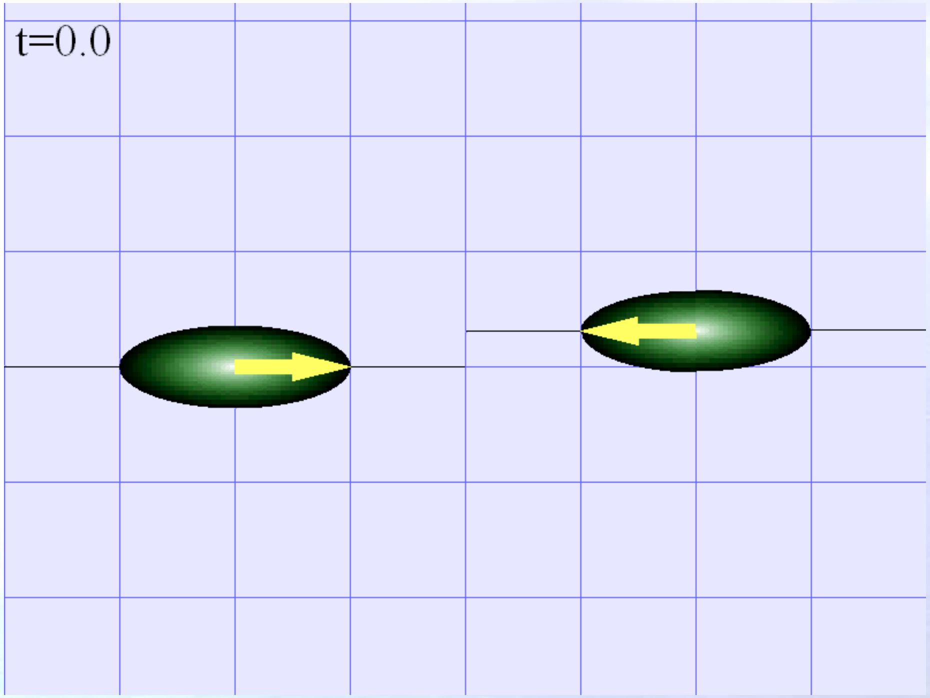
q : single-layer potential

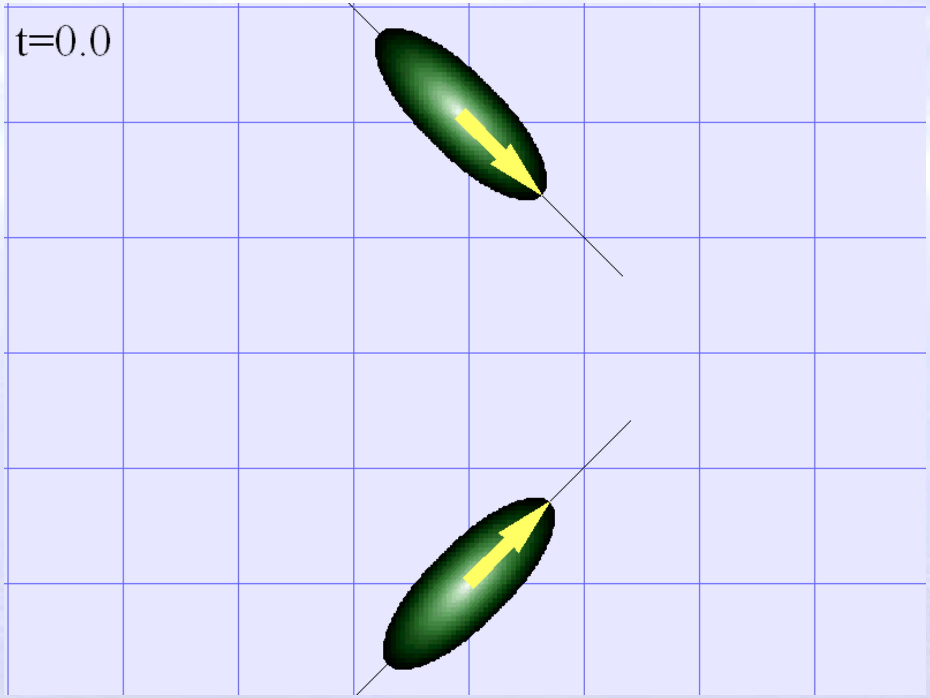
A : surface of a particle

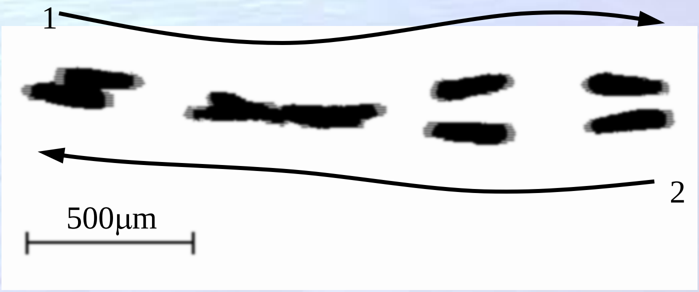
u : velocity

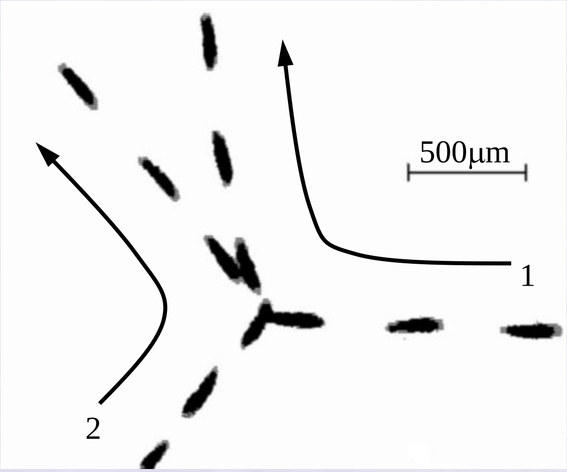
J : Green function

Numerical Results







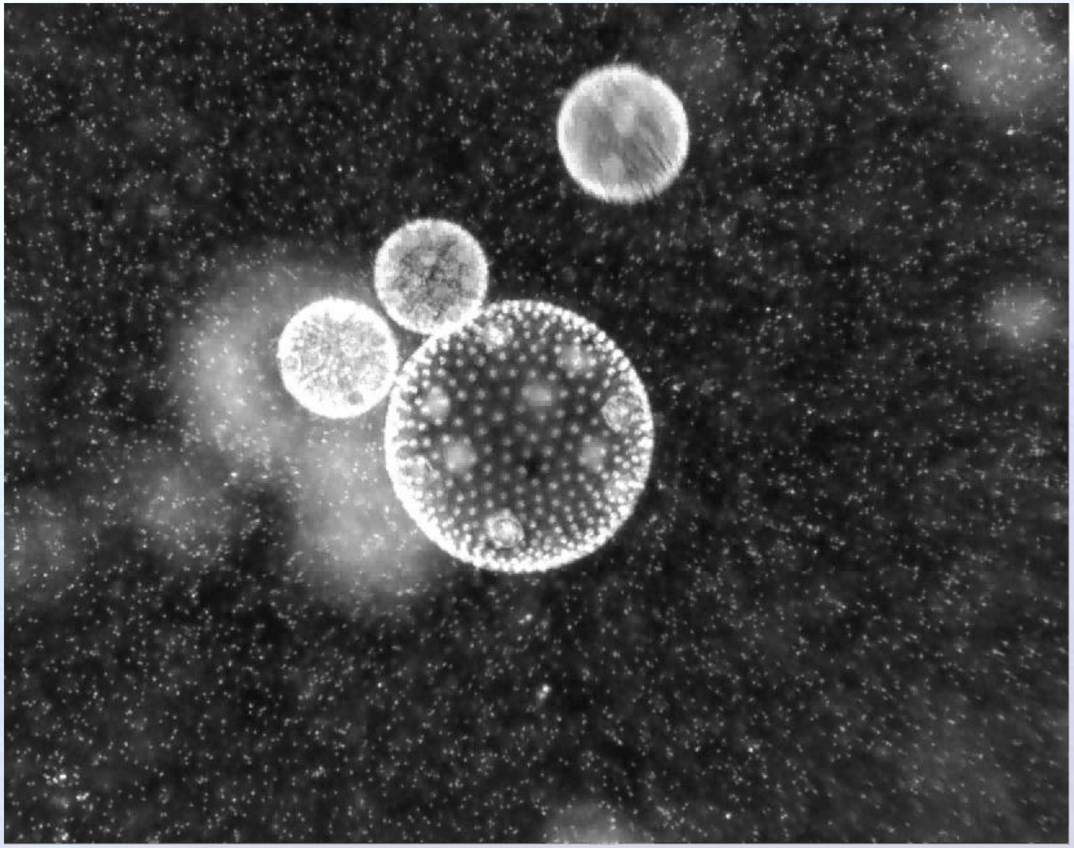


Agree with the experiment

Ishikawa and Hota, *J. Exp. Biol.* (2006)

Waltzing motion of *Volvox*

A waltzing motion was found by R.E.Goldstein's group.



