

## A black and white comic panel. In the upper right, a stick figure is shown in mid-air, falling or flying. A speech bubble next to it says "BASILISK!". In the lower left, another stick figure stands on the ground, looking up and asking "YOU'RE FLYING! HOW?". The background is filled with dense, diagonal hatching lines, suggesting a dark, stormy sky. A small, dark, spiky tree or bush is visible on the ground in the lower right.

francesco.picella@sorbonne-universite.fr

The comic strip consists of three panels, each with a stick figure character.

- Panel 1:** The stick figure is shown from the back, looking down at the ground. The text reads: "I LEARNED IT LAST NIGHT! EVERYTHING IS SO SIMPLE!" Below this, the code `hello world is just printf(stderr, "hello world \n");` is written.
- Panel 2:** The stick figure is standing upright and looking forward. The text reads: "I DUNNO... darcs, MACROS... and the BVIEW thing!" Below this, the stick figure says: "COME JOIN US! PROGRAMMING IS FUN AGAIN! IT'S A WHOLE NEW WORLD UP HERE!" Below the figure, the text reads: "BUT HOW ARE YOU FLYING?"
- Panel 3:** The stick figure is standing upright. The text reads: "I JUST TYPED basilisk.fr/sandbox/Antoonvh/README THAT'S IT?" Below this, the stick figure says: "... I ALSO SAMPLED EVERYTHING IN THE MEDICINE CABINET FOR COMPARISON." Below the figure, the text reads: "BUT I THINK THIS IS THE **BASILISK**"

# BGUM - Oxford - July 2025

comic adapted from [xkcd.com](http://xkcd.com)

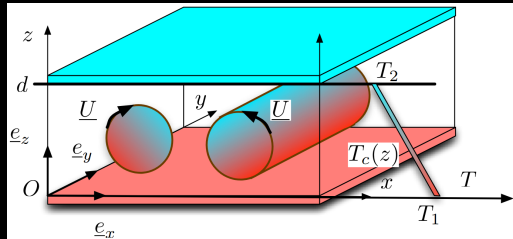
# Thermal-Convection

Passive fluid: external energy supply



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Passive fluid: external energy supply



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**Buoyancy-Driven** ( $T \propto \rho$ )  
i.e.: *Rayleigh-Bénard*

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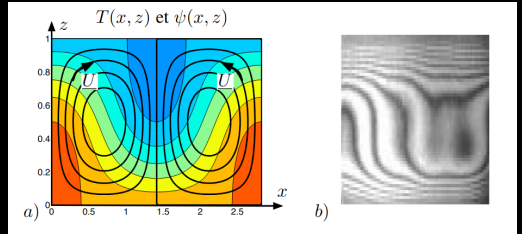
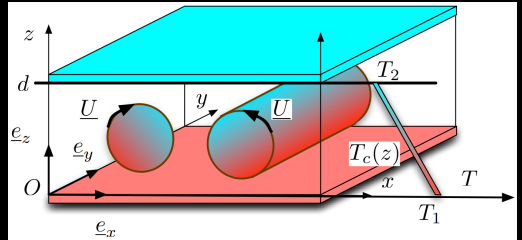
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Passive fluid: external energy supply



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downwelling, dense fluid → "plume"



Boussinesq 1903, Thuval 2020



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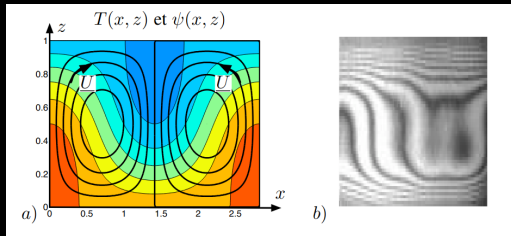
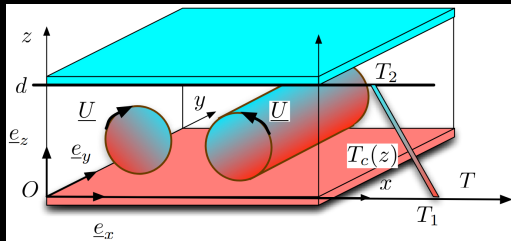
Passive fluid: external energy supply



All the spaghetti was eaten

**Buoyancy-Driven** ( $T \propto \rho$ )  
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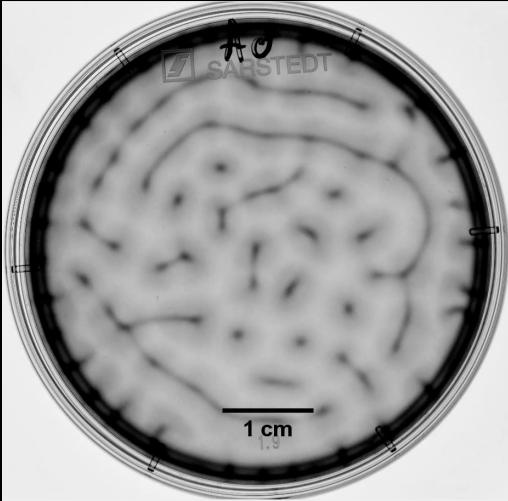
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# Bio-convection

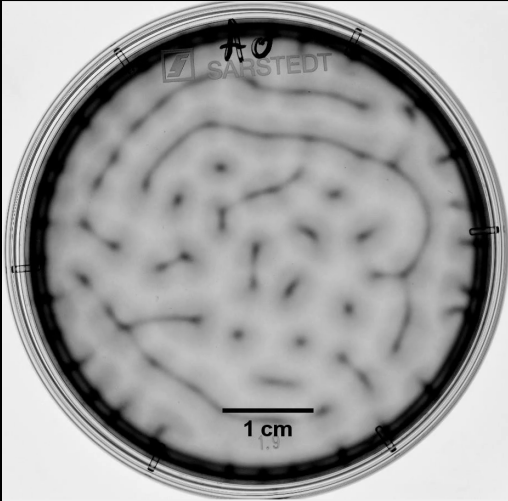
Active fluid: a colony of *Chlamydomonas Reinhardtii* (CR)



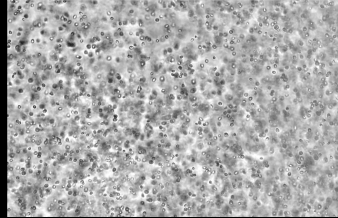
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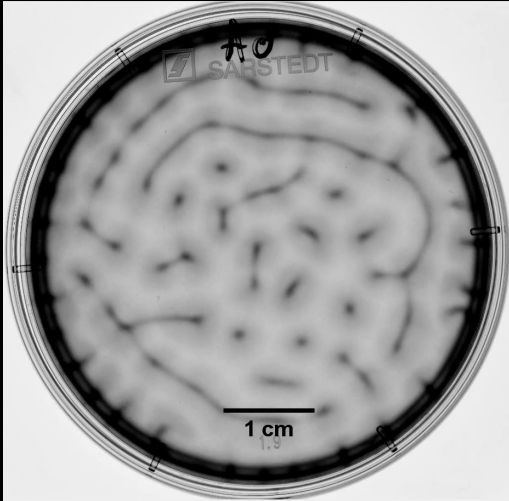
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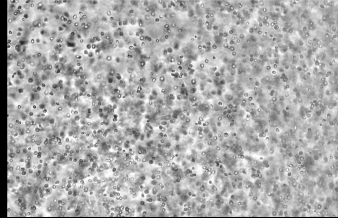
A. Givaudan, 2x. Window size 400 $\mu$ m

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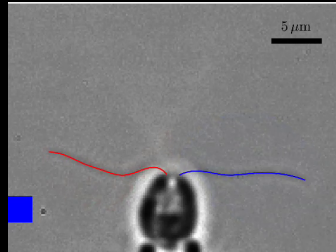
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A. Huygues-Despointes, 100x, top view



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Leptos *et al.* 2013, real time.

