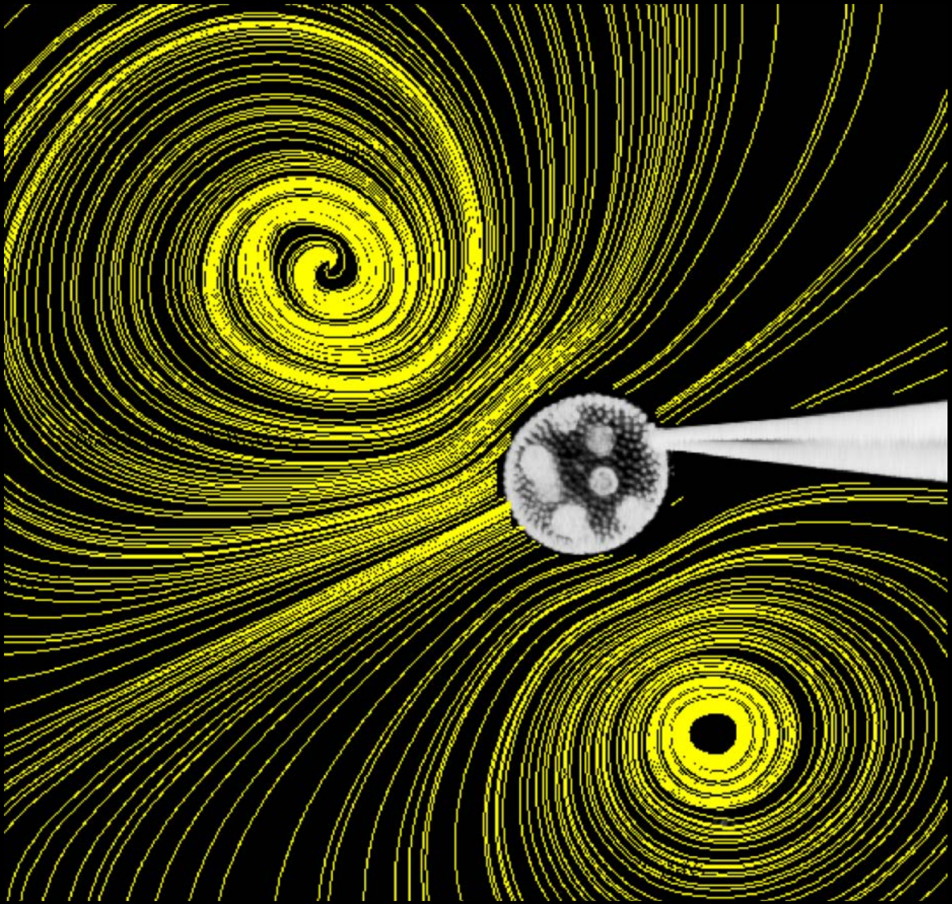
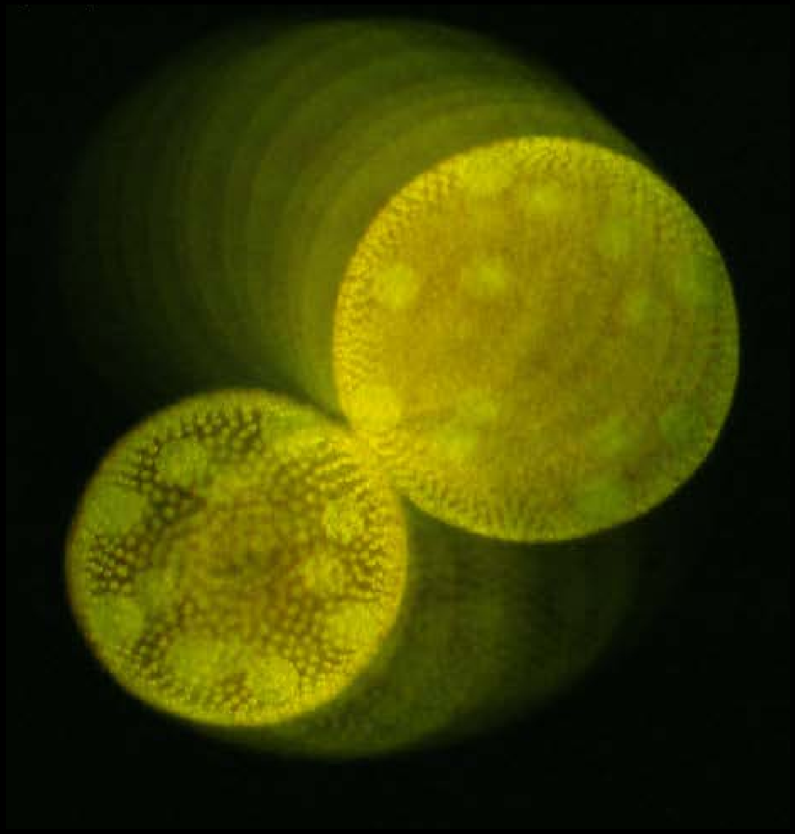
Emergent Collective Behaviour in *Volvox*



Raymond E Goldstein

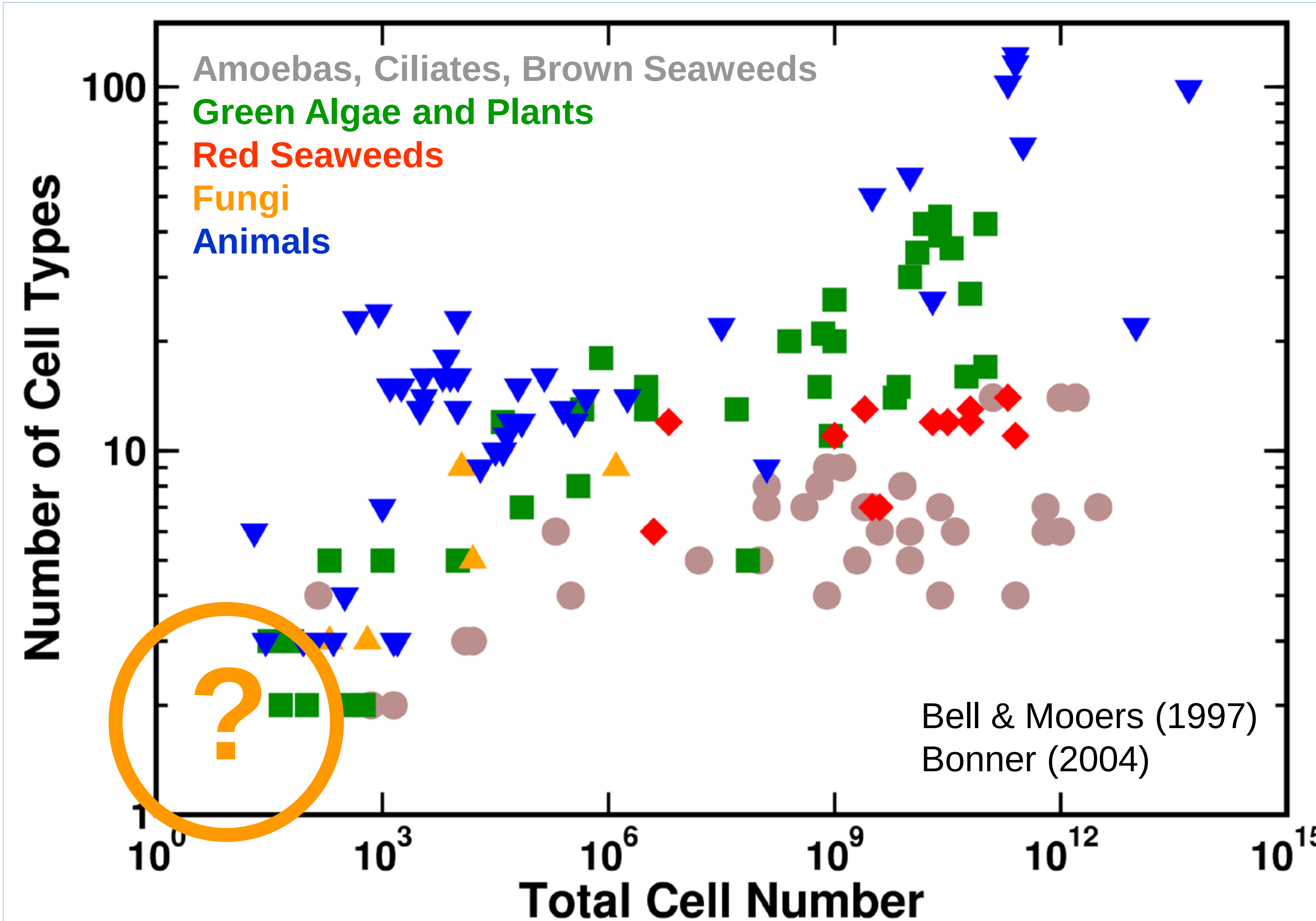
Department of Applied Mathematics and Theoretical Physics