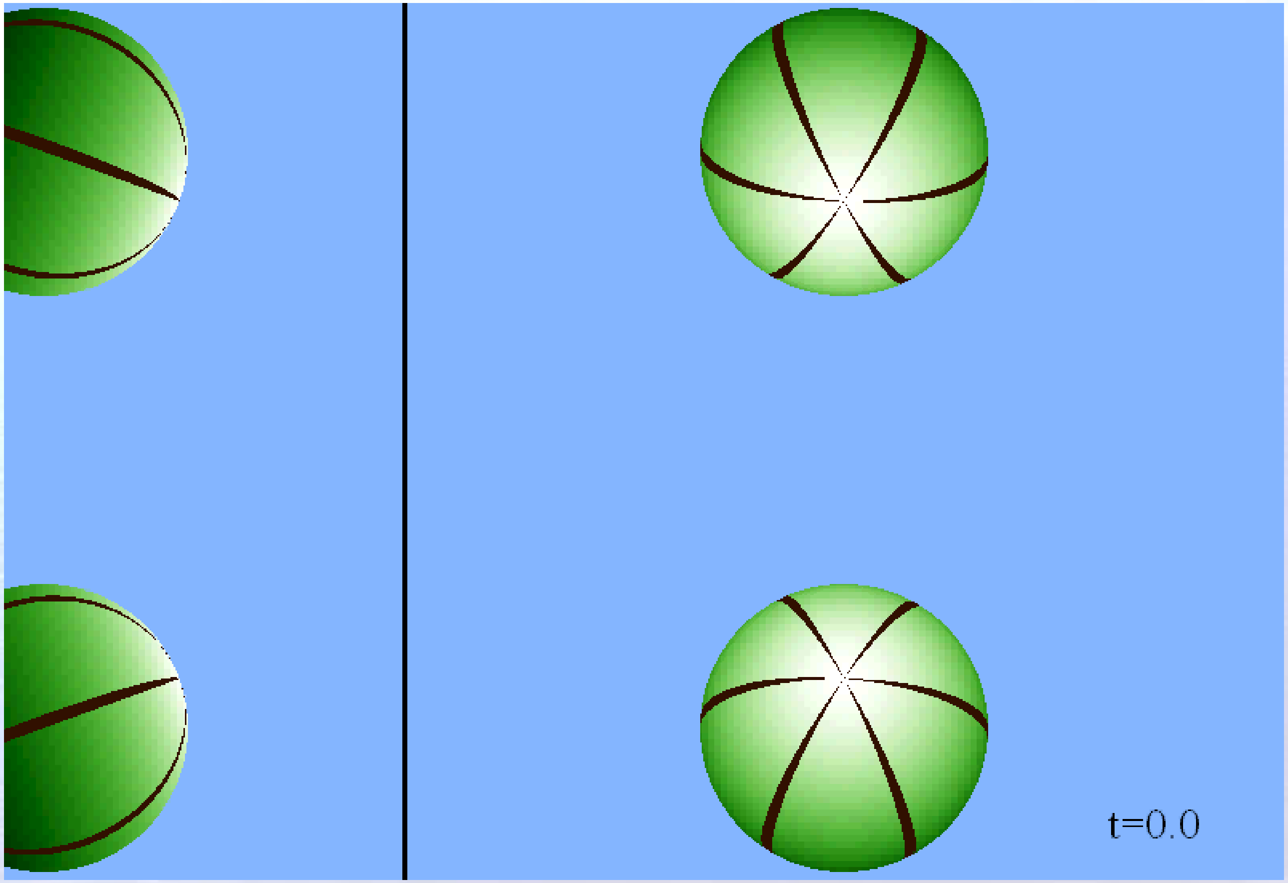
for fertilization?

http://www.damtp.cam.ac.uk/user/gold/

Mechanism: Biological? Hydrodynamical?

Resluts : effect of Bottom-heaviness

G_{bh}=50 : bottom-heavy $(\lambda = 5\text{deg})$



Waltzing motion does appear

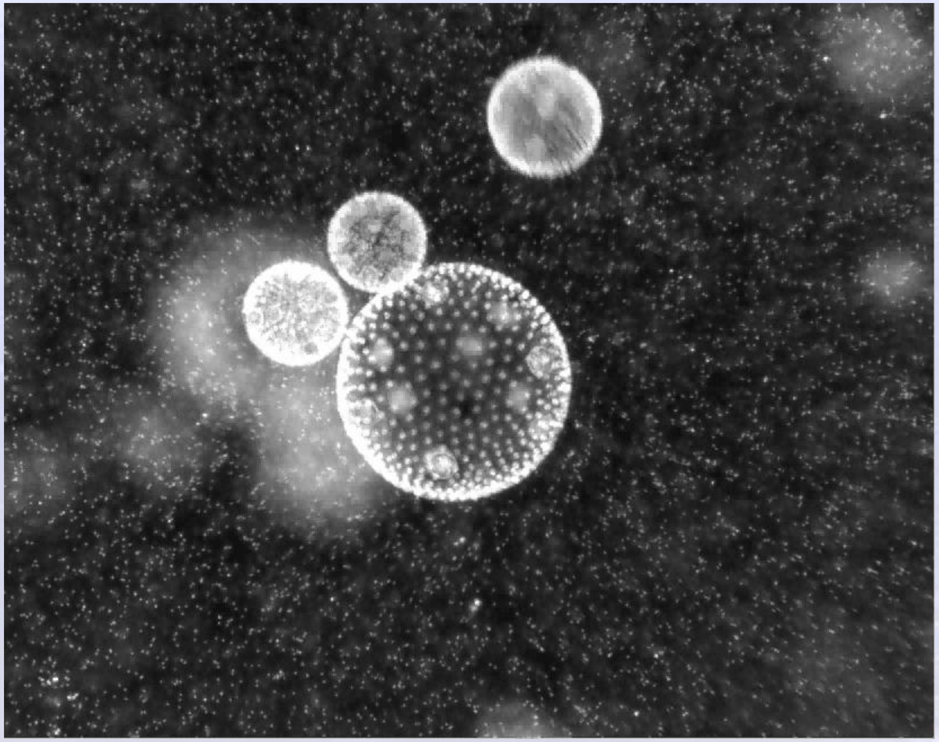
Waltzing motion of *Volvox*

The waltzing motion can be reproduced by introducing:

(a) A wall boundary

(b) Bottom-heaviness

(c) Swirl velocity



Mechanism
= Hydrodynamics

Drescher *et al.*, *Phys. Rev. Lett.* (2009)

Outline of the talk

- Introduction
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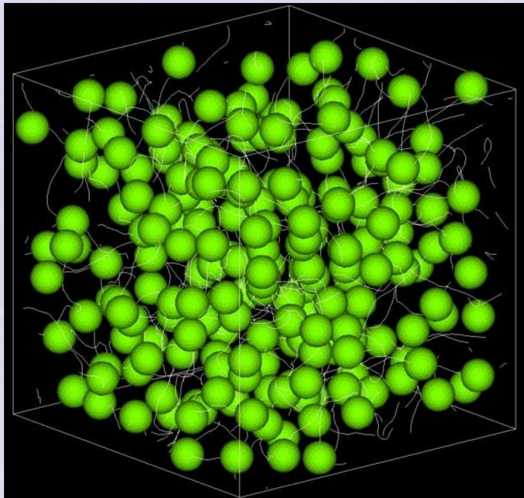
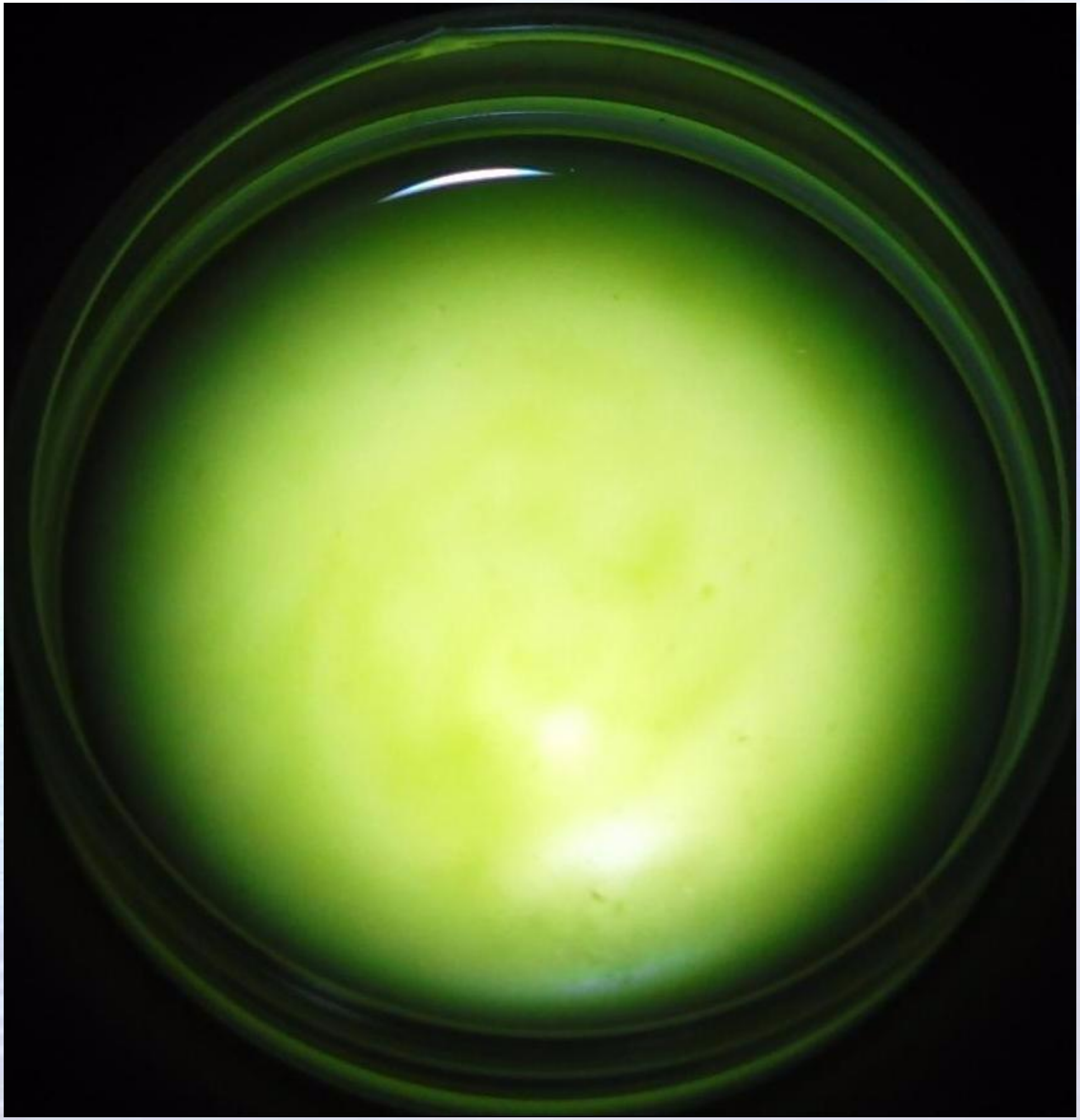
- **Macroscopic properties** of a suspension of micro-organisms
- Conclusions