# Bio-convection, triggering mechanisms\*

(\*) Present state-of-the-art

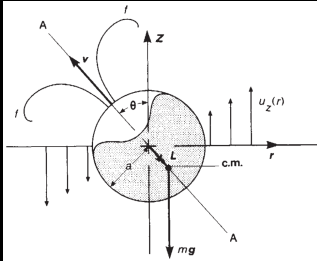
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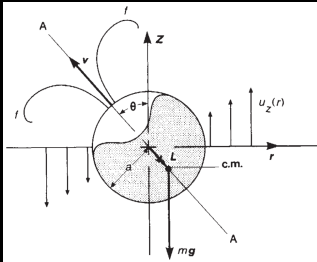


Kessler 1985

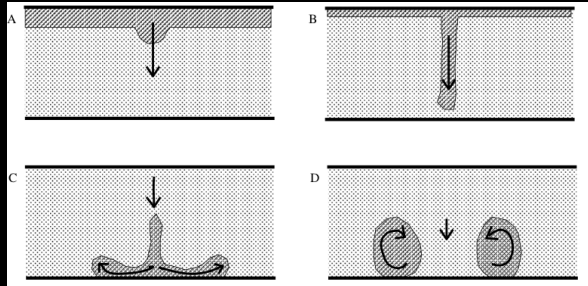
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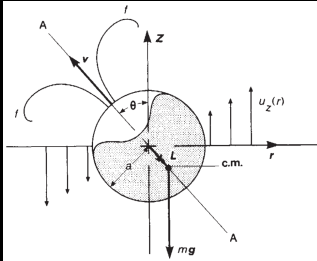


Bees & Hill 1997

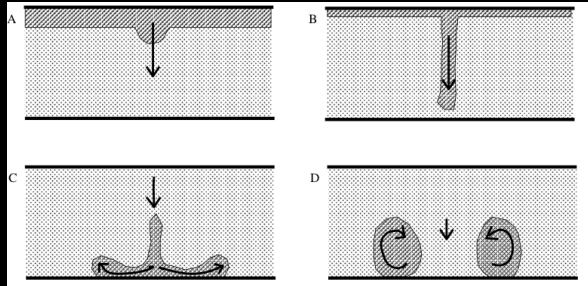
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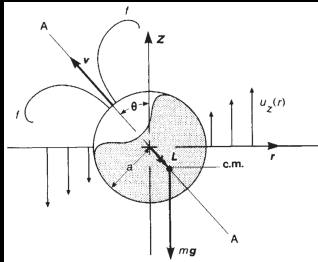
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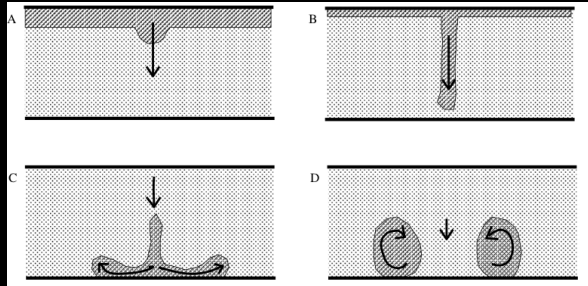
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4. **Plumes** impact the bottom, recirculation and rise of convection pattern.



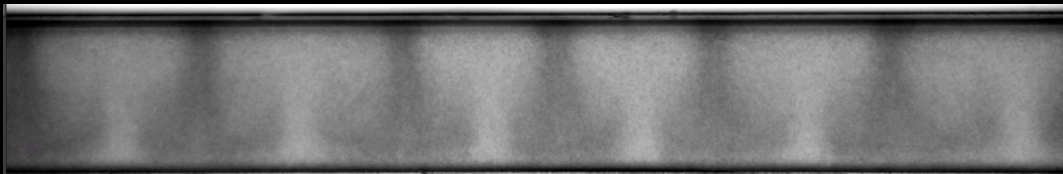
Kessler 1985



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## Experiments Are plumes *really* triggered by the *dense layer*?

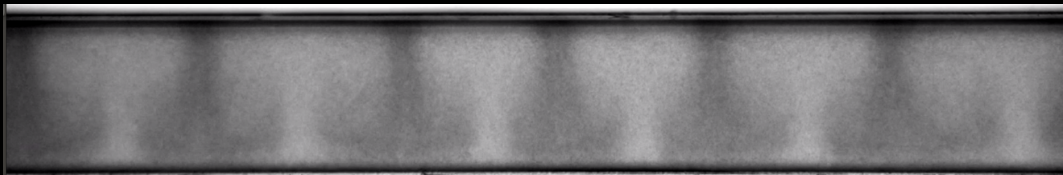
Dark spots (cell concentration) first occurring **far** from the dense layer?



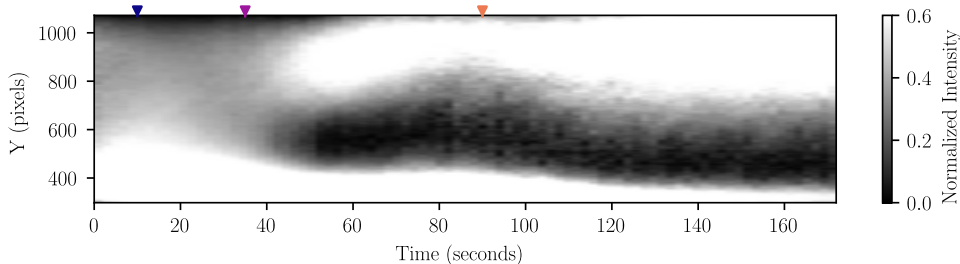
Side view. Height =  $1\text{mm}$ ,  $\Delta t = 2\text{s}$ , 10fps. Experiment by H. de Maleprade.

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Dark spots (cell concentration) first occurring **far** from the dense layer?



Side view. Height = 1mm,  $\Delta t = 2s$ , 10fps. Experiment by H. de Maleprade.



Spanwise-averaged intensity. Simultaneous dense layers forming at top and bulk

# Modelling bio-convection: a **microswimmer**-driven flow

**Agent-resolved**,  $Re \ll 1$

- ▶ **Fluid-Solid coupling:**  $\nabla \cdot \mathbf{u} = 0$ ,  $\nabla^2 \mathbf{u} = \nabla p$

# Modelling bio-convection: a **microswimmer**-driven flow

## Agent-resolved, $Re \ll 1$

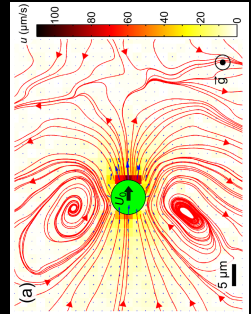
- ▶ **Fluid-Solid coupling:**  $\nabla \cdot \mathbf{u} = 0$ ,  $\nabla^2 \mathbf{u} = \nabla p$  + boundary conditions
  - ▶ *meshless* methods (e.g. **Stokesian Dynamics**, Ishikawa 2020, ...)

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## Modelling flagellate microswimmers



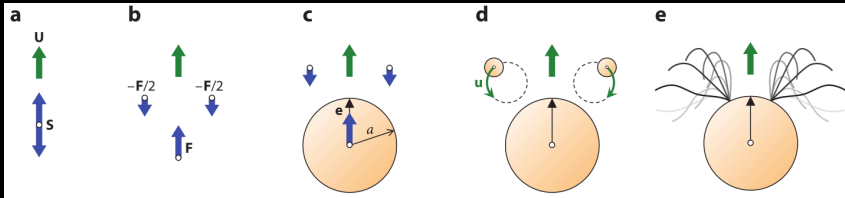
Time-averaged flow field around a biflagellate.  
Drescher *et al.* 2010.

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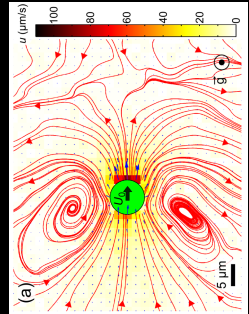
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## Modelling flagellate microswimmers

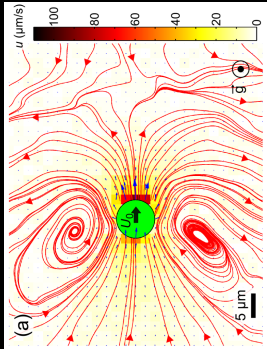


(a) Lushi & Peskin 2012, (b) Drescher *et al.* 2010, (c) Jibuti *et al.* 2014, (d) Wan *et al.* 2019, Friedrich & Julicher 2012. From Ishikawa 2024.