University of Cambridge



www.damtp.cam.ac.uk/user/gold
www.youtube.com/Goldsteinlab

The Size-Complexity Relation



The Recent Literature

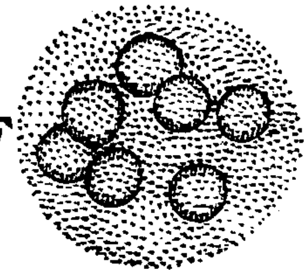
IV. *Part of a Letter from* Mr Antony Van Leeuwenhoek, *concerning the Worms in Sheeps Livers, Gnats, and Animalcula in the Excrements of Frogs.*

When I brought theſe particles before the Magnifying-glaſs, I did not only ſee that they were round, but that the outward skin of them was quite ſet over with many protuberant parts, which did ſeem to me to be triangular, and pointed towards the end; ſo that it ſeemed to me, that in the great circle of the roundneſs, ſtood ſuch particles, all orderly and equally from each other; ſo that on a ſmall body did ſtand about two thouſand of the before-mentioned convex or protuberant particles.

This was to me a very pleaſant ſight, becauſe the ſaid particles, as often as I did look on them, did never lye ſtill, and that their motion did proceed from their turning round; and that the more, becauſe I did fancy at firſt that they were ſmall animals, and the ſmaller theſe particles were, the greener was their colour; and on the contrary, in the greateſt, that were as big as a great corn of ſand, there was no green colour at all to be diſcerned on the outſide.

Theſe particles had each of them within included 5, 6, 7, nay, ſome to 12 ſmall round globules, of the ſame ſhape as the body was wherein they were included.

Fig: 5

F  E

Phil. Trans. **22**, 509-518 (1700)

CAROLI LINNÆI

EQUITIS DE STELLA POLARI,
ARCHIATRI REGII, MED. & BOTAN. PROFESS. UPSAL.;
ACAD. UPSAL. HOLMENS. PETROPOL. BEROL. IMPER.
LOND. MONSPEL. TOLOS. FLORENT. SOC.

SYSTEMA NATURÆ

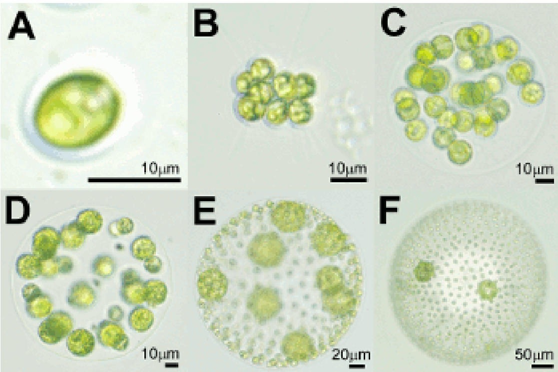
(1758)

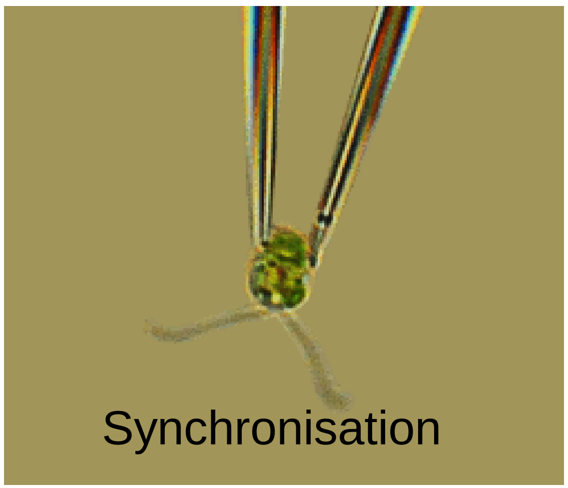
312. VOLVOX. *Corpus* liberum, gelatinoſum, rotundatum, artubus deſtitutum.
Proles ſubrotundi, nidulantes, ſparſi.

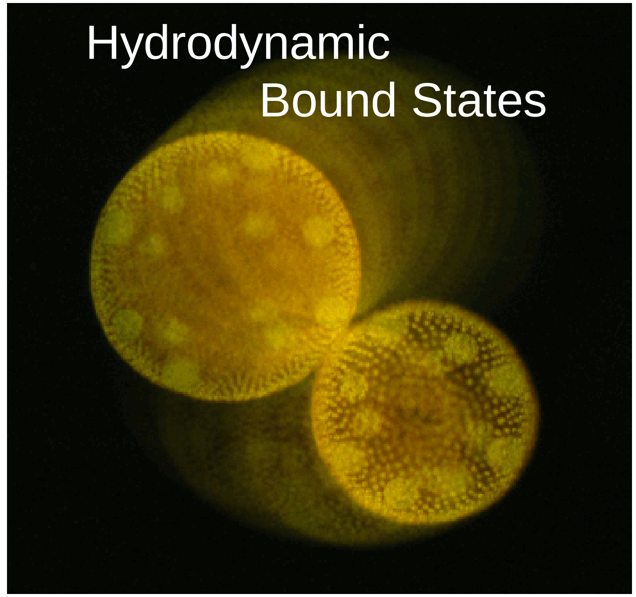
Volvendo ſeque rotando celeriter movens abſque artubus! viviparus natis, nepotibus, pronepotibus, abnepotibus conſpicuis intra animalculum minutiſſimum.