Bio-convection

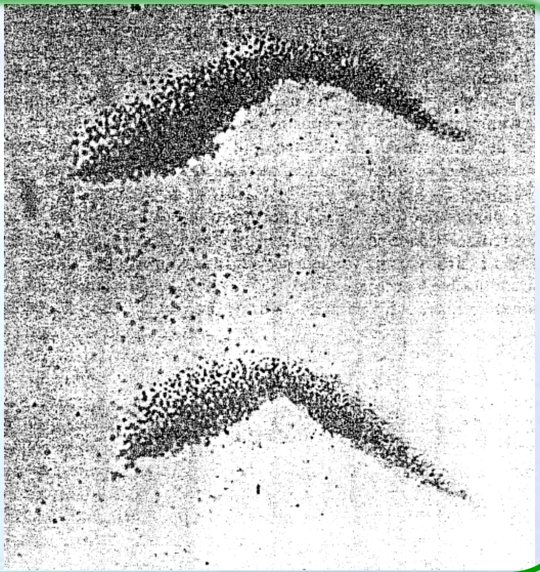


A suspension of *Chlamydomonas*

Mechanism:
upswimming of cells that are slightly denser than water generates unstable density stratification which leads to overturning

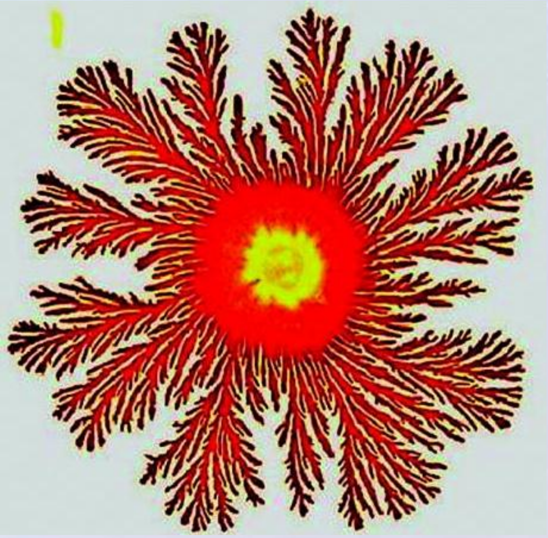
Other collective motions

Band formation



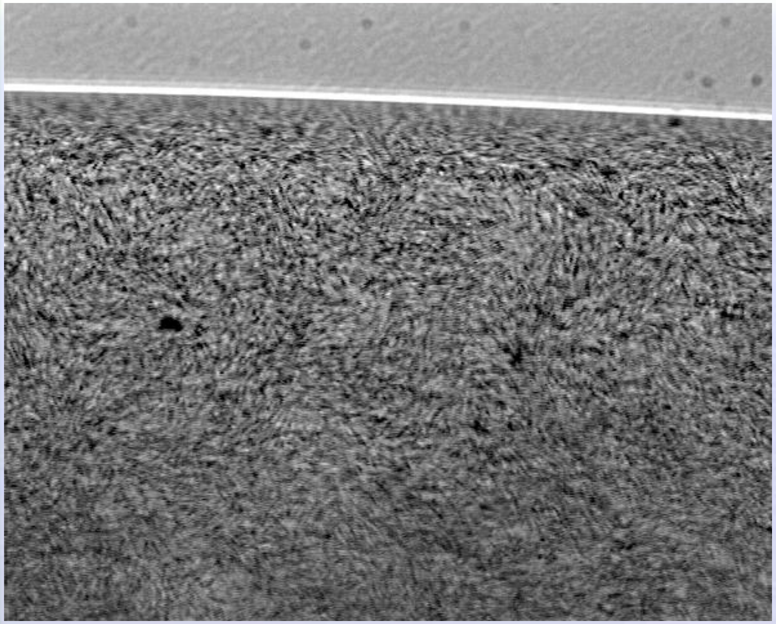
Band formation of magnetotactic bacteria. Picture from Guell *et al*., *J. Theor. Biol*. (1988)

Colonies on agar gel



Complex patten of bacterial colonies. Picture from Ben-Jacob & Levine (2006)

Slow turbulence



Cell motions of *Bacillus subtilis*. Movie from Goldstein Lab,

Mechanism
= Physics? Mechanics?

Stokesian-dynamics simulation

Micro-organism : Spherical squirmer model

Multipole Expansion of the boundary integral equation

$$u_i(\mathbf{x}) - \langle u_i(\mathbf{x}) \rangle = -\frac{1}{8\pi\mu} \sum_{\alpha=1}^{N} \int_{A_\alpha} J_{ij}(\mathbf{x}-\mathbf{y}) q_j(\mathbf{y}) dA_y \quad : \textit{Ewald sumation}$$

$$= \frac{1}{8\pi\mu} \left[\left(1 + \frac{a^2}{6}\nabla^2\right) J_{ij} F_j^\alpha + R_{ij} L_j^\alpha + \left(1 + \frac{a^2}{10}\nabla^2\right) K_{ijk} S_{jk}^\alpha + \nabla_k \nabla_l J_{ij} Q_{klj}^\alpha + \cdots \right]$$

+

Faxen Laws

$$U_i^\alpha - \langle u_i(\mathbf{x}^\alpha) \rangle = \frac{F_i^\alpha}{6\pi\mu a} + \frac{2}{3} B_1^\alpha e_i^\alpha + \left(1 + \frac{a^2}{6}\nabla^2\right) u_i'(\mathbf{x}^\alpha)$$

$$\Omega_i^\alpha - \langle \omega_i(\mathbf{x}^\alpha) \rangle = \frac{L_i^\alpha}{8\pi\mu a^3} + \frac{1}{2} \varepsilon_{ijk} \nabla_j u_k'(\mathbf{x}^\alpha)$$

$$-\langle E_{ij}(\mathbf{x}^\alpha) \rangle = \frac{S_{ij}^\alpha}{\frac{20}{3}\pi\mu a^3} + \frac{1}{5}\mu a^2 B_2^\alpha \left(3 e_i^\alpha e_j^\alpha - \delta_{ij}\right) + \frac{1}{2}\left(1 + \frac{a^2}{10}\nabla^2\right)\left(\nabla_j u_i'(\mathbf{x}^\alpha) + \nabla_i u_j'(\mathbf{x}^\alpha)\right)$$

Ishikawa *et al.*, *J. Fluid Mech.* (2008)

Stokesian-dynamics simulation

Then, inclusion of near-field lubrication forces

$$\begin{pmatrix} \mathbf{F} \\ \mathbf{L} \\ \mathbf{S} \end{pmatrix} = \left[\mathbf{R}^{far} - \mathbf{R}_{2B}^{far} + \mathbf{R}_{2B}^{near} \right] \begin{pmatrix} \mathbf{U} - \langle \mathbf{u} \rangle \\ \mathbf{\Omega} - \langle \boldsymbol{\omega} \rangle \\ -\langle \mathbf{E} \rangle \end{pmatrix} + \left[\mathbf{R}^{far} - \mathbf{R}_{2B}^{far} \right] \begin{pmatrix} -\frac{2}{3} B_1 \mathbf{e} + \mathbf{Q}_{sq} \\ 0 \\ -\frac{1}{5} B_2 \left(3\mathbf{ee} - \mathbf{I} \right) \end{pmatrix} + \begin{pmatrix} \mathbf{F}_{sq}^{near} \\ \mathbf{L}_{sq}^{near} \\ \mathbf{S}_{sq}^{near} \end{pmatrix}$$

Database compiled by BEM

Effect of squirming motion

cf. Brady & Bossis, *Annu. Rev. Fluid Mech*. (1988)

For details : Ishikawa *et al.*, *J. Fluid Mech.* (2008)

Results: Aggregation

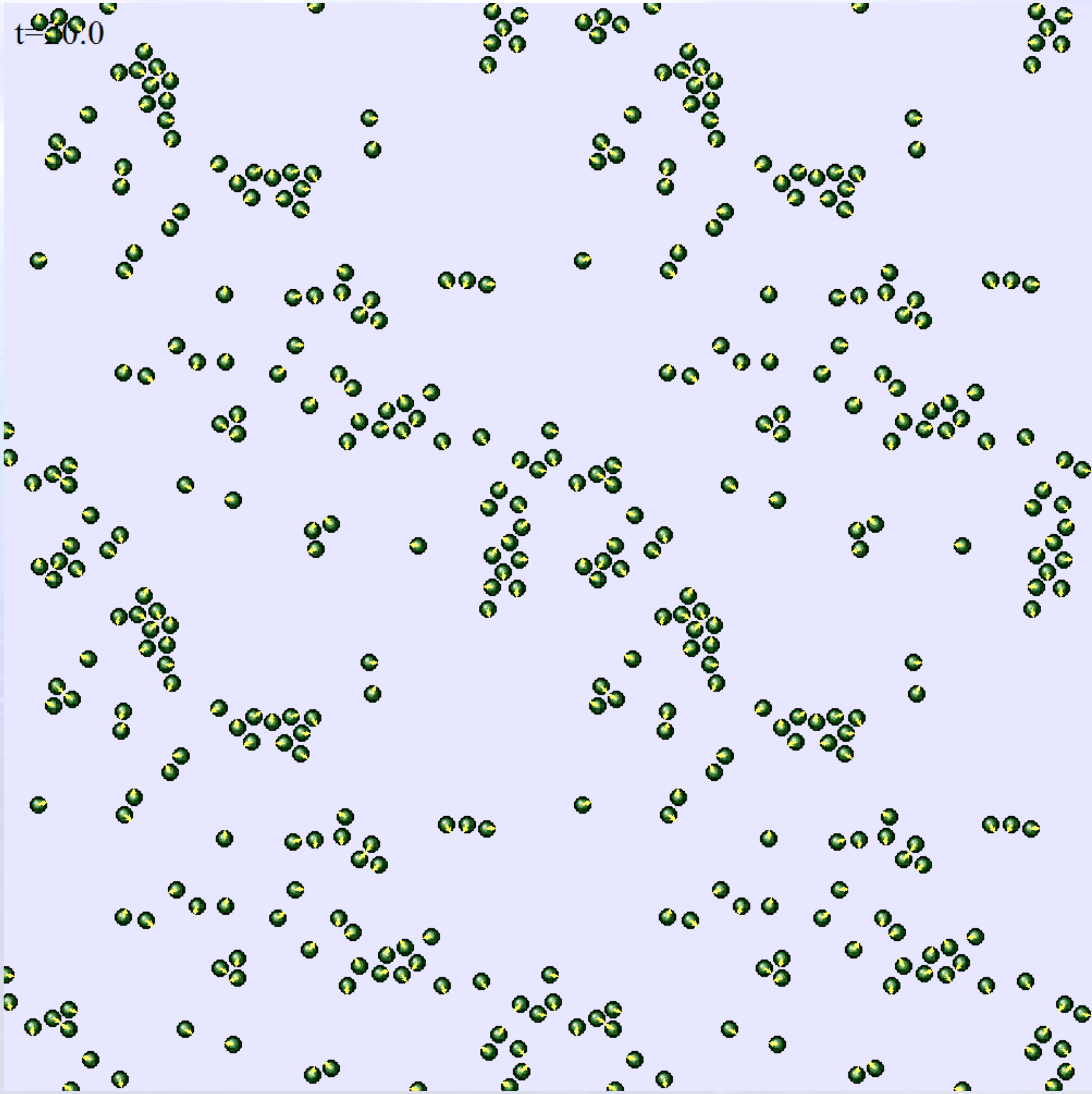
Monolayer

Non-bottom-heavy

ϕ_a=0.1

Periodic B.C.