Time-averaged flow field around a biflagellate. Drescher *et al.* 2010.

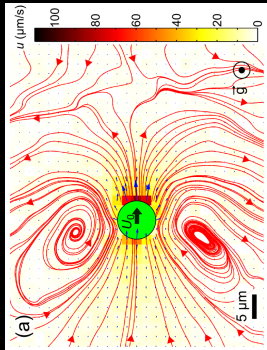
# Introducing the tHree model



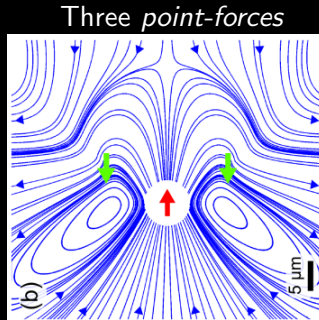
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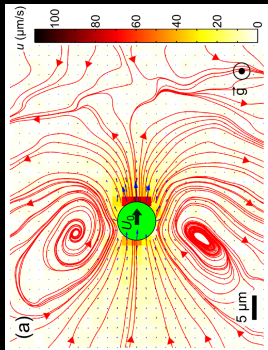


Drescher *et al.* 2010.

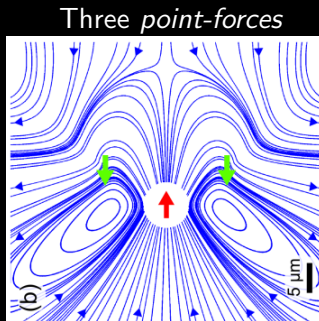


Drescher *et al.* 2010.

# Introducing the **tHree** model

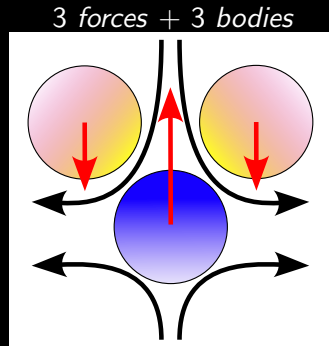


Drescher *et al.* 2010.



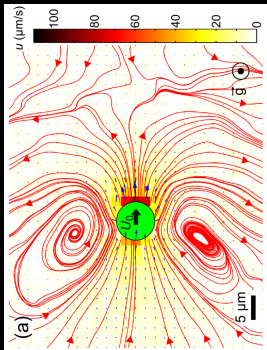
Three point-forces

Drescher *et al.* 2010.

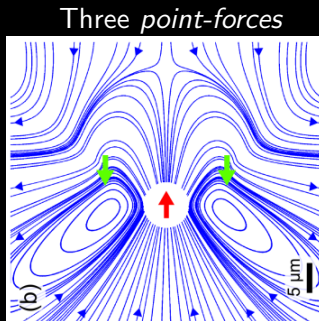


**tHree** model of a biflagellate puller.

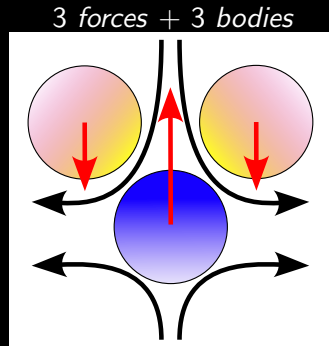
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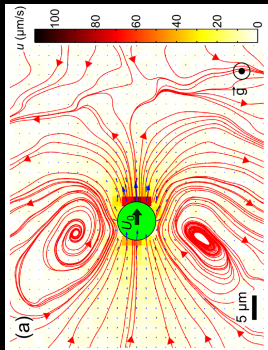
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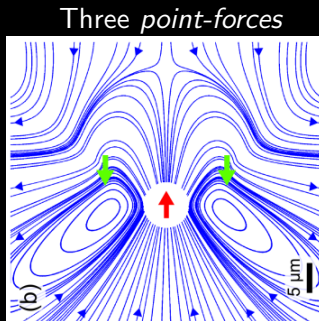
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Why still another model?

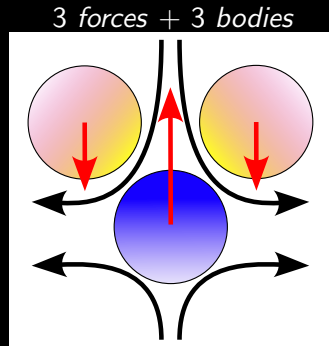
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Drescher *et al.* 2010.



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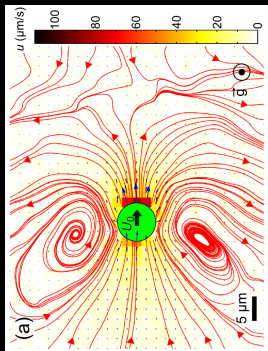


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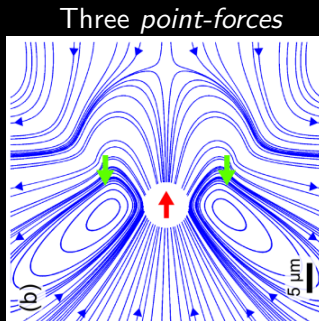
Why still another model?

- Same physical **model**, **compatible** with **multiple** resolution **methods/scales**

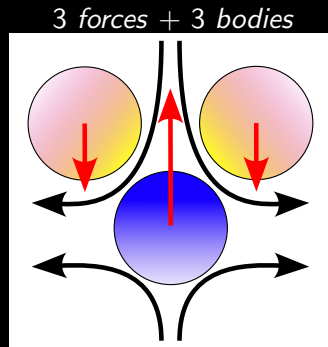
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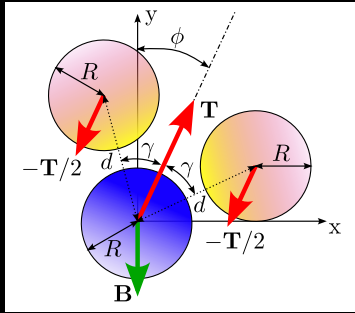
**tHree** model of a  
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## Why still another model?

- ▶ Same physical **model**, **compatible** with **multiple** resolution **methods/scales**
- ▶ Access to **complex physics** (confinement, light, non-linearities...)

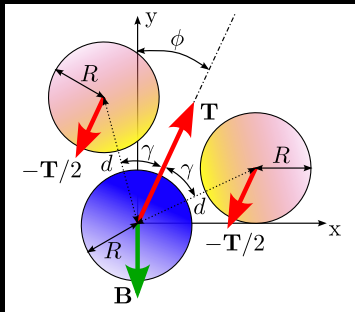
# Characterising tHree model. Single, force free swimmer's velocity $U$

A. Palotai 2025 internship.



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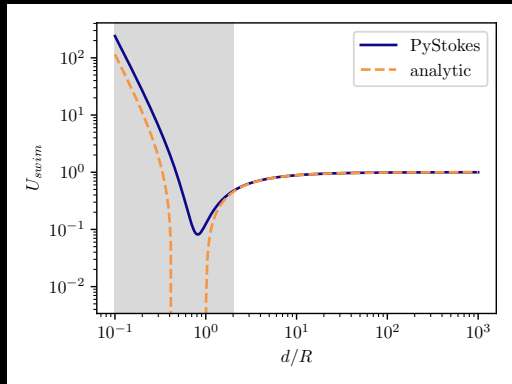
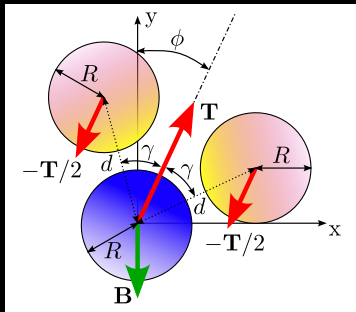
## Analytical solution

$$U = \frac{F}{6\pi\mu R} \left( 1 - \frac{3R \sin^2(\alpha)}{2d} - \frac{3R \cos^2(\alpha)}{4d} + \frac{R^3 \sin^2(\alpha)}{2d^3} - \frac{R^3 \cos^2(\alpha)}{4d^3} \right)$$