Green Algae as Model Organisms

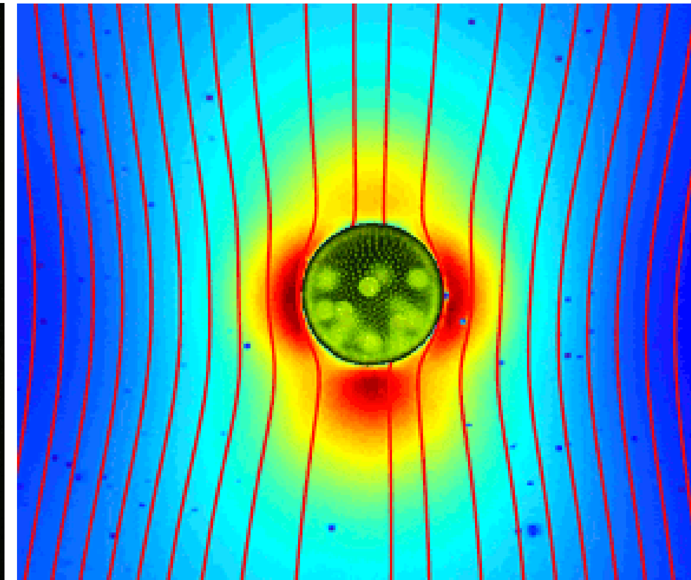
Multicellularity



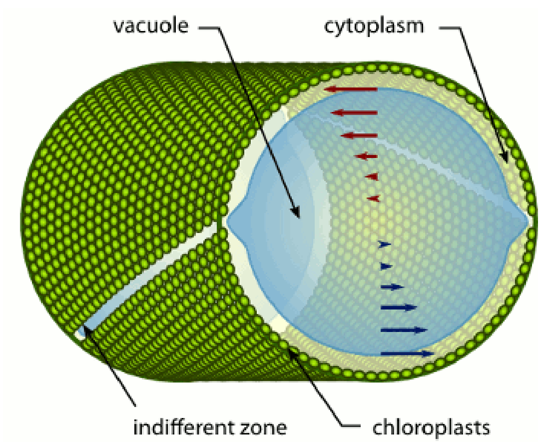




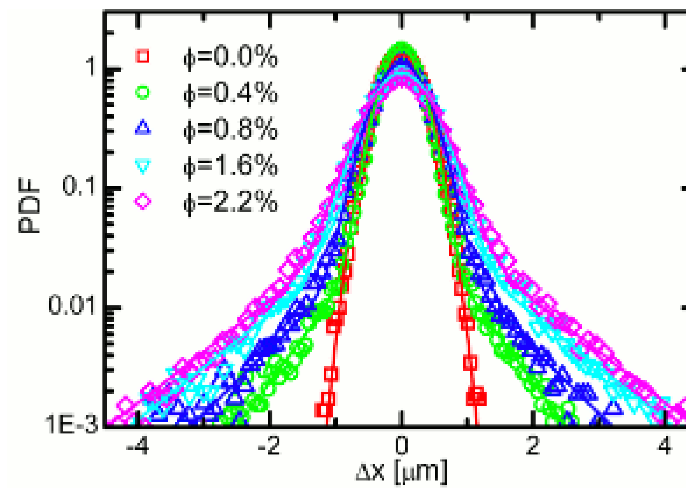
Flow Fields



Cytoplasmic Streaming



Tracer Statistics



REG, et al., Annual Review of Fluid Mechanics (2014)

Advection & Diffusion

If a fluid has a typical velocity **U**, varying on a length scale **L**, with a molecular species of diffusion constant **D**. Then there are two times:

$$t_{advection} = \frac{L}{U}$$

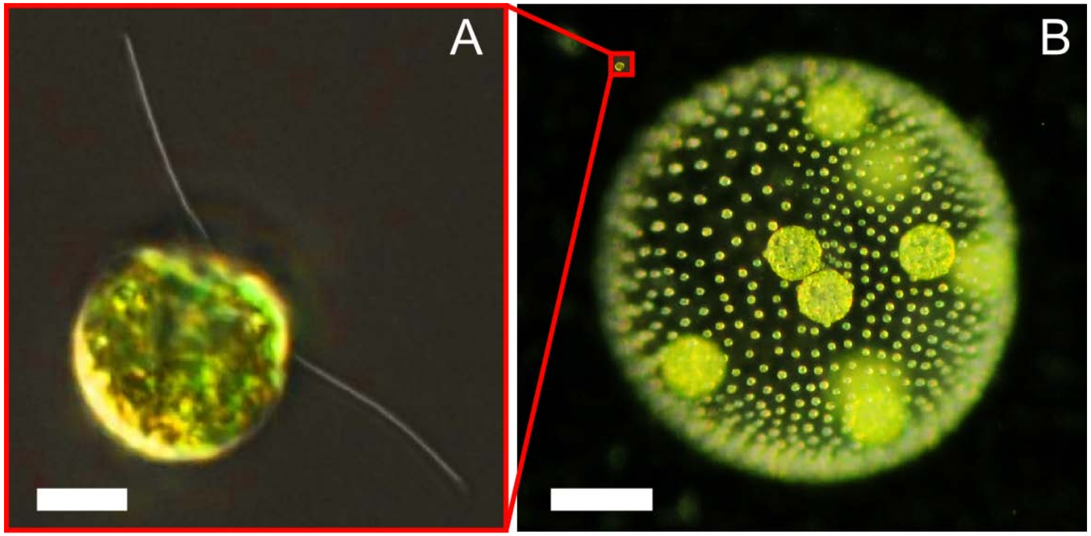
$$t_{diffusion} = \frac{L^2}{D}$$

We define the Péclet number as the ratio:

$$Pe = \frac{t_{diffusion}}{t_{advection}} = \frac{UL}{D}$$

This is like the Reynolds number comparing inertia to viscous dissipation:

$$Re = \frac{UL}{\nu}$$



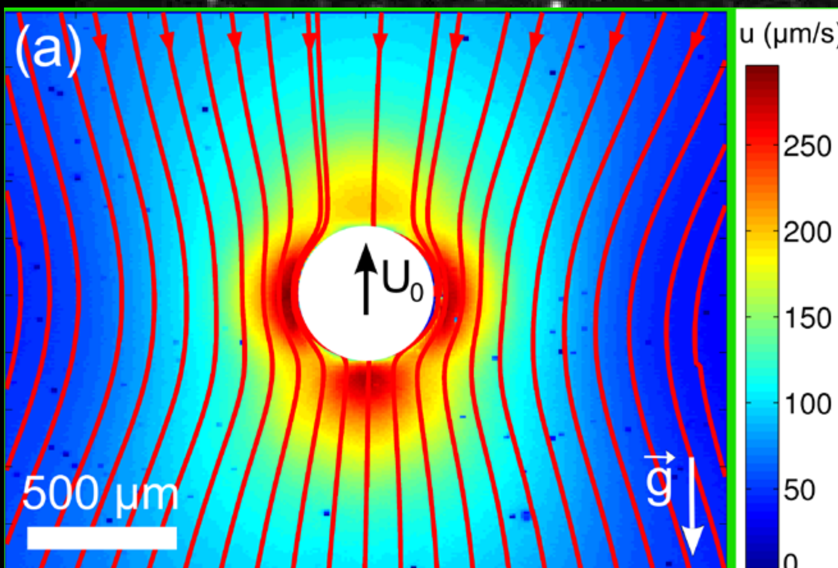
If U=100 μm/s, L=10 μm,
Re ~ 10^{-3}, Pe ~ 1
At the scale of an individual cell, diffusion dominates advection.

The opposite holds for ***multicellularity****…*

Solari, Ganguly, Michod, Kessler, Goldstein, *PNAS* (2006)
Short, Solari, Ganguly, Powers, Kessler & Goldstein, *PNAS* (2006)

Volvox In Its Own Frame

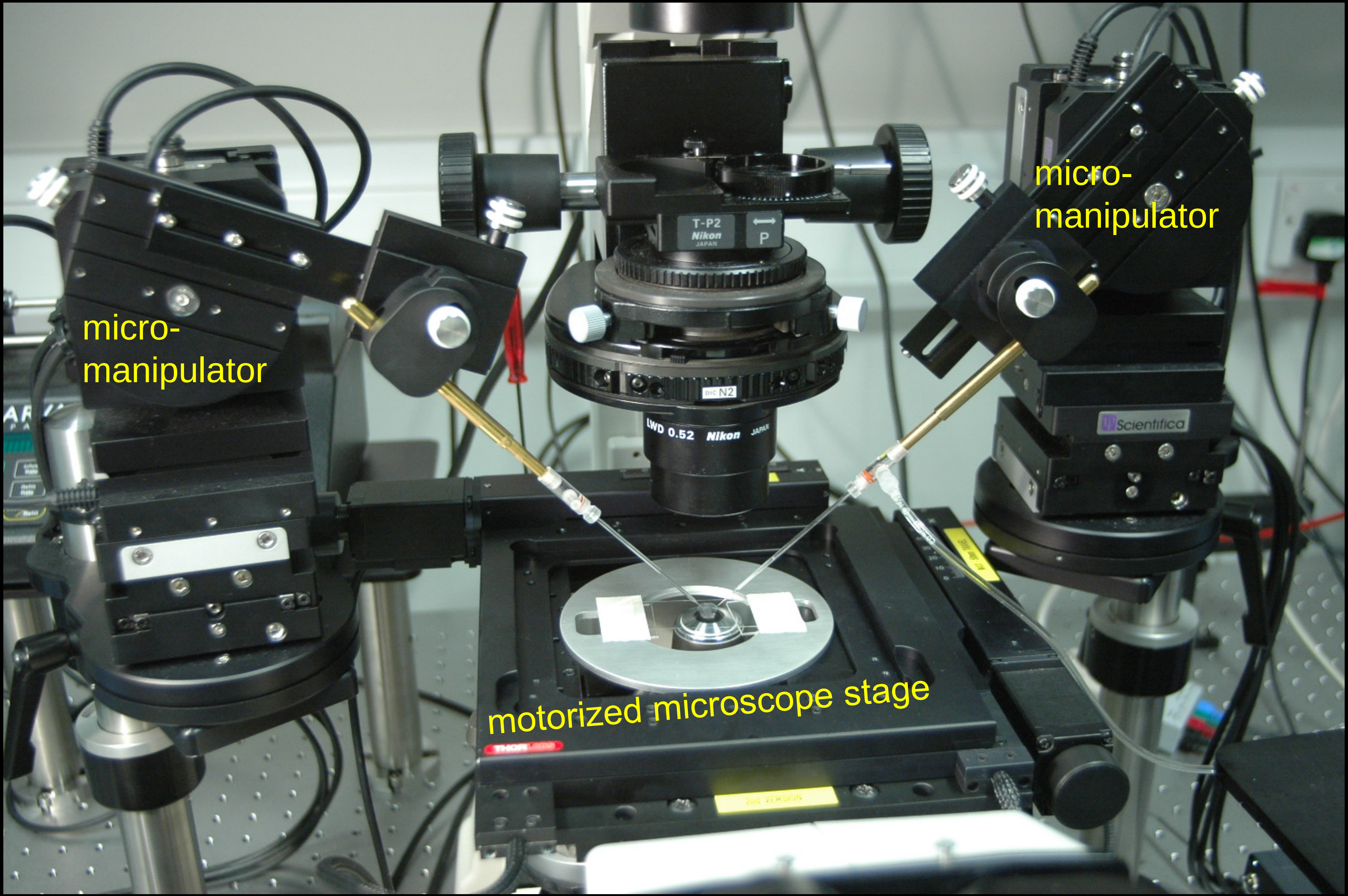
Tracking microscope
 in vertical orientation
Laser sheet illumination
 of microspheres