Hydrodynamic interaction only



Ishikawa & Pedley
Phys. Rev. Lett. (2008)

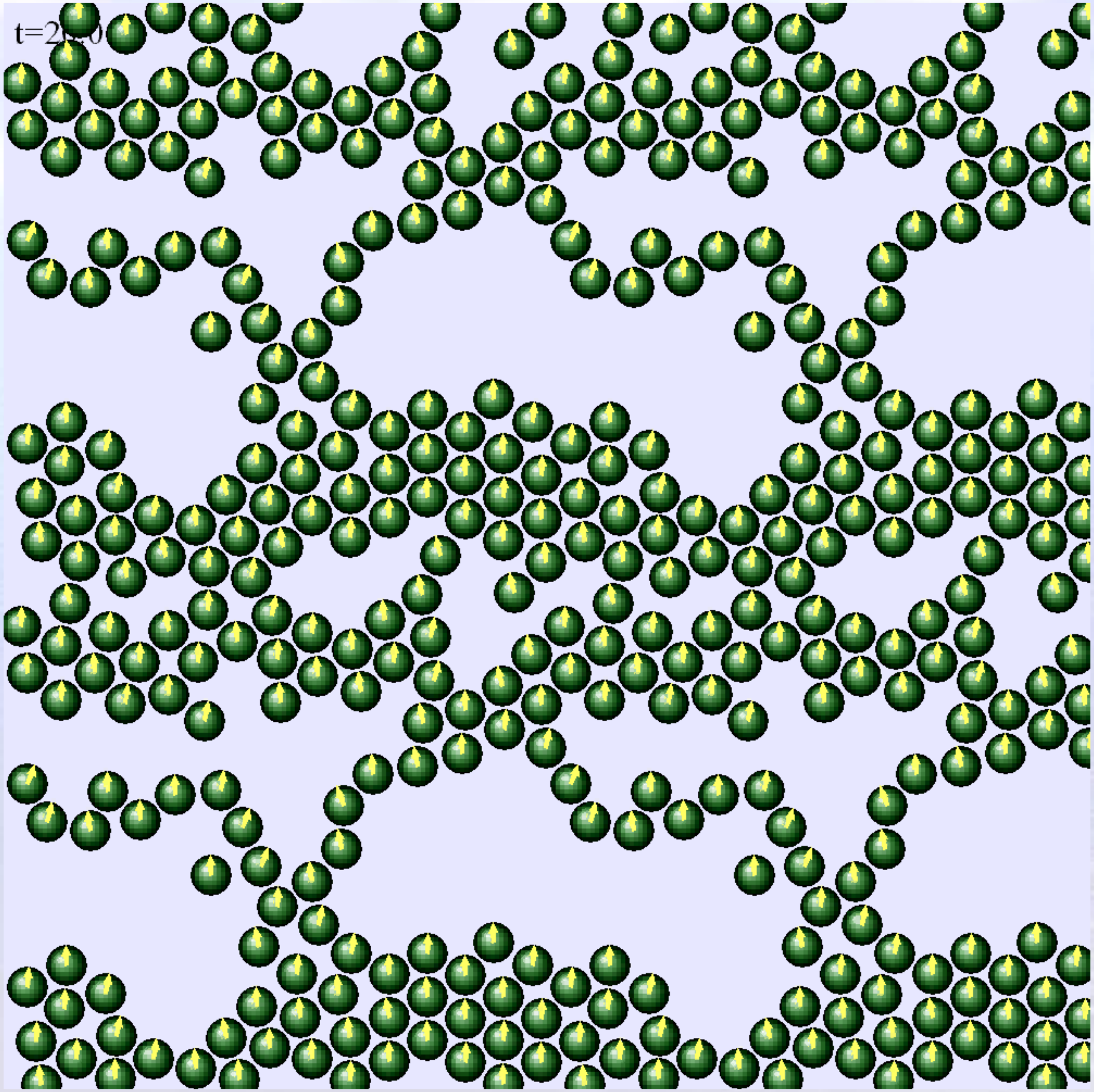
Results: Band formation

Monolayer

Bottom-heavy

ϕ_a=0.5, G_{bh} =100

$$G_{bh} = \frac{2\pi\rho g a h}{\mu B_1}$$

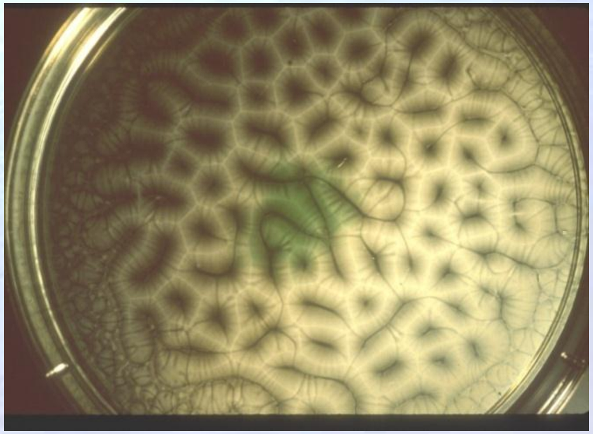


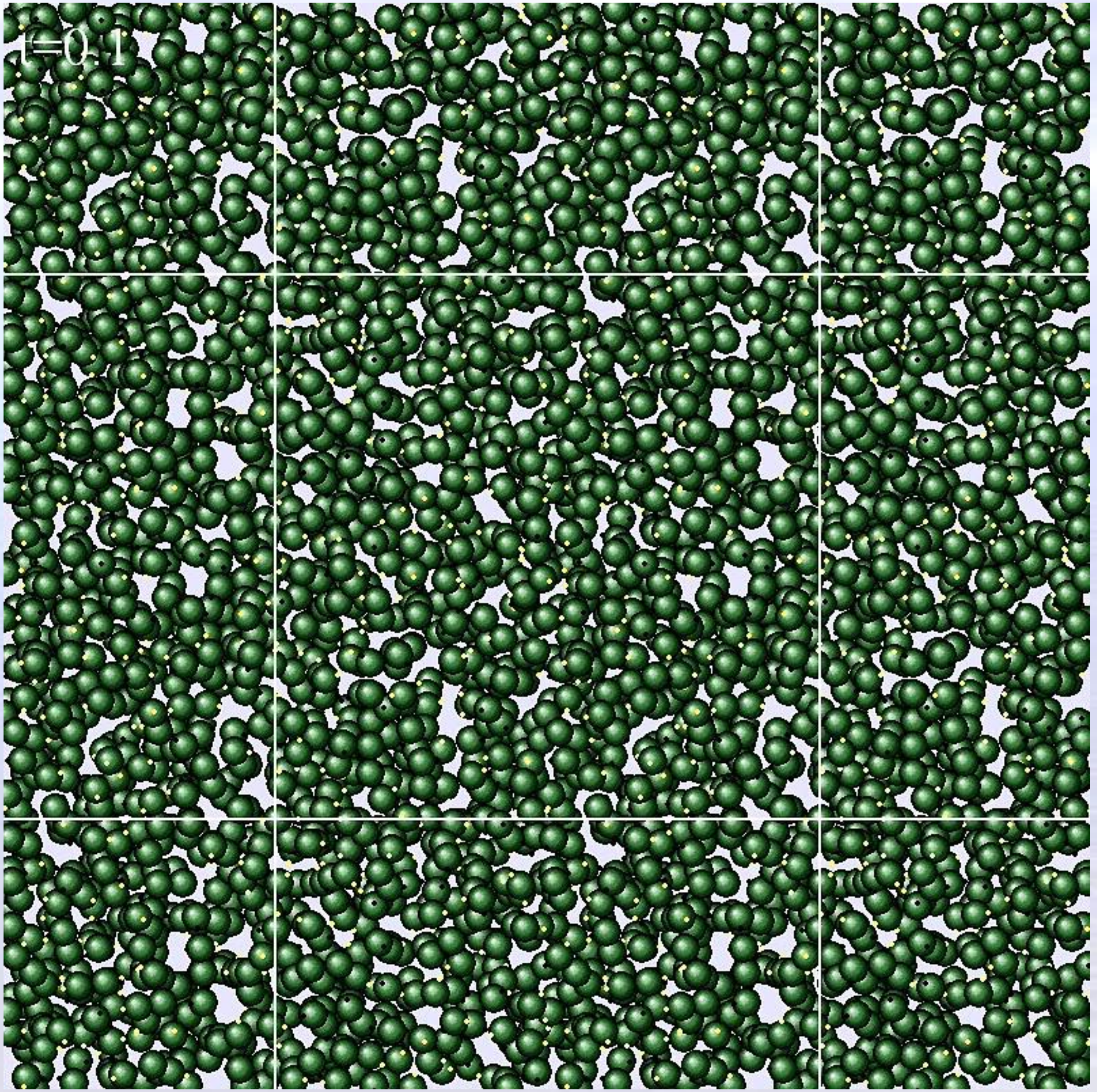
Ishikawa & Pedley
Phys. Rev. Lett. (2008)

Results: 3D Large scale

Bioconvection

Bottom-Heavy
Sedimentation
Periodic B.C.