following Kim & Karilla 1991

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## Analytical solution

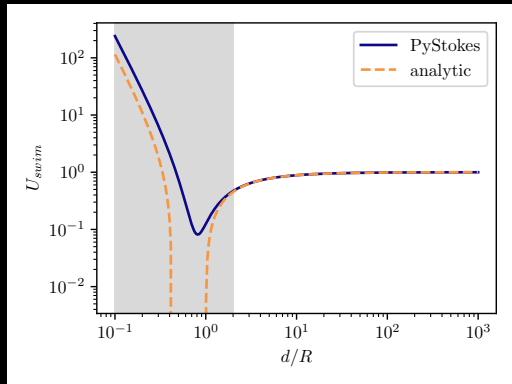
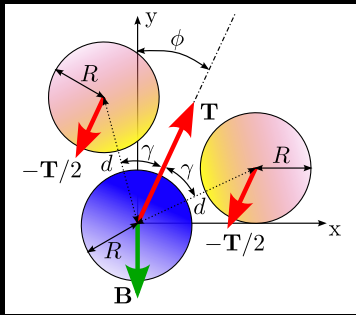
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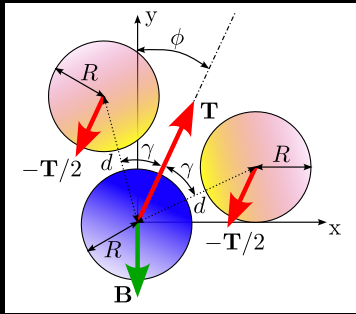
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- Numerical validation with Stokesian Dynamics  
<https://github.com/rajeshrinet/pystokes>

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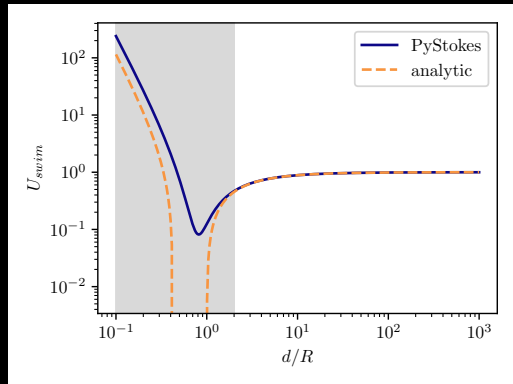
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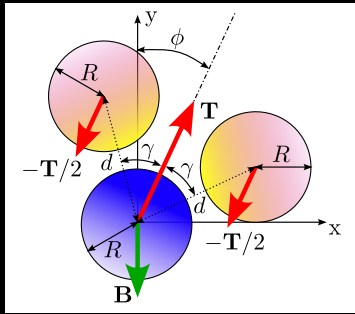


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- **Velocity  $U$  decreases when  $d/R \rightarrow 0$**

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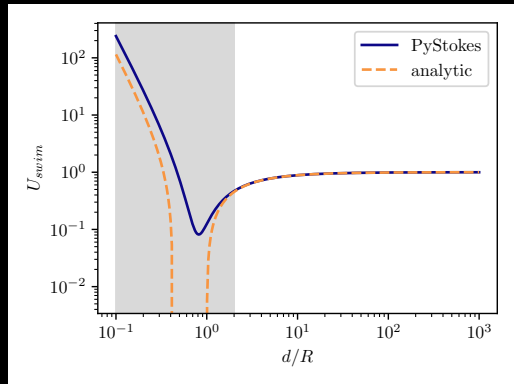
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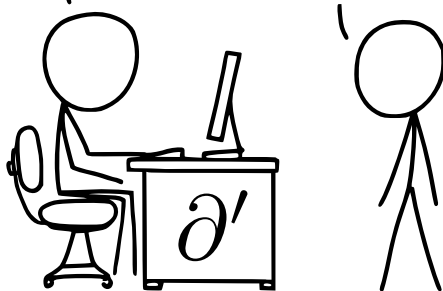


- Numerical validation with Stokesian Dynamics  
<https://github.com/rajeshrinet/pystokes>
- **Velocity  $U$  decreases when  $d/R \rightarrow 0$**
- Particle collapsing = 0 thrust = 0 efficiency

# HOW I MADE MY FIRST *push*

HI STEPHANE,  
ROUGH DAY?

YEAH, BETTER  
UNLEASH *basilisk/src*  
BEFORE PAPERWORKS  
TURNS ME TO STONE.



# Microhydrodynamics with Basilisk

A number of validation available on `sandbox/fpicella/README/...`

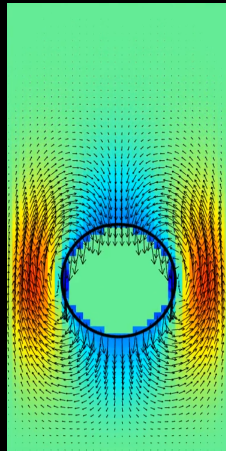
```
#include "grid/quadtree.h"
#include "ghigo/src/myembed.h"
#include "ghigo/src/mycentered.h"
// -> myviscosity-embed.h -> mypoisson.h
#include "fpicella/src/driver-myembed-particles.h"
// adapted from sandbox/Antoonvh/tracer-particles.h
int main () {stokes = true;}
```

Velocity BC on embed: `ghigo/src/mypoison.h`

projection step: from  $\mathbf{u}^*$  ( $\nabla \cdot \mathbf{u}^* \neq 0$ , no BC on embed...)

$$\nabla \cdot (\alpha \nabla p) = \frac{\nabla \cdot \mathbf{u}^* + \mathbf{u}_{\text{embed}} \cdot \mathbf{n}}{\Delta t} \quad (1)$$

$$\mathbf{u} \leftarrow \mathbf{u}^* - \Delta t \alpha \nabla p \quad (2)$$

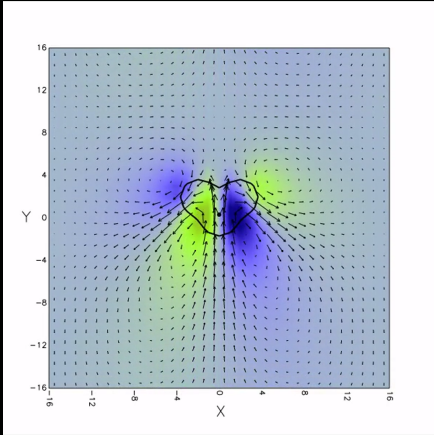


A sedimenting cylinder.  
Validation: Dvinsky Popel 1987.

# A general-purpose framework for the tHree model

## tHree in Basilisk

finite volume, adaptive mesh...

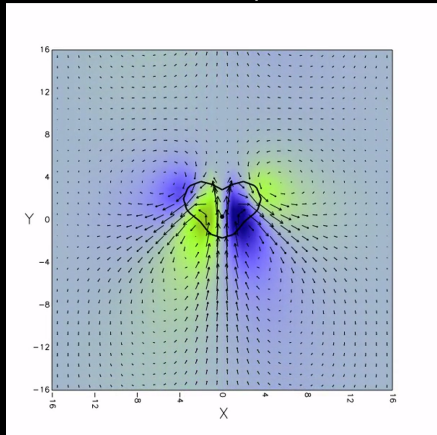


[basilisk.fr/sandbox/fpicella](http://basilisk.fr/sandbox/fpicella)

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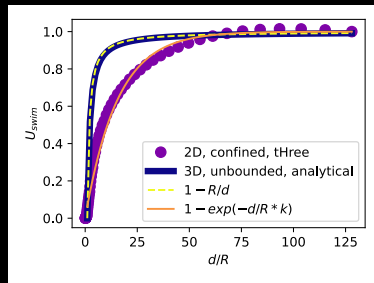
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[basilisk.fr/sandbox/fpicella](http://basilisk.fr/sandbox/fpicella)

- ▶ quasi-steady Stokes solver  
`basilisk.fr/src/navier-stokes/centered.h`
- ▶ Forces: *smooth kernel* (Cortez 2001)
- ▶ Body: high-viscosity blobs (Tanaka & Araki 2000)
- ▶ Multiple-particle tracking  
`basilisk.fr/sandbox/Antoonvh/tracer-particles.h`



tHree swimming velocity.  
2D Basilisk vs 3D analytic prediction.