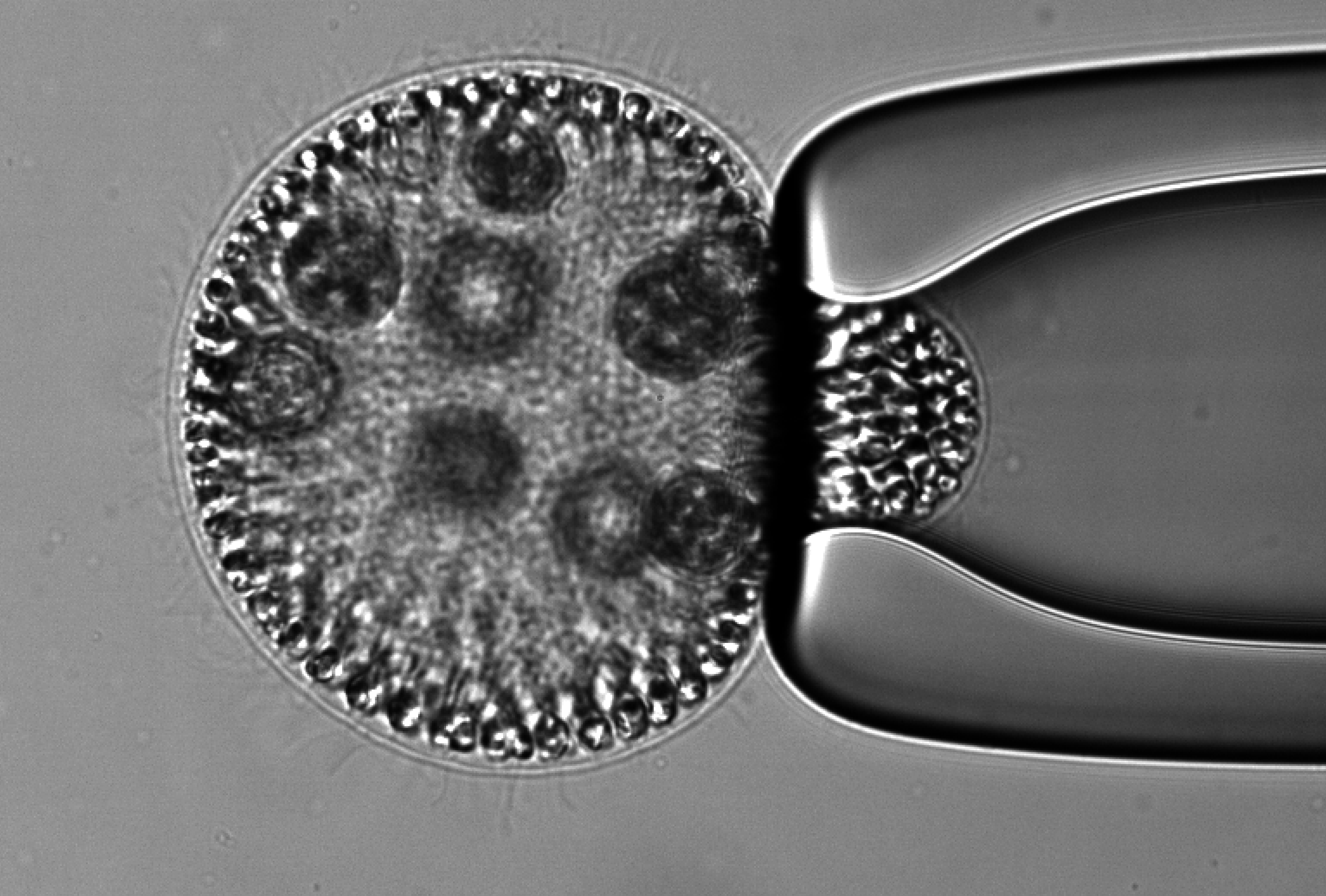
Drescher, Goldstein, Michel, Polin, and Tuval, *PRL* **105,** 168101 (2010)
Rushkin, Kantsler, Goldstein, *PRL* **105**, 188101 (2010)