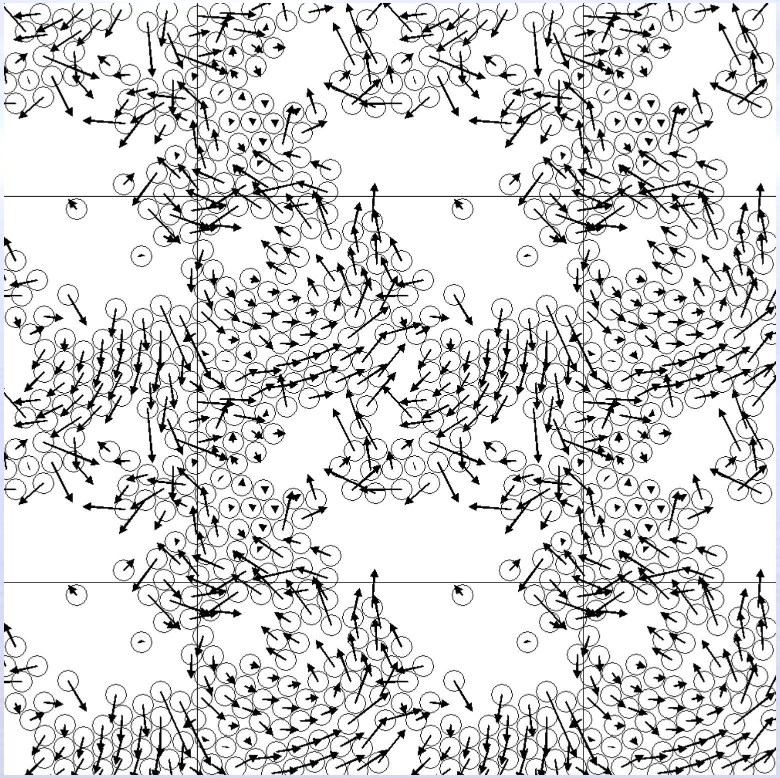




Coherent structures

Various collective motions observed in former experiments can be expressed

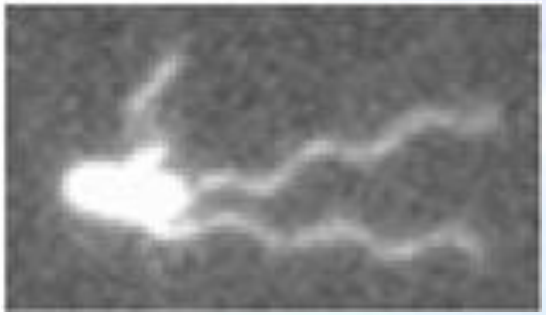
- Meso-scale spatiotemporal motion
- Ordered motion



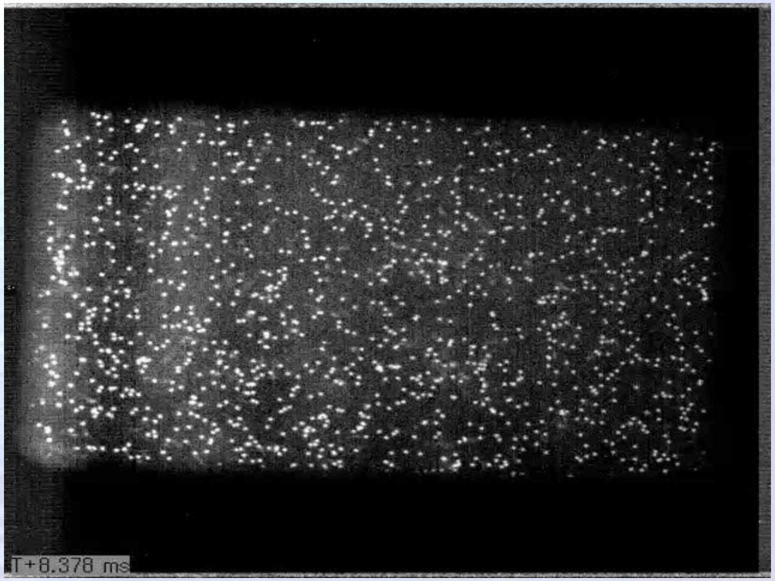
How coherent structures affect transport phenomena?

- Diffusion of particles Wu & Libchaber (2000)
- Energy is transported towards larger scale?

Energy transport in a bacterial bath

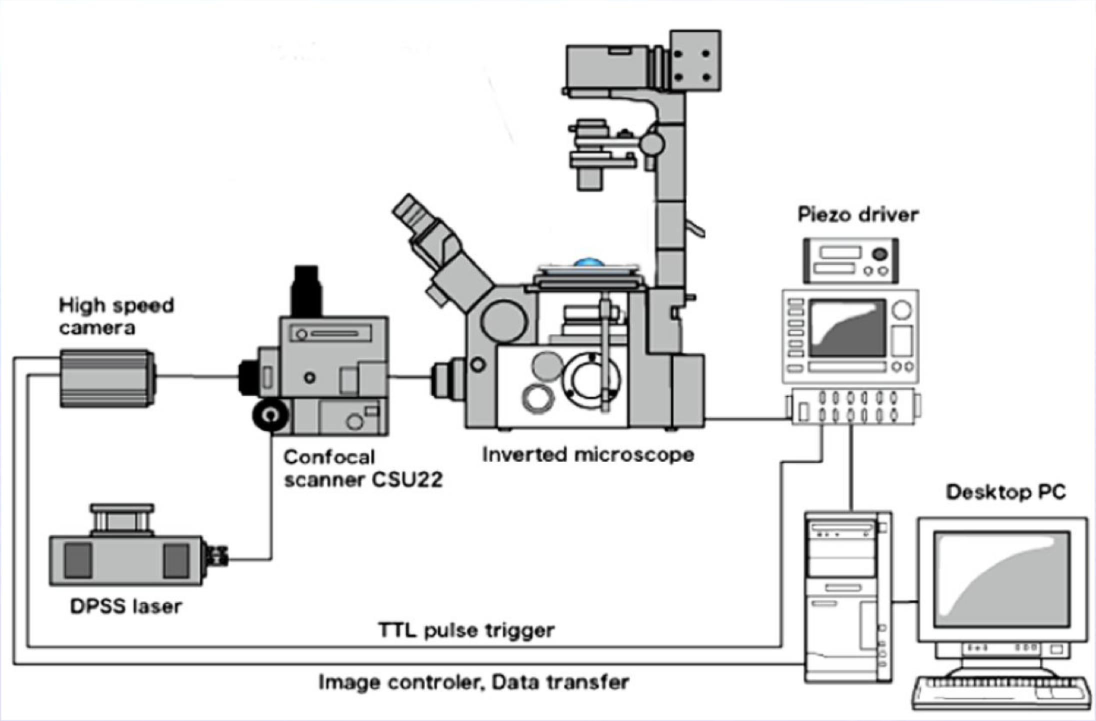


E. coli : MG1655 (wildtype)



Sample confocal image

Confocal μPIV system



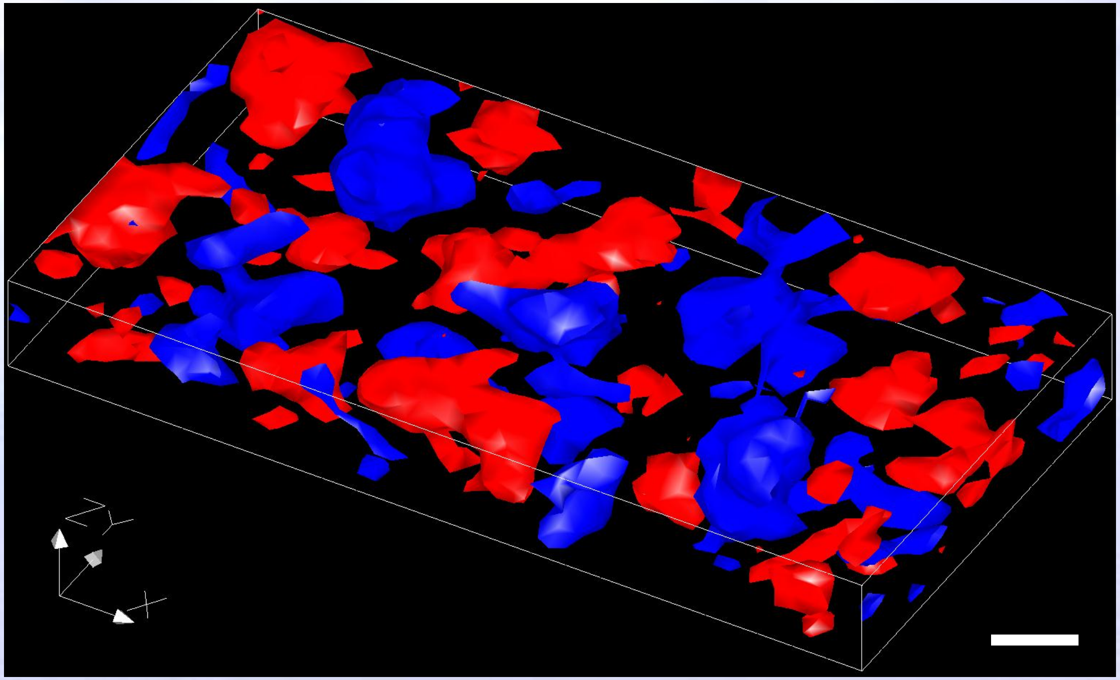
Lima, *et al.*, *Meas. Sci. Technol*. (2006)

3D velocity field can be measured with high spacial and time resolutions

Energy transport in a bacterial bath

In-plane vorticity

Iso-surfaces of Ω_z = 1.3 and -1.3 s^{-1} are drawn by red and blue, respectively.



Energy dissipation on meso-scale

$$\nu\,|\mathrm{rot}\,\mathbf{v}|^2 \approx 5 \times 10^{-9}\ \mathrm{J/(s.mL)}$$

/ number density of 3×10^{10}

= individual bacteria dissipate energy of 2×10^{-19} J/(s.cell) on the meso-scale.