# Simulating bio-convection: tHree model

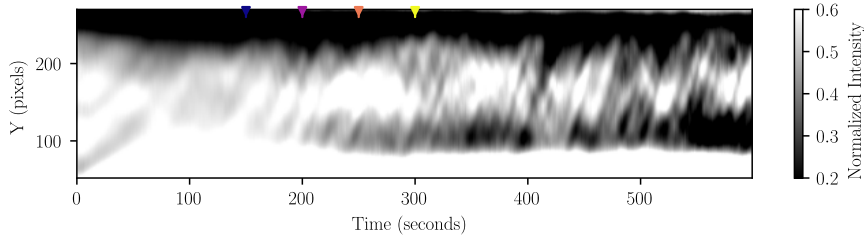
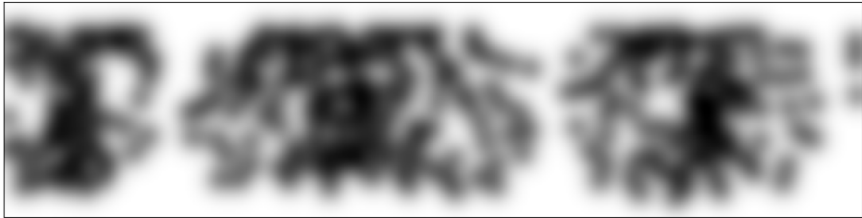
microswimmer-driven instabilities. Cell height  $64 \cdot R$ , cell width  $512 \cdot R$ , 512 tHree microswimmers.





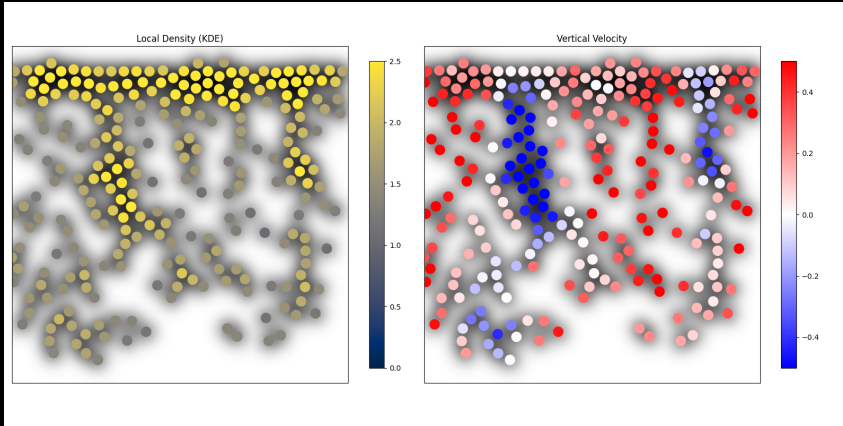
# Simulating bio-convection: tHree model

microswimmer-driven instabilities. Cell height  $64 \cdot R$ , cell width  $512 \cdot R$ , 512 tHree microswimmers.



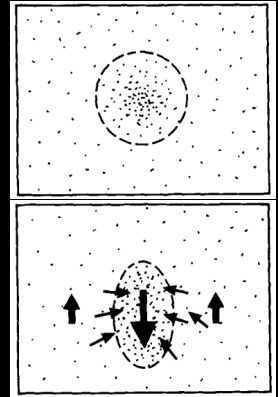
Spanwise-averaged intensity. Dense layers forming simultaneously at top and bulk. (statistics ok?)

# Local concentration fluctuation triggers plumes (?)



Before the onset of *plumes*, local high cell concentration:

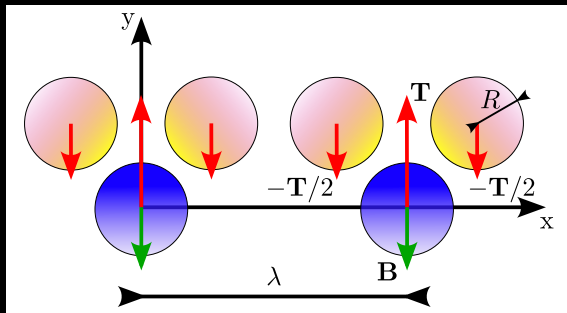
1. observed **far from free-surface** (role of microhydrodynamics!)
2. → **negative velocity**



Kessler 1985

# Binary interactions

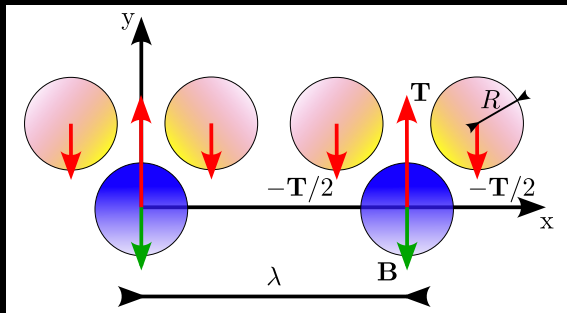
Loss of *hydrodynamic efficiency*



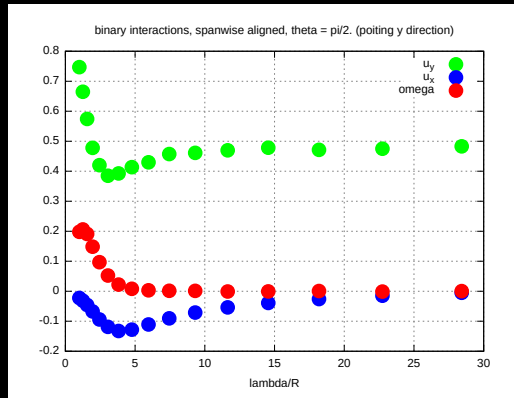
- ▶  $\phi = 0$ , aligned, variable distance  $\lambda$ .
- ▶  $\mathbf{T} = [0, 4, 0]$ ,  $\rho = \mu = 1$
- ▶ zero buoyancy  $\mathbf{B} = \mathbf{0}$
- ▶ identical blob sizes  
 $R = 1.$ ,  $d = 1.$ ,  $\beta = 1.$

# Binary interactions

Loss of *hydrodynamic efficiency*



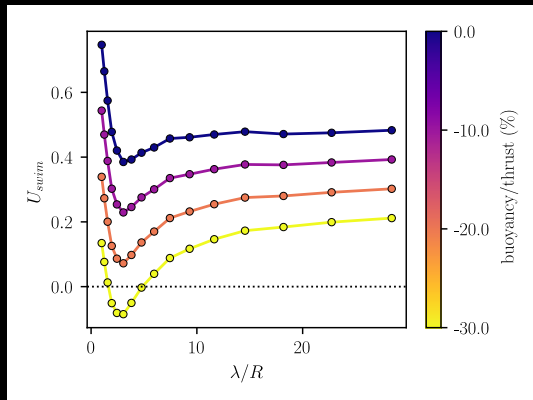
- ▶  $\phi = 0$ , aligned, variable distance  $\lambda$ .
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- ▶ zero buoyancy  $\mathbf{B} = \mathbf{0}$
- ▶ identical blob sizes  
 $R = 1.$ ,  $d = 1.$ ,  $\beta = 1.$



- ▶ below  $\lambda/R = 3$ , contact (unphysical)
- ▶ Repulsion ( $u_x$ ) @ approach (puller)
- ▶ Efficiency ( $u_y$ ) drops @ approach

# Binary interactions + negative buoyancy

Identical to previous slide, but with  $B < 0$

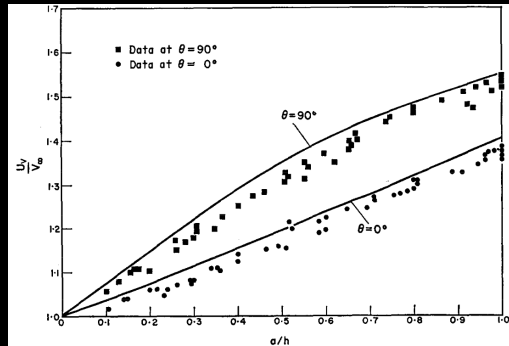
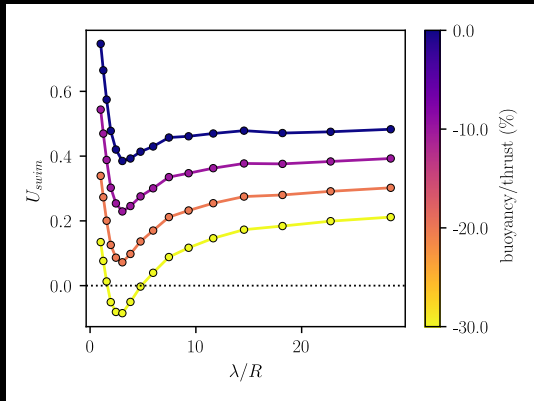


## Confinement + added gravity

- ▶ decrease swimming **velocity**...
- ▶ ... up to **negative** @ approach!