LONG PASS
LWD 0.52
Nikon
WARNING

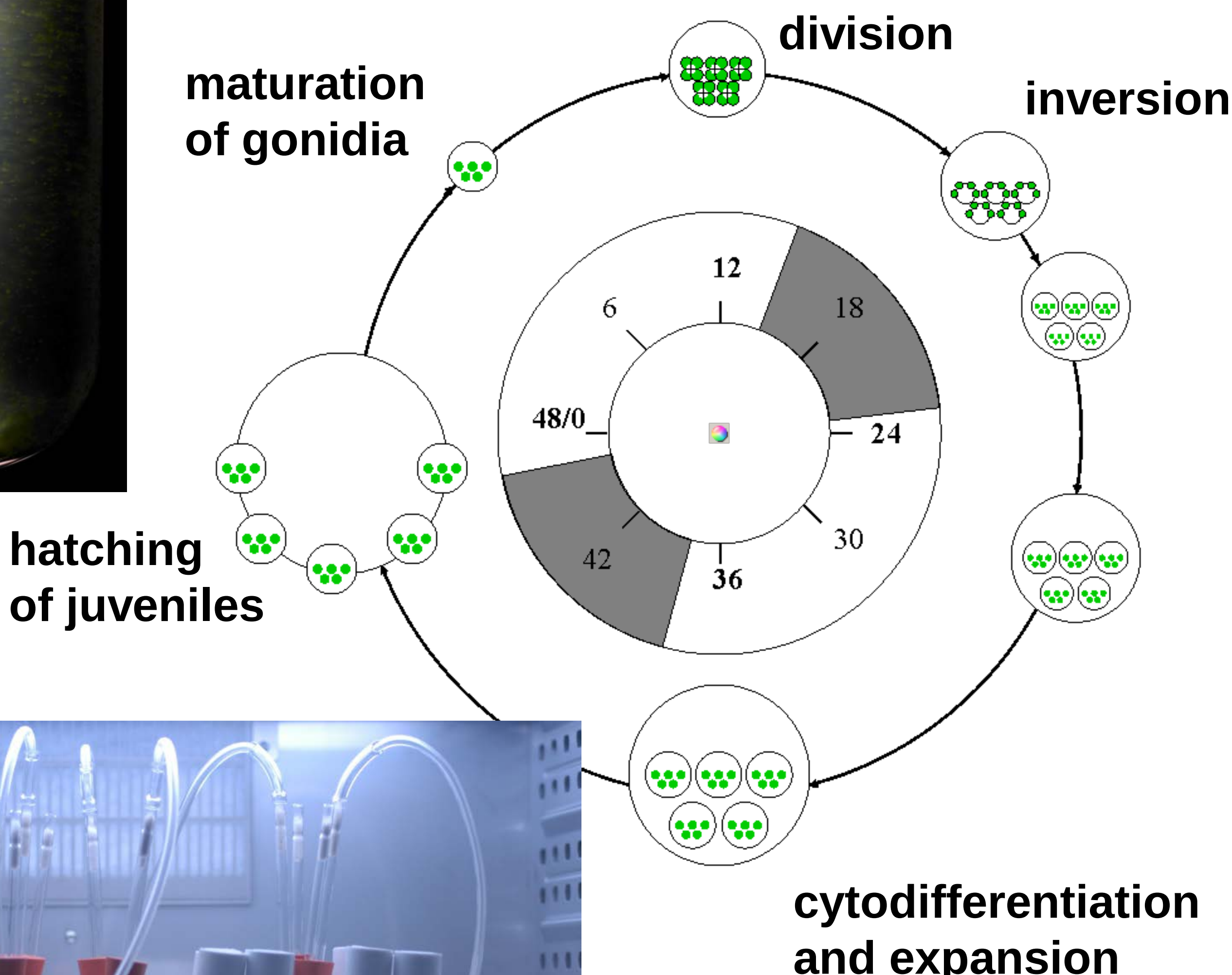
Microscopy & Micromanipulation



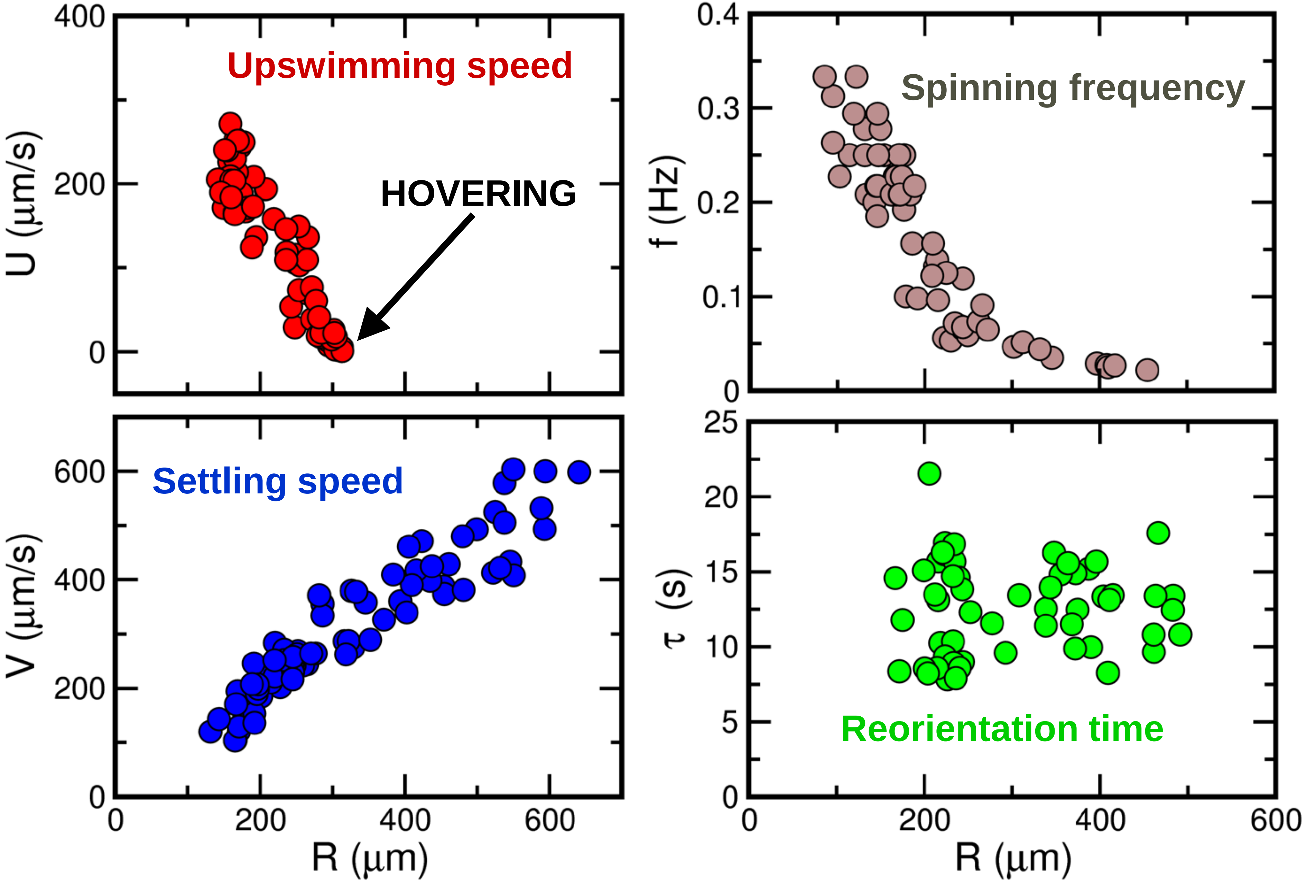
Volvox on a Micropipette



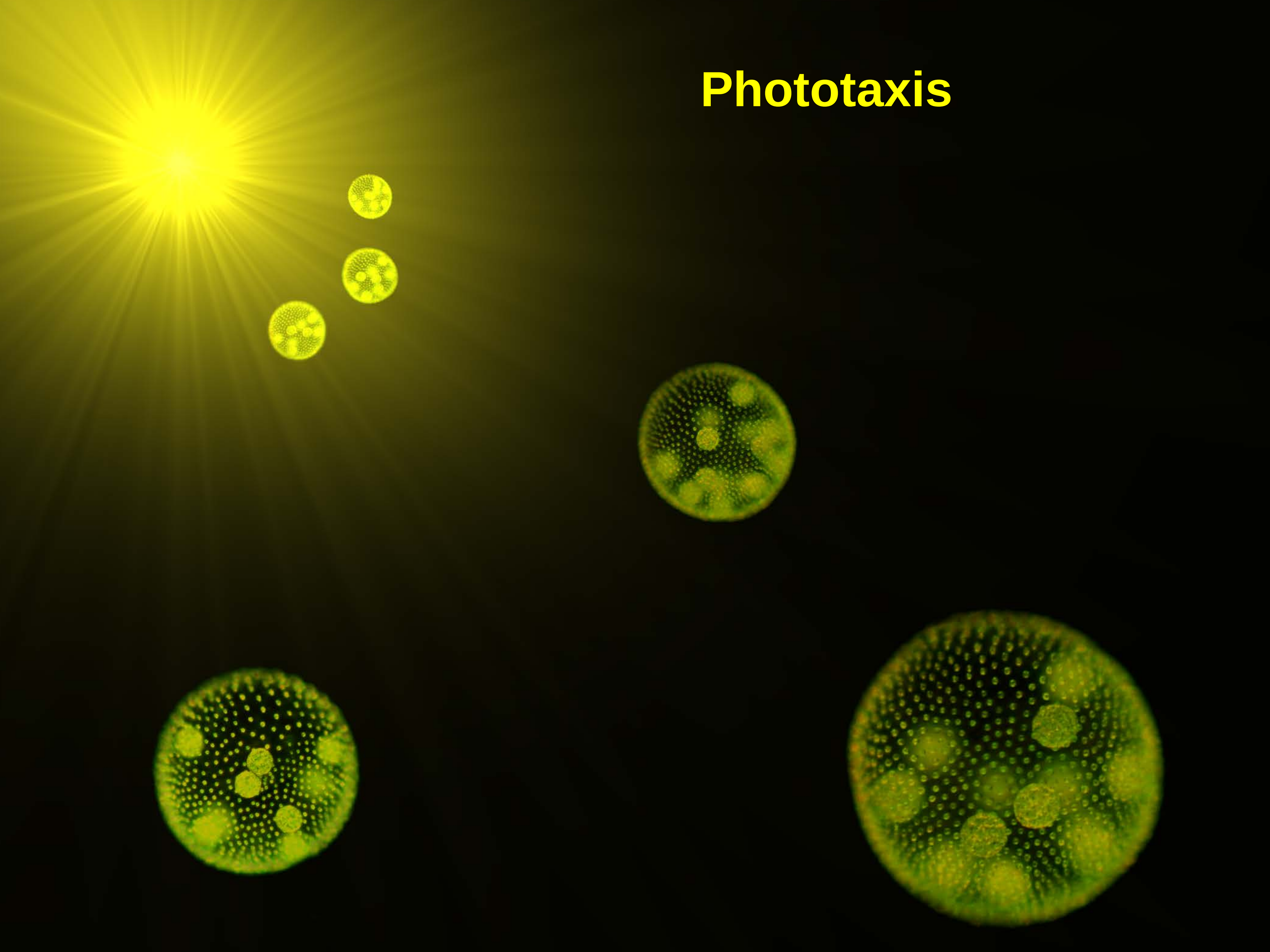
Life Cycles of the Green and Famous



Systematics of *Volvox*

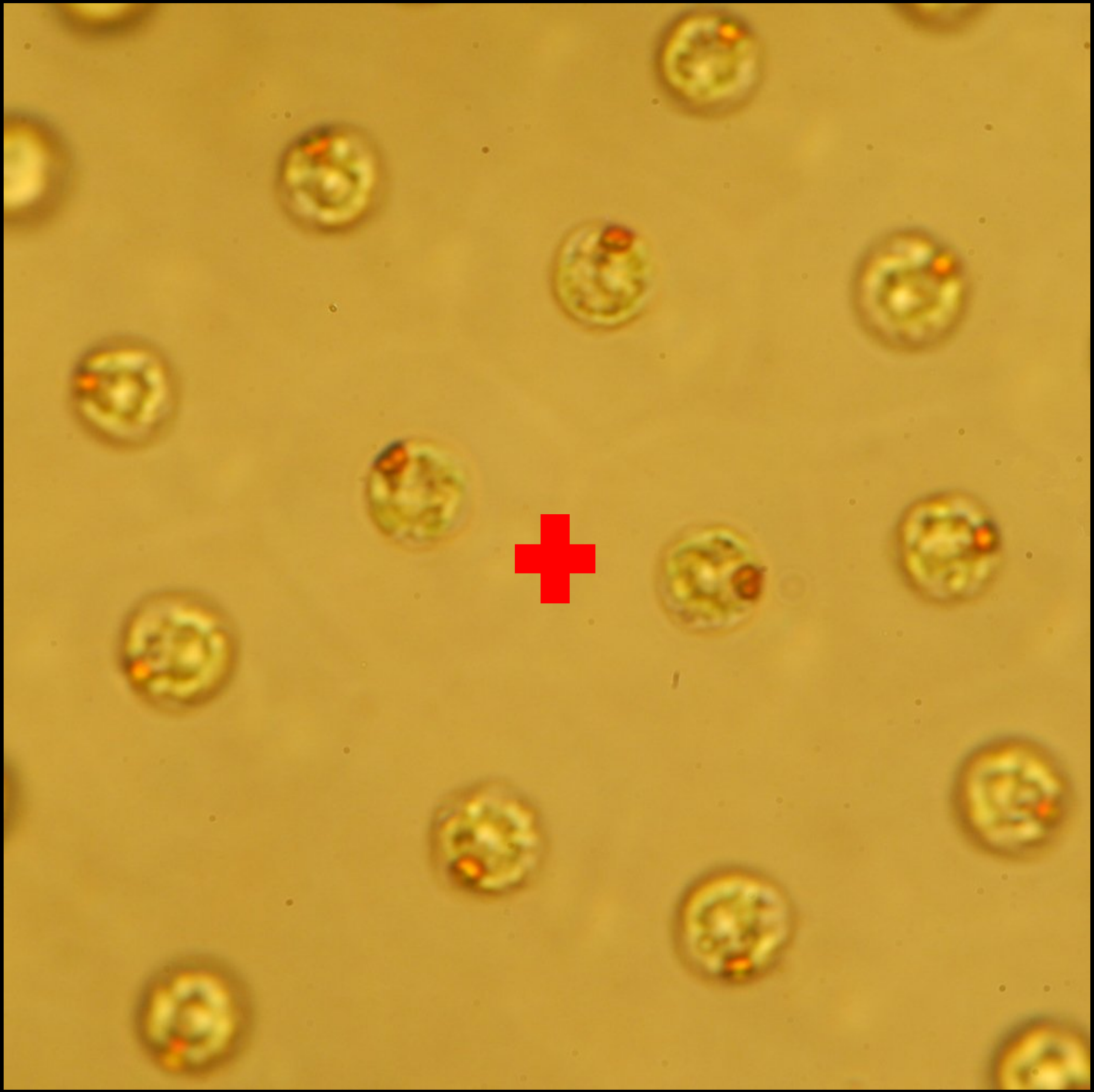


Phototaxis

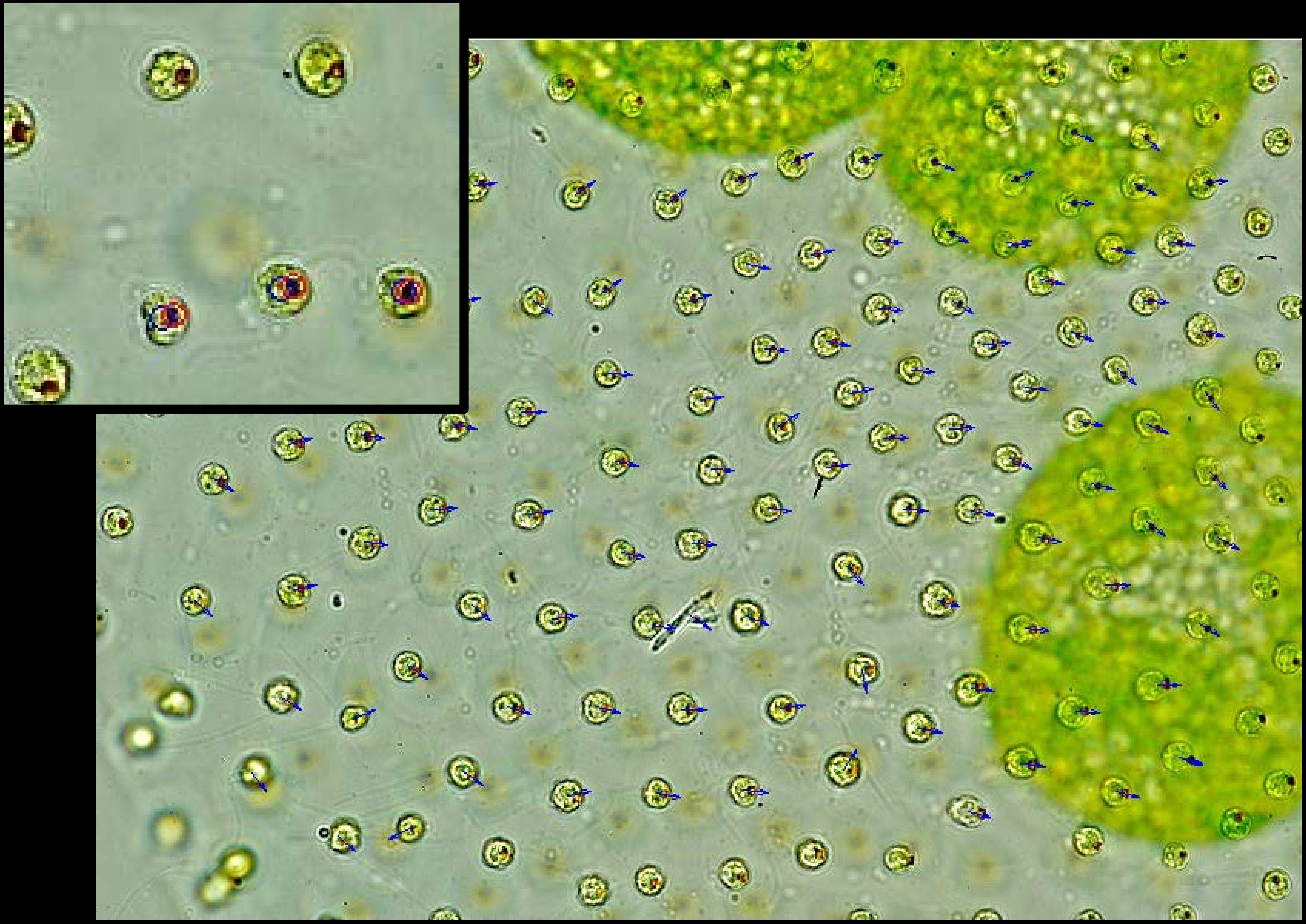


Volvox Eyespots

Top view at anterior pole



Planar Cell Polarity in *Volvox carteri*



Hugo Wioland

The Mathematics of Turning

angular velocity · *direction of gravity* · *axis direction* · *surface normal* · *surface fluid velocity*

$$\mathbf{\Omega}(t) = \frac{1}{\tau_{bh}}\hat{\mathbf{g}} \times \hat{\mathbf{k}} - \frac{3}{8\pi R^3}\int \hat{\mathbf{n}} \times \mathbf{u}(\theta, \phi, t)\, dS$$