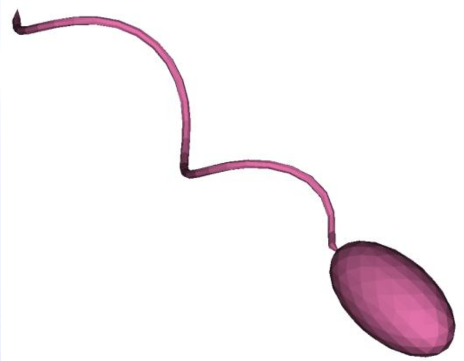
Is this a large portion of energy input?

Energy transport in a bacterial bath

Energy dissipation of a solitary bacteria

BEM model

Cell body: ellipsoid (2 × 1 μm)
Flagella length: 6 μm
Swimming velocity: 20 μm/s



Giacche *et al.*, *PRE* (2010)

Energy input: 4×10^{-16} J/s

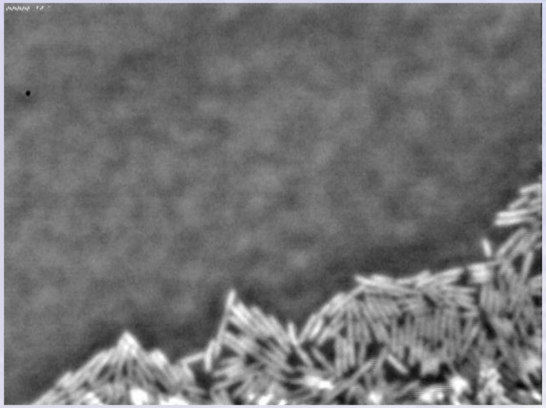
Used for swimming: 7×10^{-18} J/s (=0.36pN × 20μm/s)

Used for the coherent structure: 2×10^{-19} J/s

Gain from the coherent structure:

- Enhanced diffusion
- High swimming velocity

→ Useful to expand the biosphere?



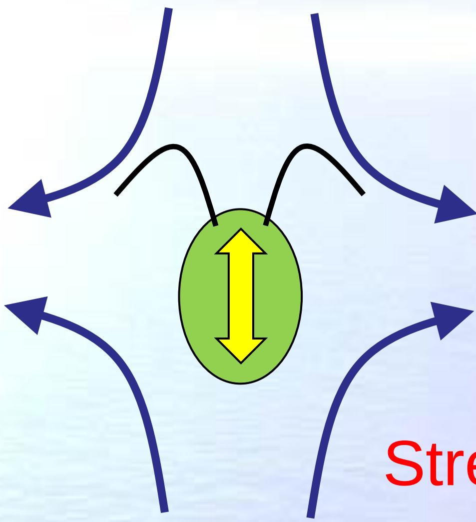
Ishikawa, *et al.*, *Phys. Rev. Lett.* (2011)

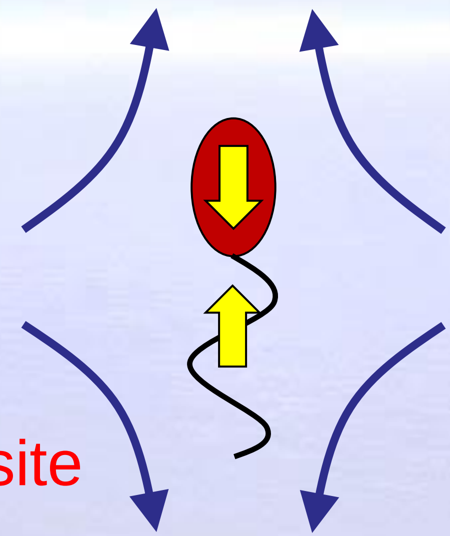
Outline of the talk

- Introduction
- Biomechanics of an **individual** and a **pair** of micro-organisms
- **Collective swimming** in meso-scale
- **Macroscopic properties** of a suspension of micro-organisms
- Conclusions

Rheological properties

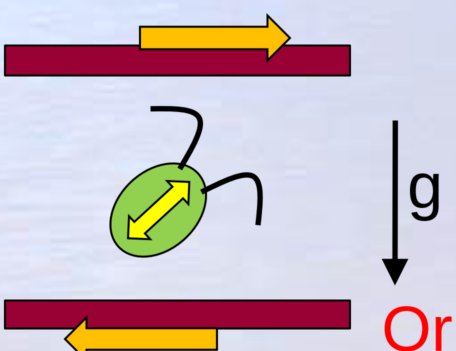
Stress field generated by a solitary cell

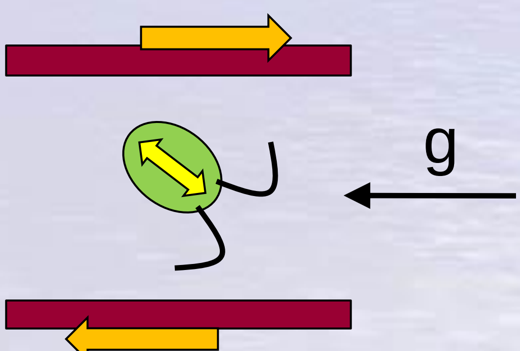




Stress field is opposite

A bottom-heavy cell in a shear flow

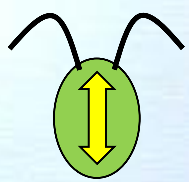
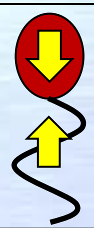




Orientation changes

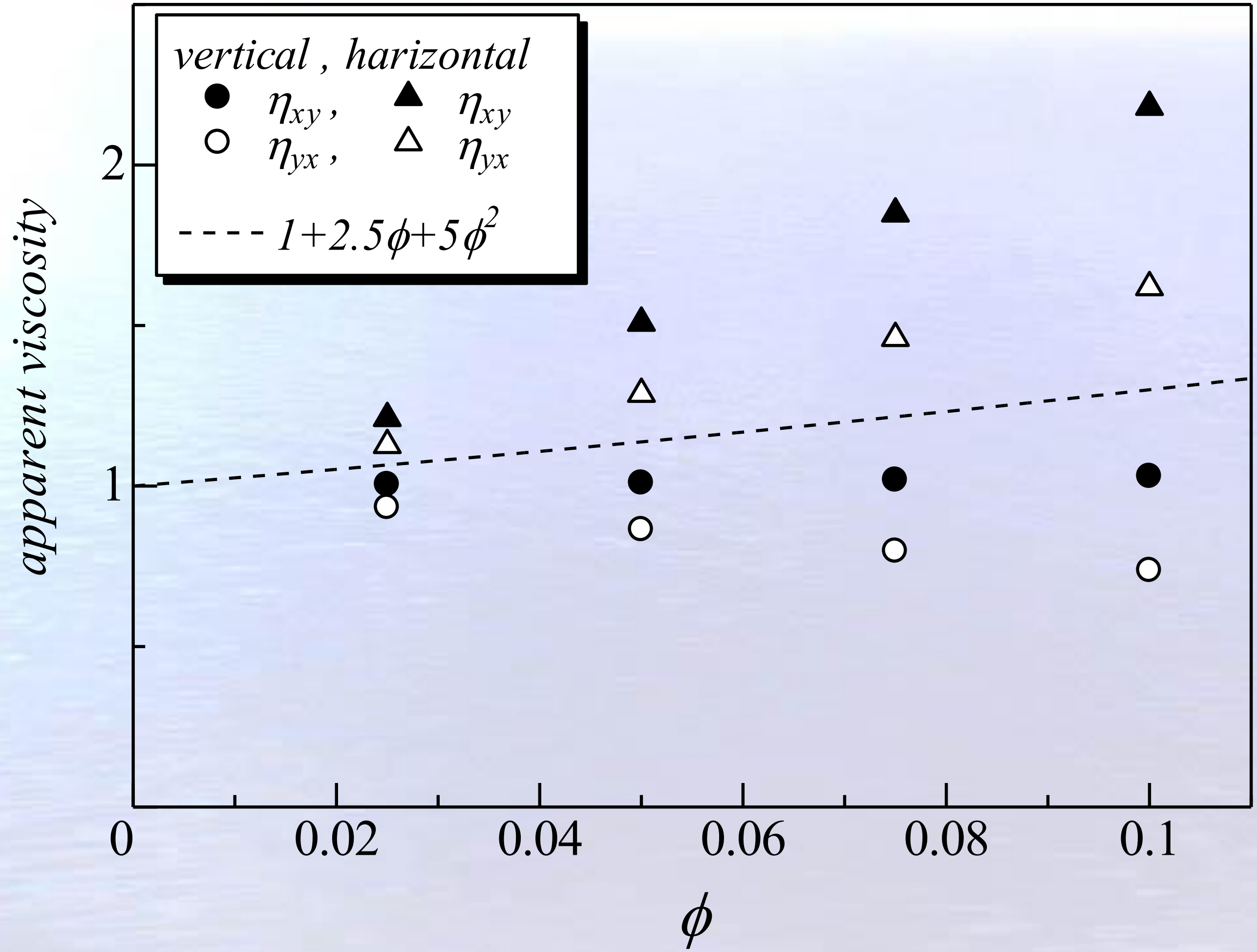
Rheological properties

Shear viscosity (compared to dead cell suspensions)

	Horizontal shear	Vertical shear
	Increase	Decrease
	Decrease	Increase

Rheological properties

Shear viscosity : Suspension of Squirmers

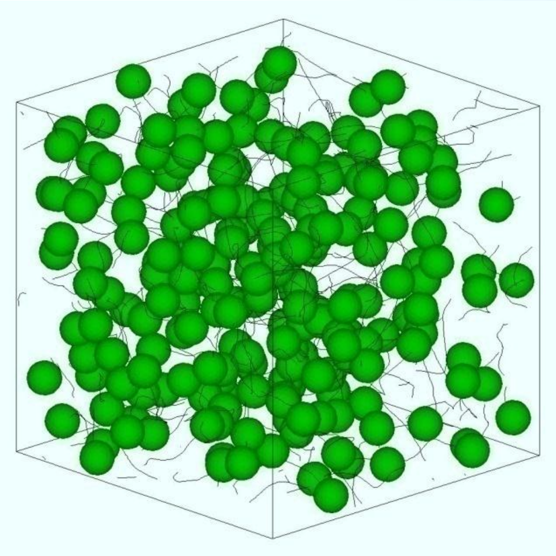


Ishikawa & Pedley, *J. Fluid Mech*. (2007)