# Binary interactions + negative buoyancy

Identical to previous slide, but with  $B < 0$



Goldman, Cox & Brenner, 1966

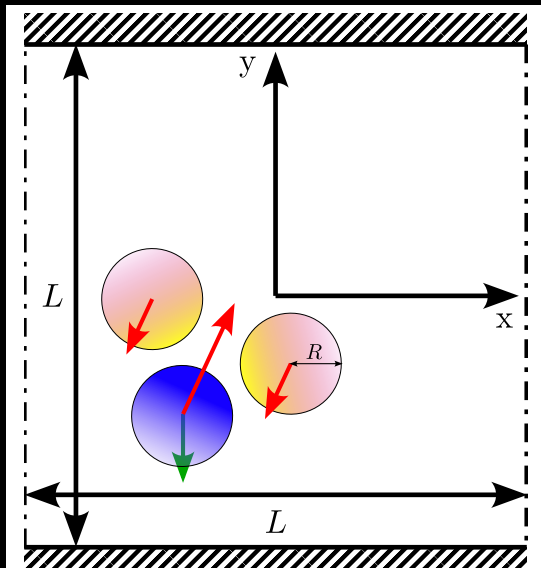
## Confinement + added gravity

- ▶ decrease swimming **velocity**...
- ▶ ... up to **negative** @ approach!

- ▶ Purely sedimenting particles
- ▶  $a/h = \frac{1}{\lambda/R}$
- ▶ As particle approaches (right), increase in sedimentation speed!

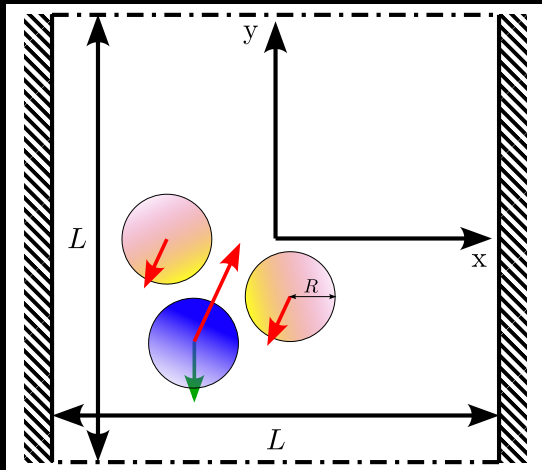
# Plumes without a free-surface

Single Swimmer



# Plumes without a free-surface

Single Swimmer

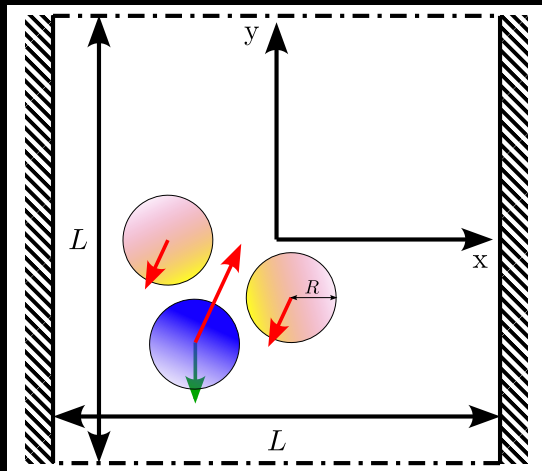


*"infinitely tall vertical pipe"*

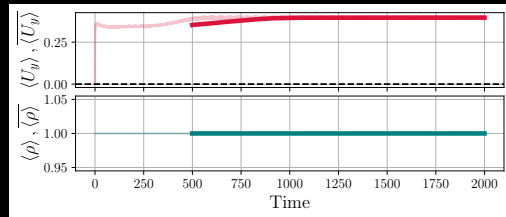


# Plumes without a free-surface

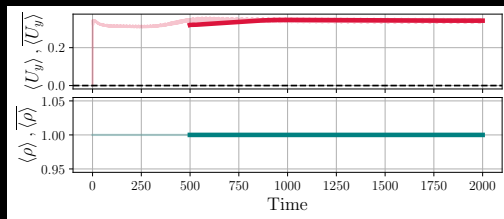
Single Swimmer



"infinitely tall vertical pipe"



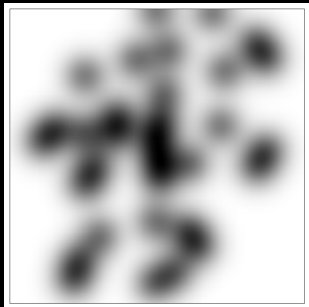
$$|B| = |T| \cdot 0.0\%$$



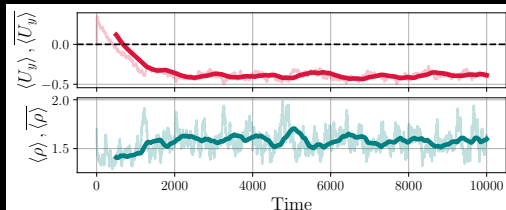
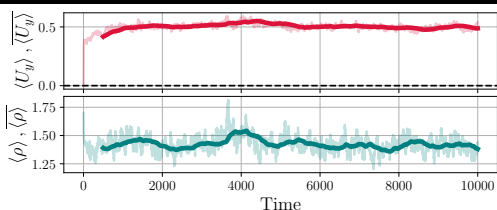
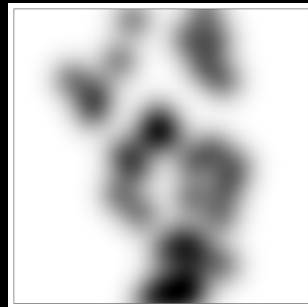
$$|B| = |T| \cdot 2.5\%$$

# Plumes without free-surfaces.

$$|\mathbf{B}| = |\mathbf{T}| \cdot 0.0\% \text{ (no-buoyancy)}$$

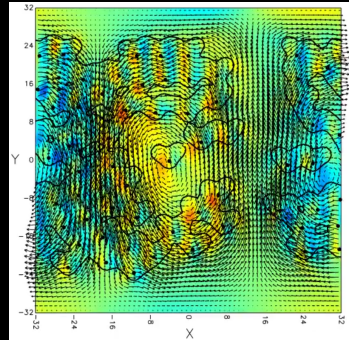
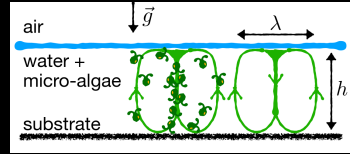


$$|\mathbf{B}| = |\mathbf{T}| \cdot 2.5\% \text{ (negative-buoyancy)}$$



# Triggering Bio-convection

take-home messages

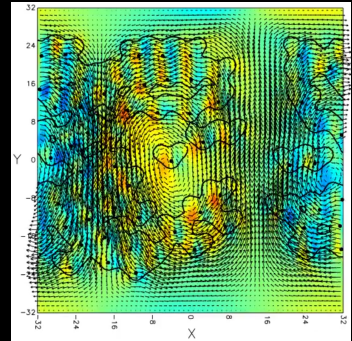
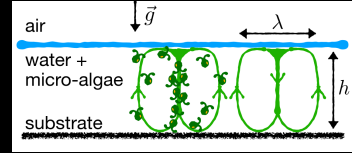


sandbox/fpicella/microswimmer\_tHree\_forces/  
plumes\_x\_periodic.c

# Triggering Bio-convection

take-home messages

1. **Hydrodynamic interaction** → **concentration fluctuation**

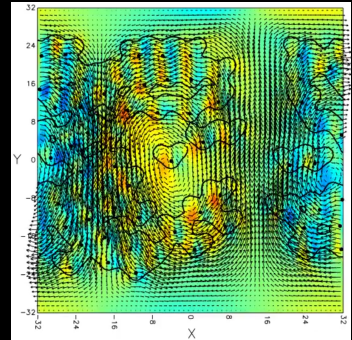
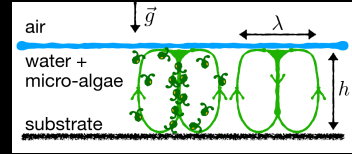


sandbox/fpicella/microswimmer\_tHree\_forces/  
plumes\_x\_periodic.c

# Triggering Bio-convection

take-home messages

1. **Hydrodynamic interaction** → **concentration fluctuation**
2. **Concentration increase** → **hydro. efficiency decrease**