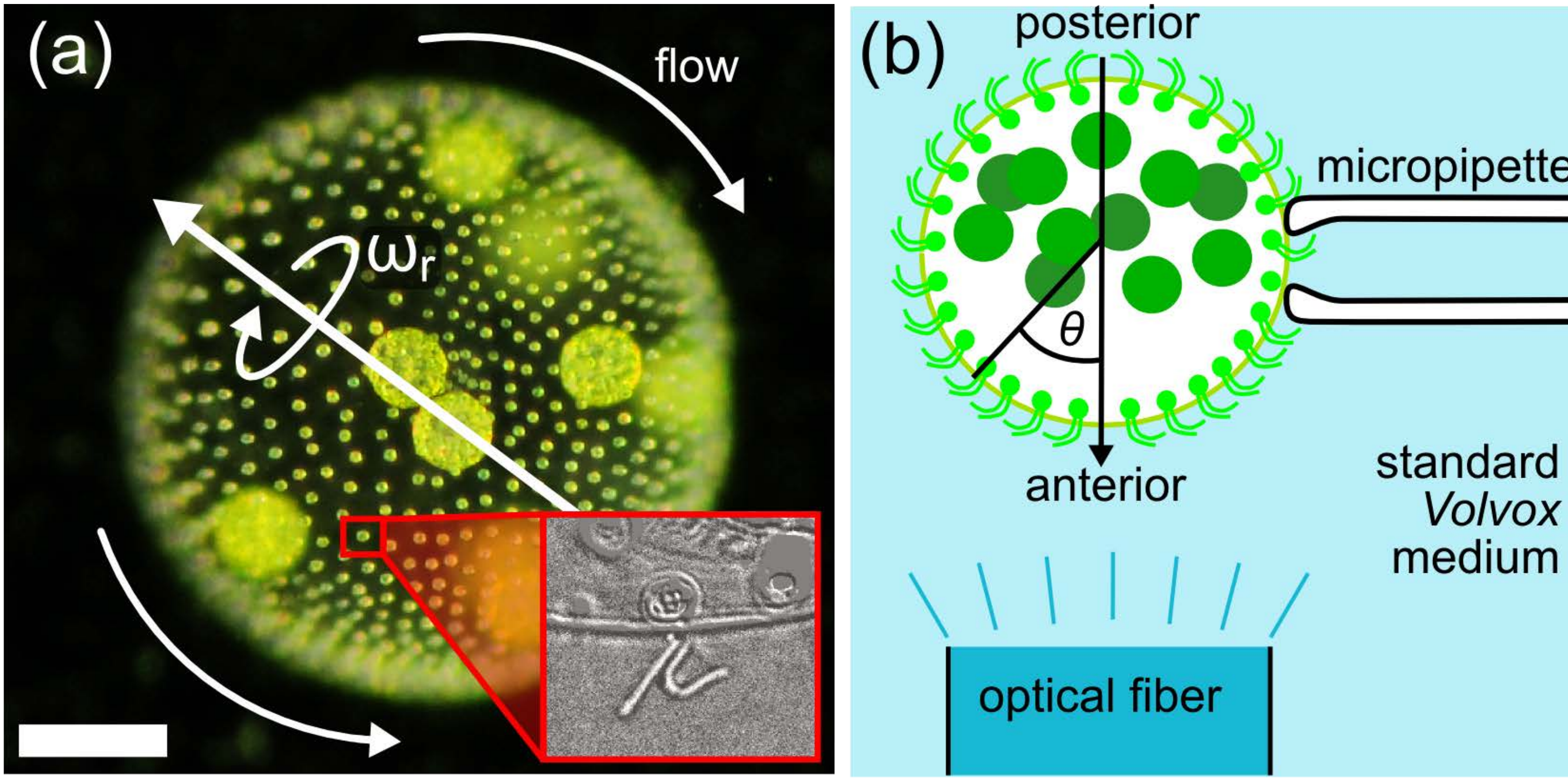
bottom-heaviness relaxation time

Based on Reciprocal Theorem (Stone & Samuel)

In the *Volvox* frame of reference, light direction evolves according to:

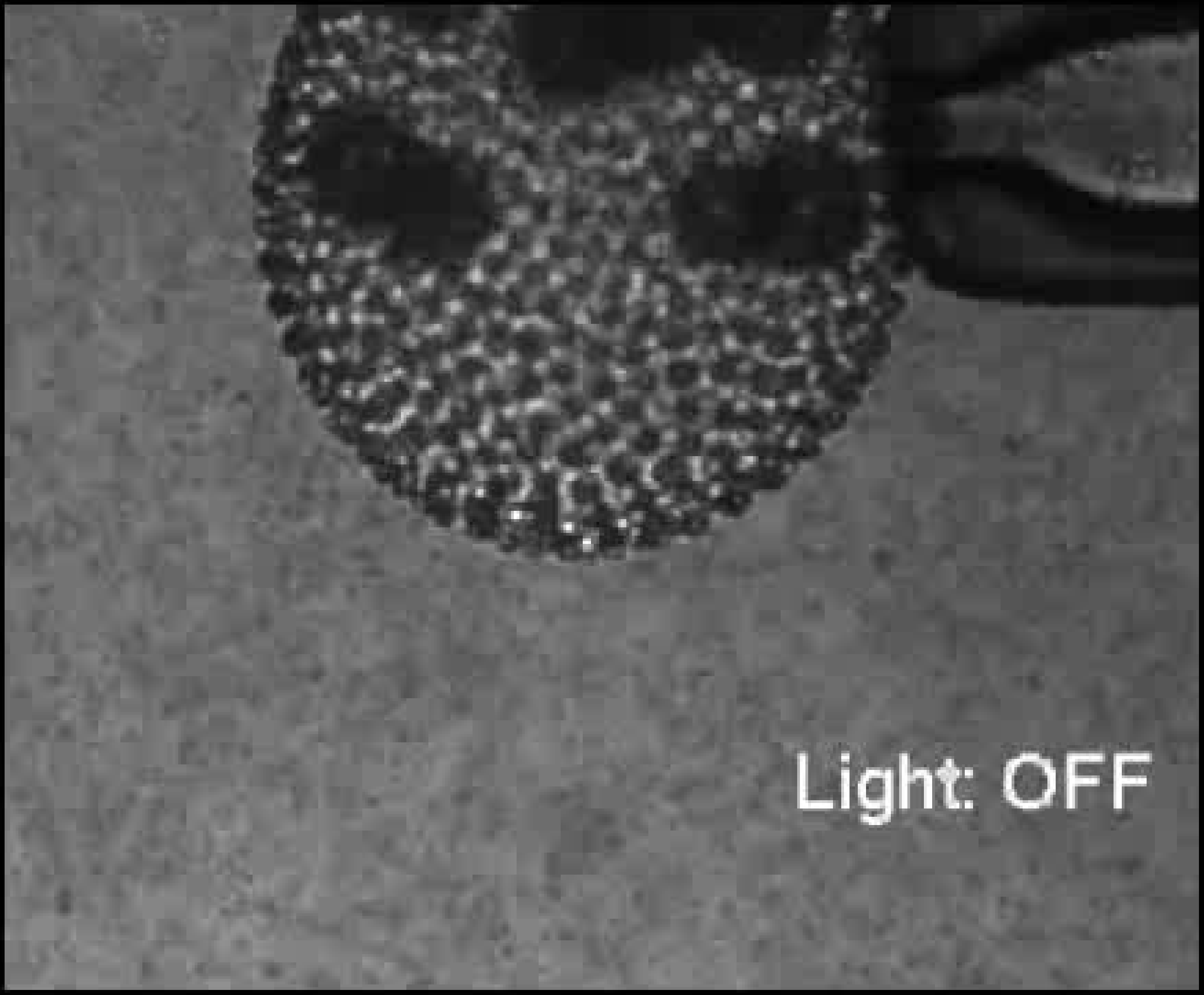
$$\frac{d\hat{\mathbf{l}}}{dt} = -\mathbf{\Omega} \times \hat{\mathbf{l}}$$