Diffusion properties

Cell Conservation (continuum model)

$$\frac{Dn}{Dt} = -\nabla \cdot \left(n\mathbf{V}_c + \mathbf{J}_r \right) \quad \text{[+ birth, death, etc]}$$



where $\mathbf{V}_c$ = mean cell swimming velocity,

$\mathbf{J}_\mathrm{r}$ = flux due to random cell swimming

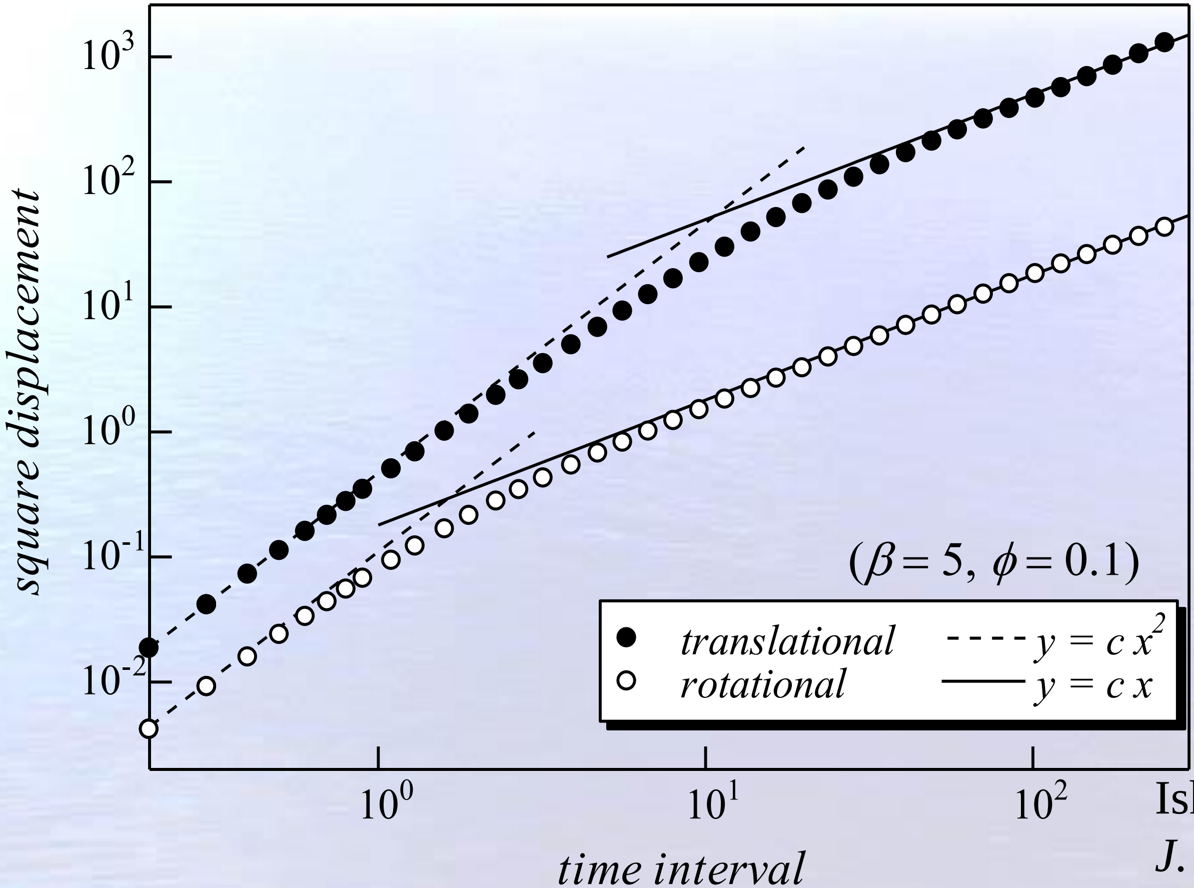
$$\mathbf{J}_r = -\mathbf{D} \cdot \nabla n \;\; ?$$

Definition of **D**

$$\mathbf{D} = \lim_{t \to \infty} \frac{\left\langle \left[\mathbf{r}(t+t_0) - \mathbf{r}(t_0) \right] \left[\mathbf{r}(t+t_0) - \mathbf{r}(t_0) \right] \right\rangle}{2t}$$

Diffusion properties

Self-diffusion of cells

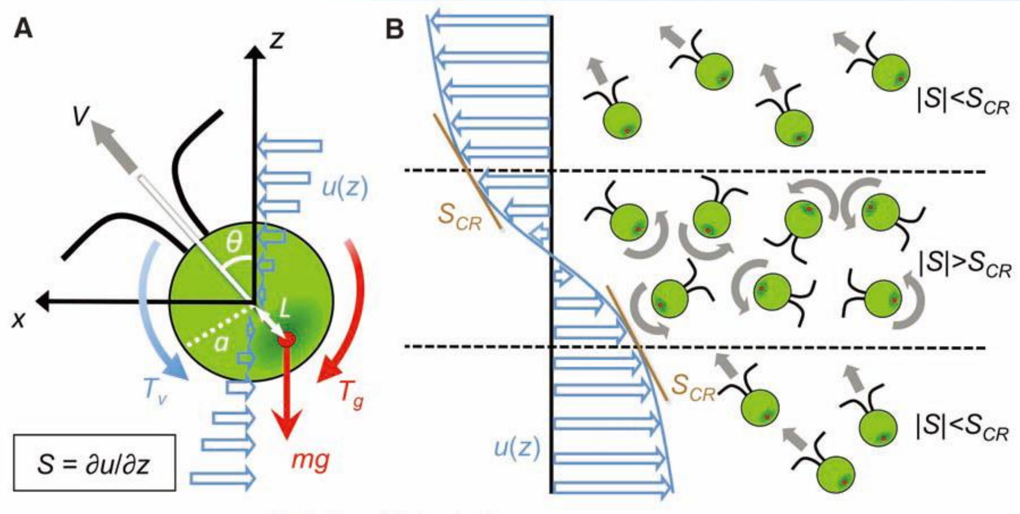


Ishikawa & Pedley, *J. Fluid Mech.* (2007)

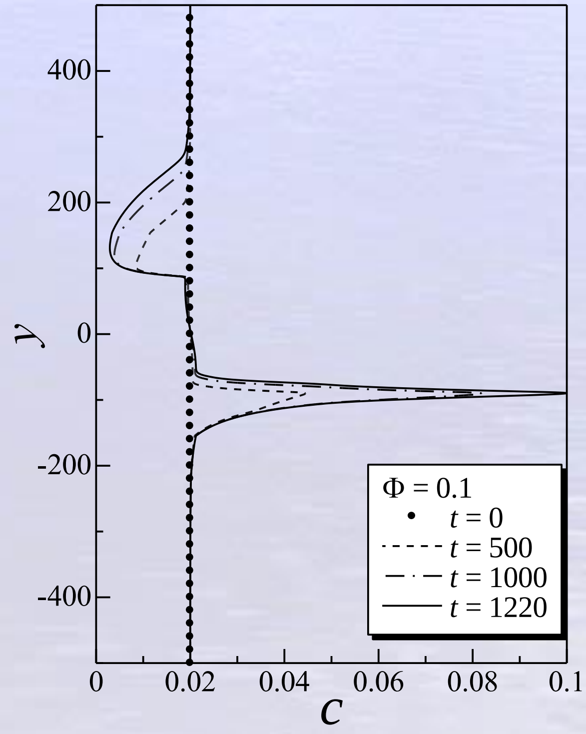
The spreading is correctly described as a diffusive process

Large Scale Example in Nature

Thin layers of plankton are important hotspots of ecological activity



Durham *et al.*, *Science* (2009)



Continuum model:

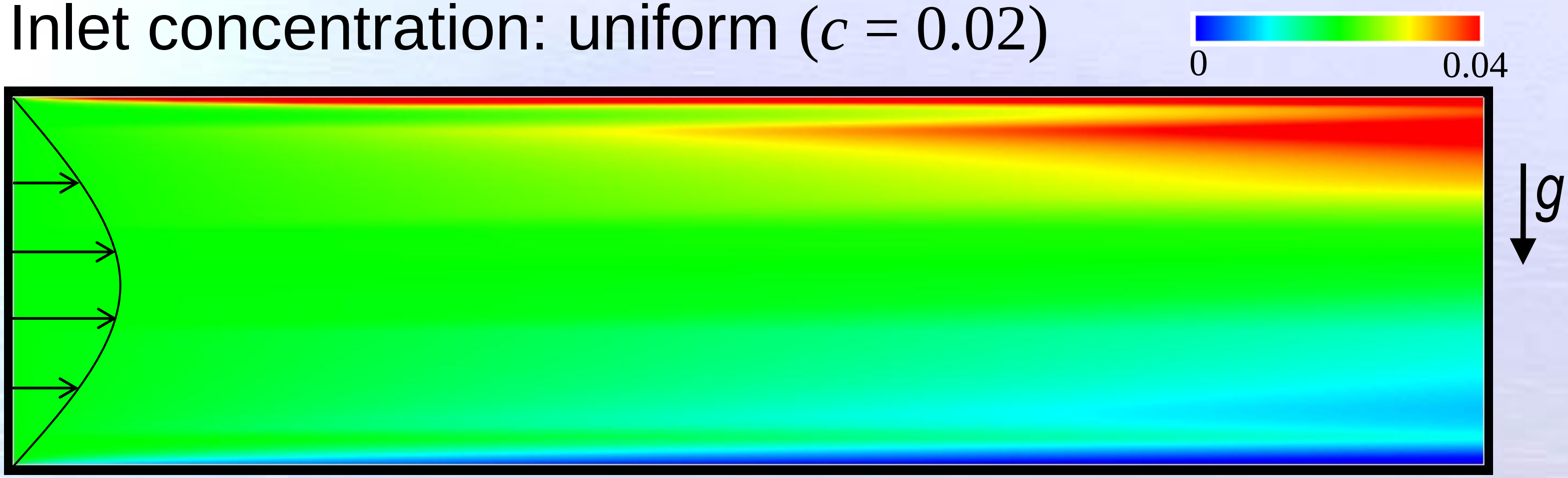
$$\frac{\partial c}{\partial t} = -\nabla.\left[\left(\mathbf{V}+\mathbf{U}_d\right)c\right] + \nabla.\left[\mathbf{D}.\nabla c\right]$$

Thin layer is also formed in this system.