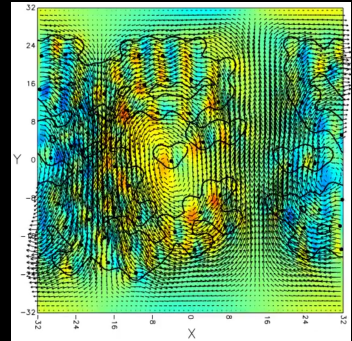
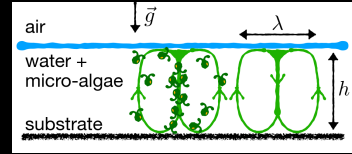


sandbox/fpicella/microswimmer\_three\_forces/  
plumes\_x\_periodic.c

# Triggering Bio-convection

take-home messages

1. **Hydrodynamic interaction** → **concentration fluctuation**
2. **Concentration increase** → **hydro. efficiency decrease**
3. → **sedimentation** kicks-in



sandbox/fpicella/microswimmer\_tHree\_forces/  
plumes\_x\_periodic.c

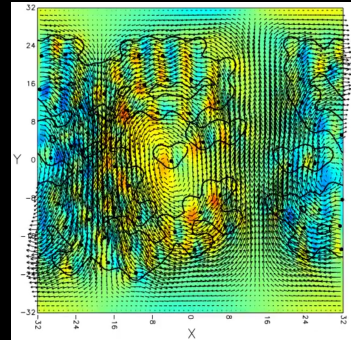
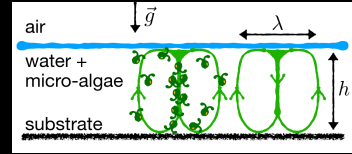
# Triggering Bio-convection

take-home messages

1. **Hydrodynamic interaction** → **concentration fluctuation**
2. **Concentration increase** → **hydro. efficiency decrease**
3. → **sedimentation** kicks-in

Persp. Numerics + Experiments

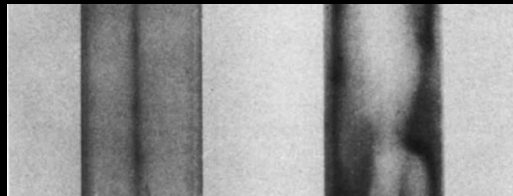
► 2D/3D effects?



sandbox/fpicella/microswimmer\_three\_forces/  
plumes\_x\_periodic.c

## Kessler 1985

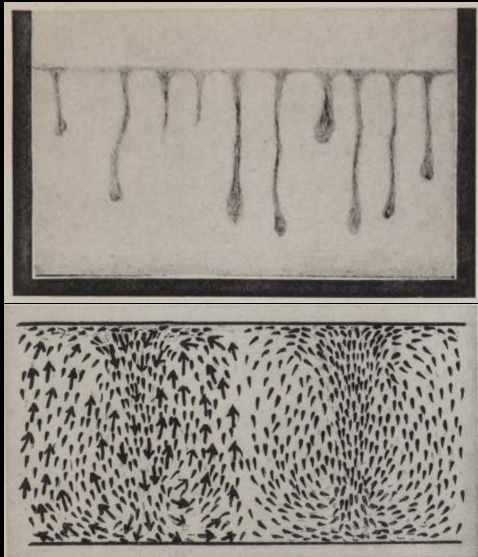
## Kessler 1985



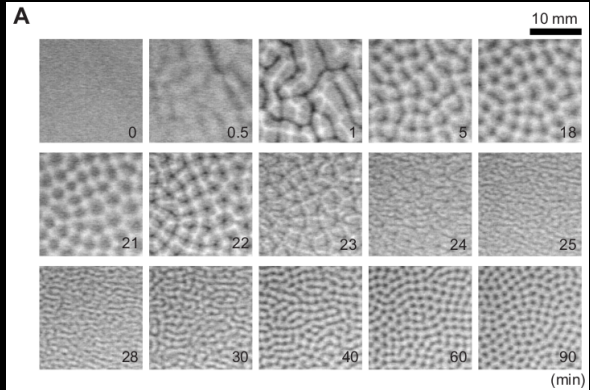
18 / 25



# Triggering plume $\neq$ sustaining bioconvection



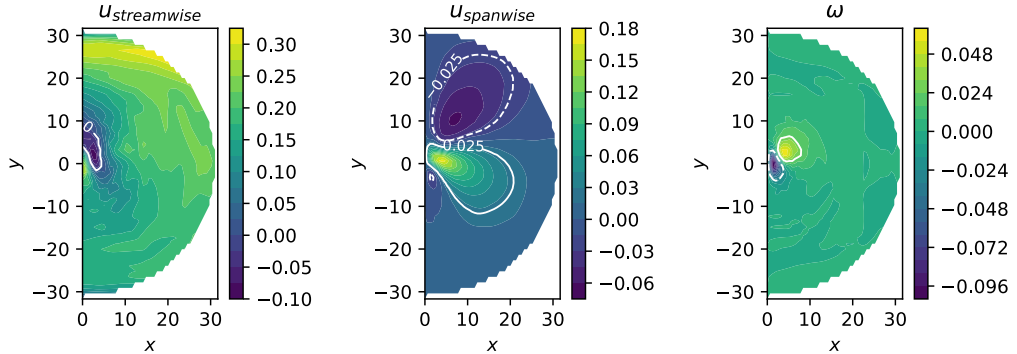
Wager 1911



Long-term bioconvection patterns. Top view.

Kage *et al.* 2013

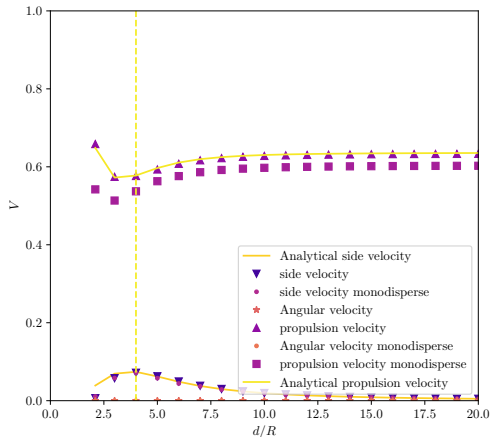
# Binary interactions, non aligned



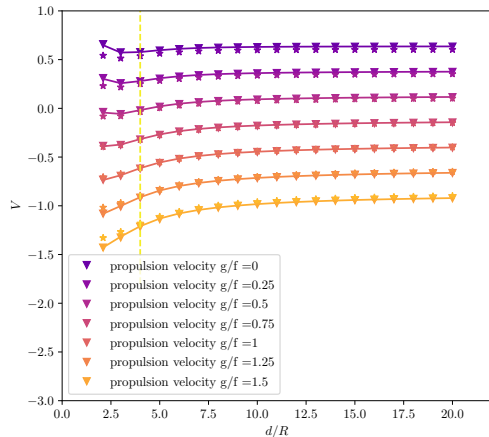
# Binary interactions, full 3D

A. Palotai

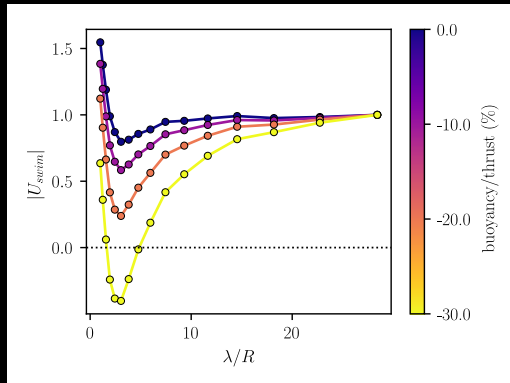
Speed of Microswimmers as a function the distance between the two microswimmers