Horizontal Poiseuille Flow

Engineering settings: Horizontal Poiseuille flow

Flow: 2D, parabolic
Cells: Bottom-heavy squirmers
Inlet concentration: uniform ($c = 0.02$)



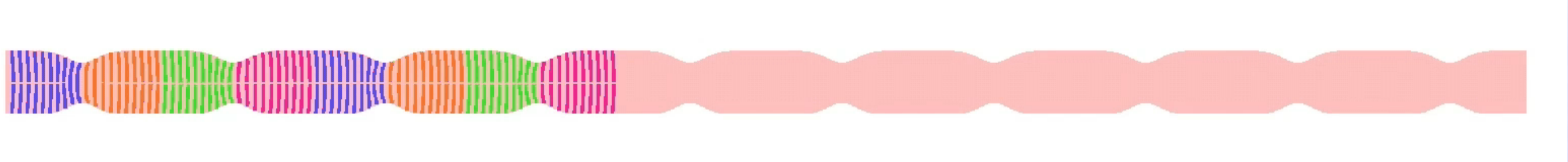
High concentration appears near the upper wall.

➡ Volume fraction of bottom-heavy cells in the channel becomes larger than that at the inlet.

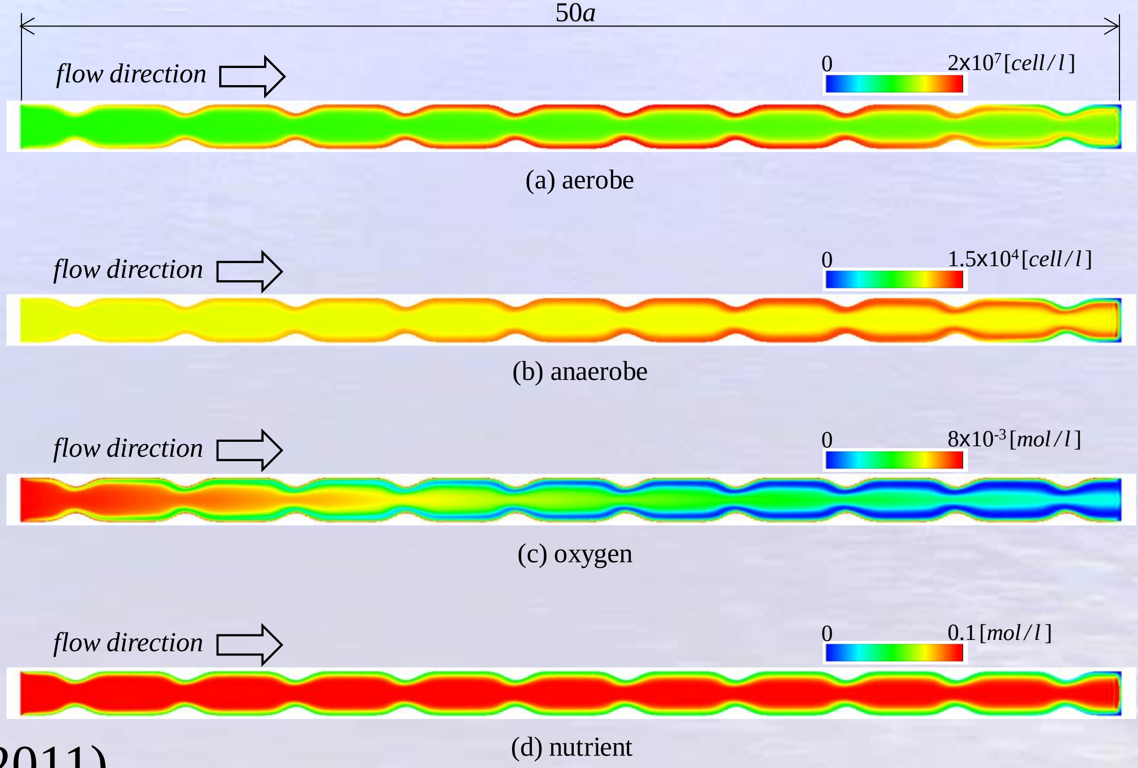
Ishikawa, *J. Fluid Mech*. (2012)

Applications: Population dynamics

Microbial flora in the intestine



Simultaneously solving:
- Flow field generated by peristalsis
- Concentrations of oxygen and nutrient
- Densities of anaerobes and aerobes



Ishikawa *et al.*, *J. Theor. Biol.* (2011)

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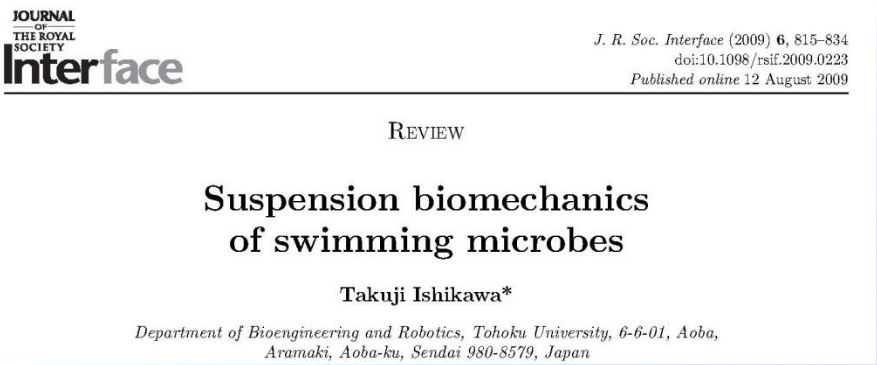
Conclusions

Physiological Flow Studies Laboratory TOHOKU UNIVERSITY

By using the bottom-up strategy, suspension biomechanics of swimming microbes can be clarified much further.


JOURNAL OF THE ROYAL SOCIETY Interface

J. R. Soc. Interface (2009) 6, 815–834
doi:10.1098/rsif.2009.0223
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REVIEW

Suspension biomechanics of swimming microbes

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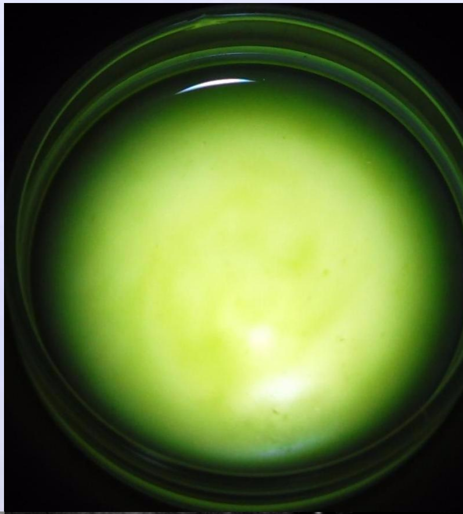
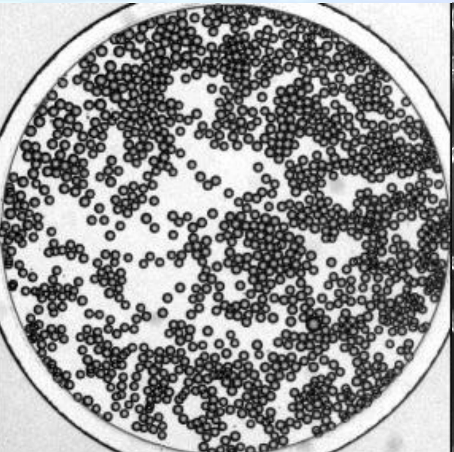
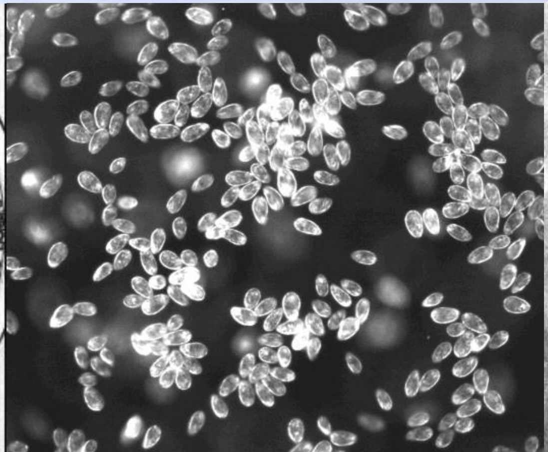
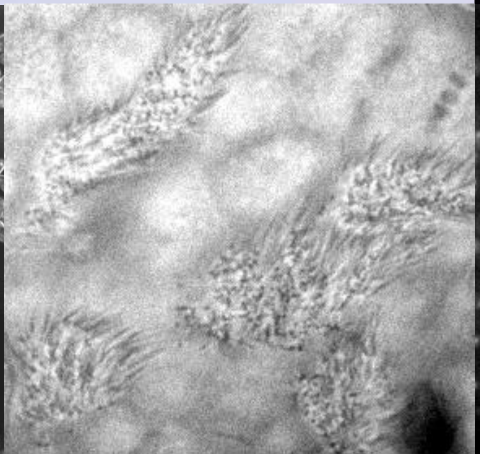
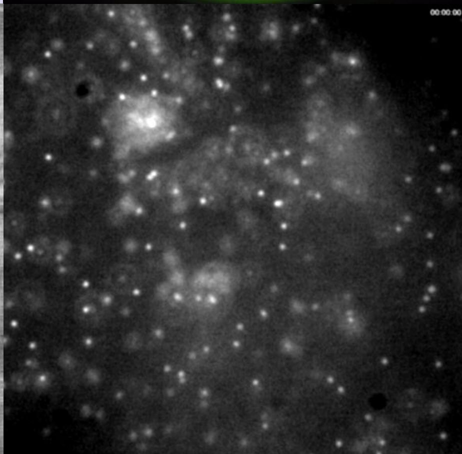


Such mathematical modeling should be expanded to various phenomena in nature.









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Lab members

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Thank you for your listening