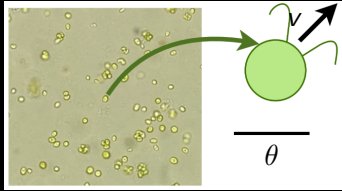
Speed of Microswimmers as a function the distance between the two microswimmers



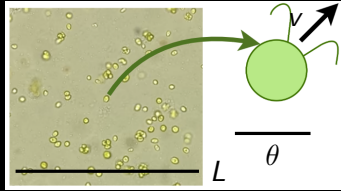
# Binary interactions + buoyancy, normalized



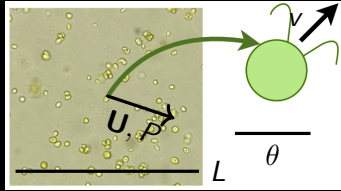
# Modelling bio-convection (1): a **buoyancy**-driven flow (?)



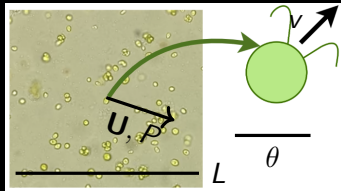
# Modelling bio-convection (1): a **buoyancy**-driven flow (?)



# Modelling bio-convection (1): a **buoyancy**-driven flow (?)



# Modelling bio-convection (1): a **buoyancy**-driven flow (?)



Eulerian, **averaged**,  $L \gg \theta$

$$\frac{D\mathbf{U}}{Dt} = -Sc\nabla P + Sc\nabla^2\mathbf{U} \quad (3)$$

$$\nabla \cdot \mathbf{U} = 0 \quad (4)$$

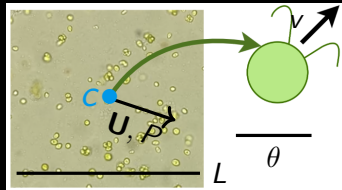
$$(5)$$

$$(6)$$

Pedley & Kessler 1990



# Modelling bio-convection (1): a **buoyancy**-driven flow (?)



Eulerian, **averaged**,  $L \gg \theta$

$$\frac{D\mathbf{U}}{Dt} = -Sc\nabla P + Sc\nabla^2\mathbf{U} - Sc \cdot Ra \, c \, \hat{\mathbf{g}} \quad (3)$$

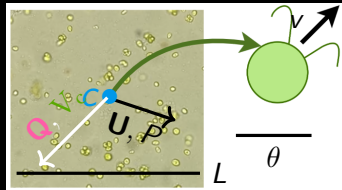
$$\nabla \cdot \mathbf{U} = 0 \quad (4)$$

$$(5)$$

$$(6)$$

Pedley & Kessler 1990

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Eulerian, **averaged**,  $L \gg \theta$

$$\frac{D\mathbf{U}}{Dt} = -Sc\nabla P + Sc\nabla^2\mathbf{U} - Sc \cdot Ra \, c \, \hat{\mathbf{g}} \quad (3)$$

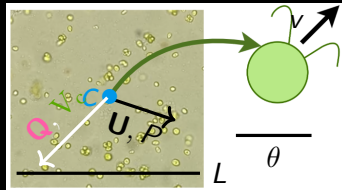
$$\nabla \cdot \mathbf{U} = 0 \quad (4)$$

$$\frac{\partial c}{\partial t} = -\nabla \cdot ((\mathbf{U} + \mathbf{V}_c \langle \mathbf{Q} \rangle) c - \nabla c) \quad (5)$$

$$(6)$$

Pedley & Kessler 1990

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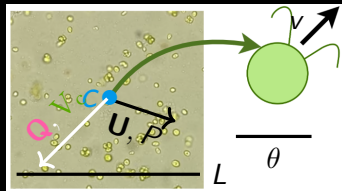
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$$\frac{\partial \mathbf{Q}}{\partial t} = \frac{1}{2G} (\hat{\mathbf{g}} - (\hat{\mathbf{g}} \cdot \mathbf{Q})) + \frac{\boldsymbol{\Omega} \times \mathbf{Q}}{2} \quad (6)$$

Pedley & Kessler 1990

# Modelling bio-convection (1): a **buoyancy**-driven flow (?)



Eulerian, **averaged**,  $L \gg \theta$

$$\frac{D\mathbf{U}}{Dt} = -Sc\nabla P + Sc\nabla^2\mathbf{U} - Sc \cdot Ra \, c \, \hat{\mathbf{g}} \quad (3)$$

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$Ra \propto$  buoyancy,  $Sc \propto$  diffusion,

$G \propto$  reorientation towards gravity .

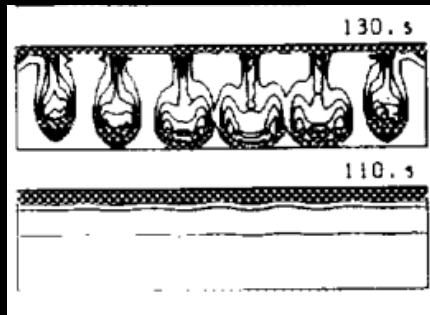
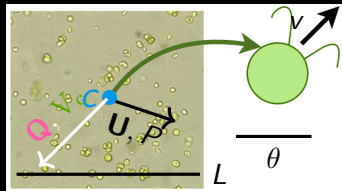
$\mathbf{V}_c$ , CR **average swimming velocity**

$\mathbf{Q}(\mathbf{x}, t)$ , CR **average orientation**

$c(\mathbf{x}, t)$ , CR **average concentration**

Pedley & Kessler 1990

# Modelling bio-convection (1): a **buoyancy**-driven flow (?)



Harashima *et al.* 1987

Eulerian, **averaged**,  $L \gg \theta$

$$\frac{D\mathbf{U}}{Dt} = -Sc\nabla P + Sc\nabla^2\mathbf{U} - Sc \cdot Ra \, c \, \hat{\mathbf{g}} \quad (3)$$

$$\nabla \cdot \mathbf{U} = 0 \quad (4)$$

$$\frac{\partial c}{\partial t} = -\nabla \cdot ((\mathbf{U} + \mathbf{V}_c \langle \mathbf{Q} \rangle) c - \nabla c) \quad (5)$$

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Pedley & Kessler 1990

# Simulating bio-convection: averaged, buoyancy-driven model

In-house implementation with Spectral Element Method Nek5000



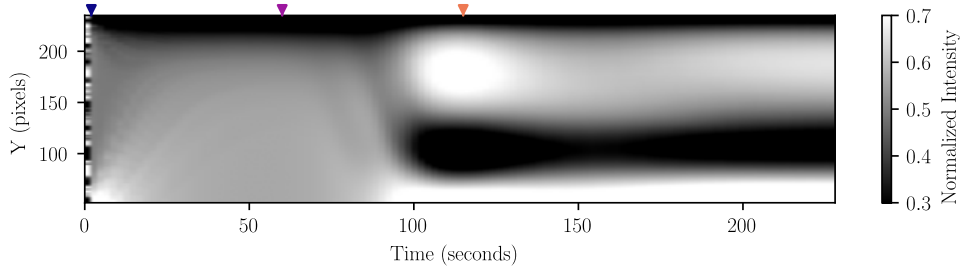
Side view.  $Ra$ ,  $Sc$ ,  $G$ ,  $V_c$  from Ghorai & Hill 1999

# Simulating bio-convection: averaged, buoyancy-driven model

In-house implementation with Spectral Element Method Nek5000



Side view.  $Ra$ ,  $Sc$ ,  $G$ ,  $V_c$  from Ghorai & Hill 1999



Spanwise-averaged intensity. First top dense layer thinning, then plumes.