Adaptive Flagellar Dynamics and the Fidelity of Multicellular Phototaxis

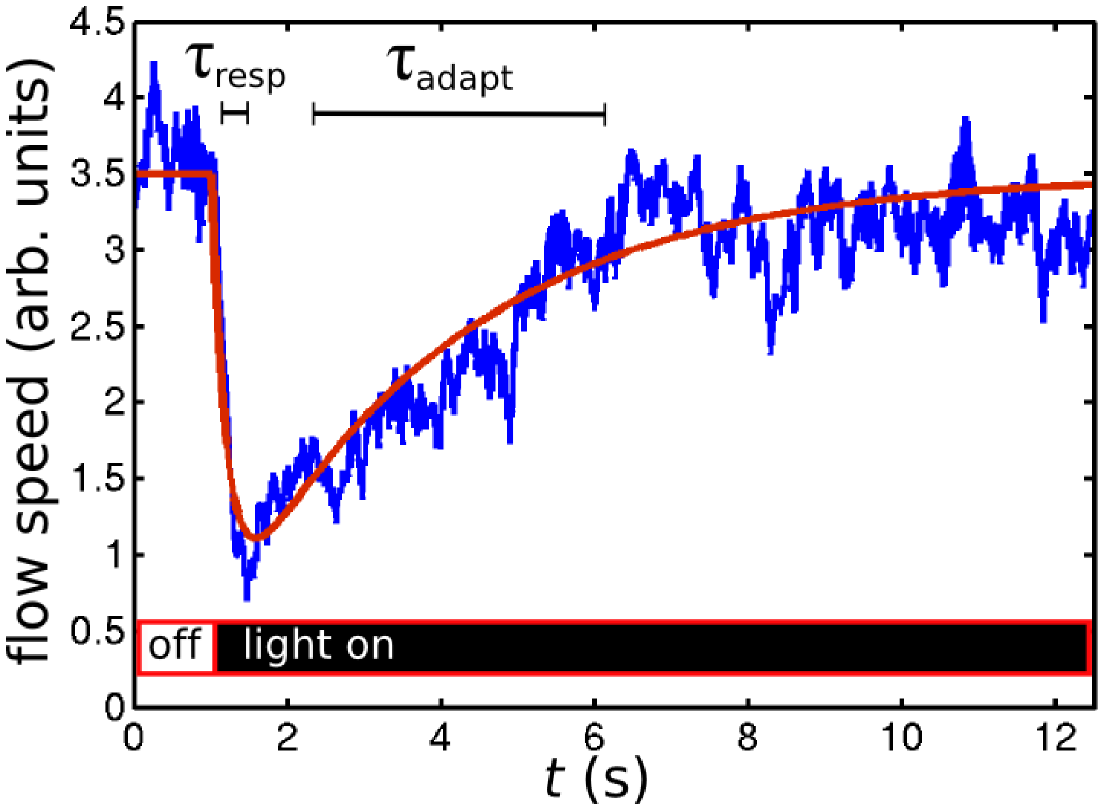


Drescher, Goldstein, Tuval, *PNAS* **107**, 11171 (2010)
See also Ueki, Matsunaga, Inouye, and Hallmann (2010)

Step Response of Flagellar Beating



Dynamic PIV Measurements – Step Response



Adaptive, two-variable model

$$\dot{p} = \frac{(s-h)-p}{\tau_r}$$

$$\dot{h} = \frac{s-h}{\tau_a}$$

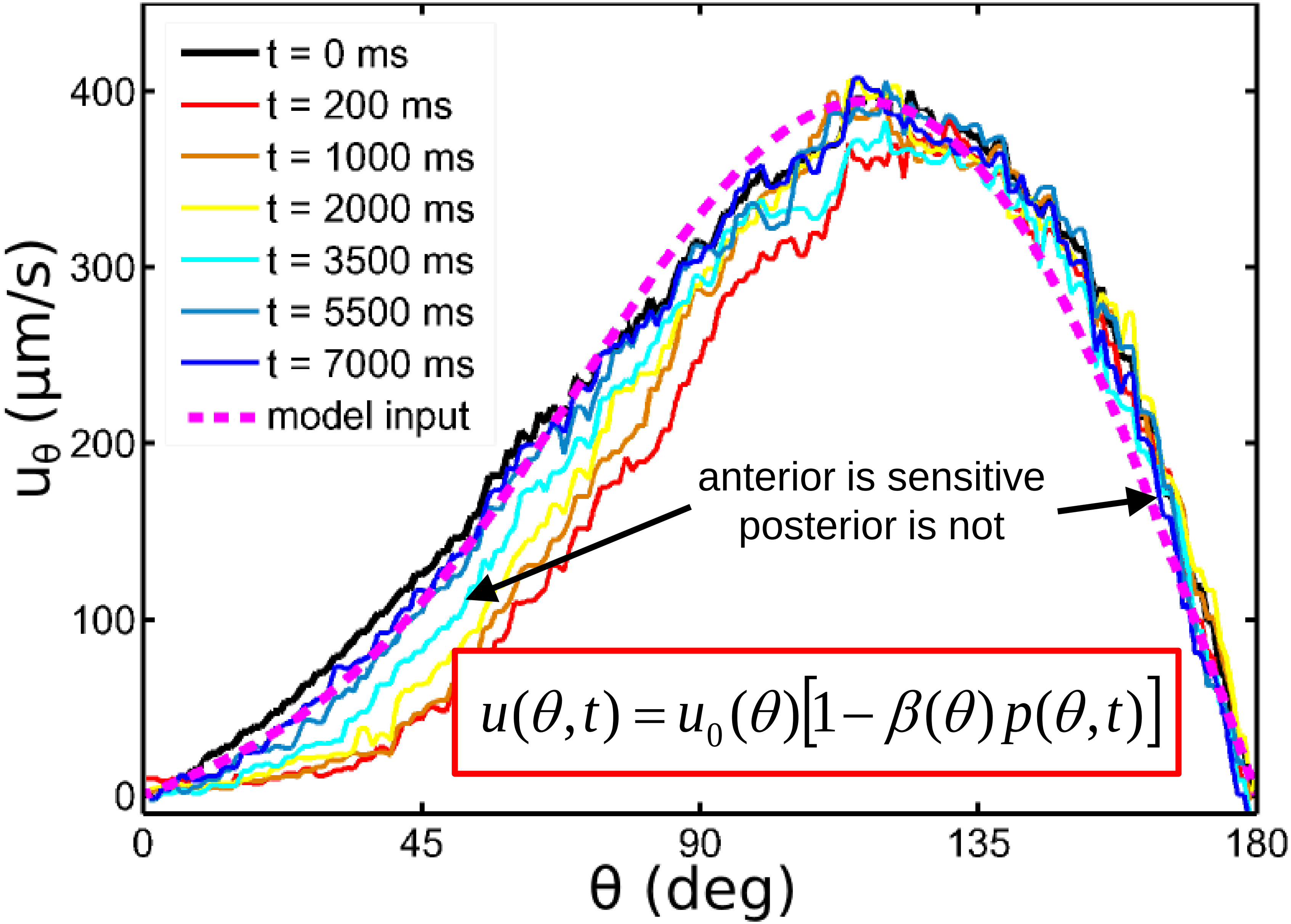
p="photoresponse" amplitude
h="hidden" biochemistry

$$u = u_0(1-\beta p)$$

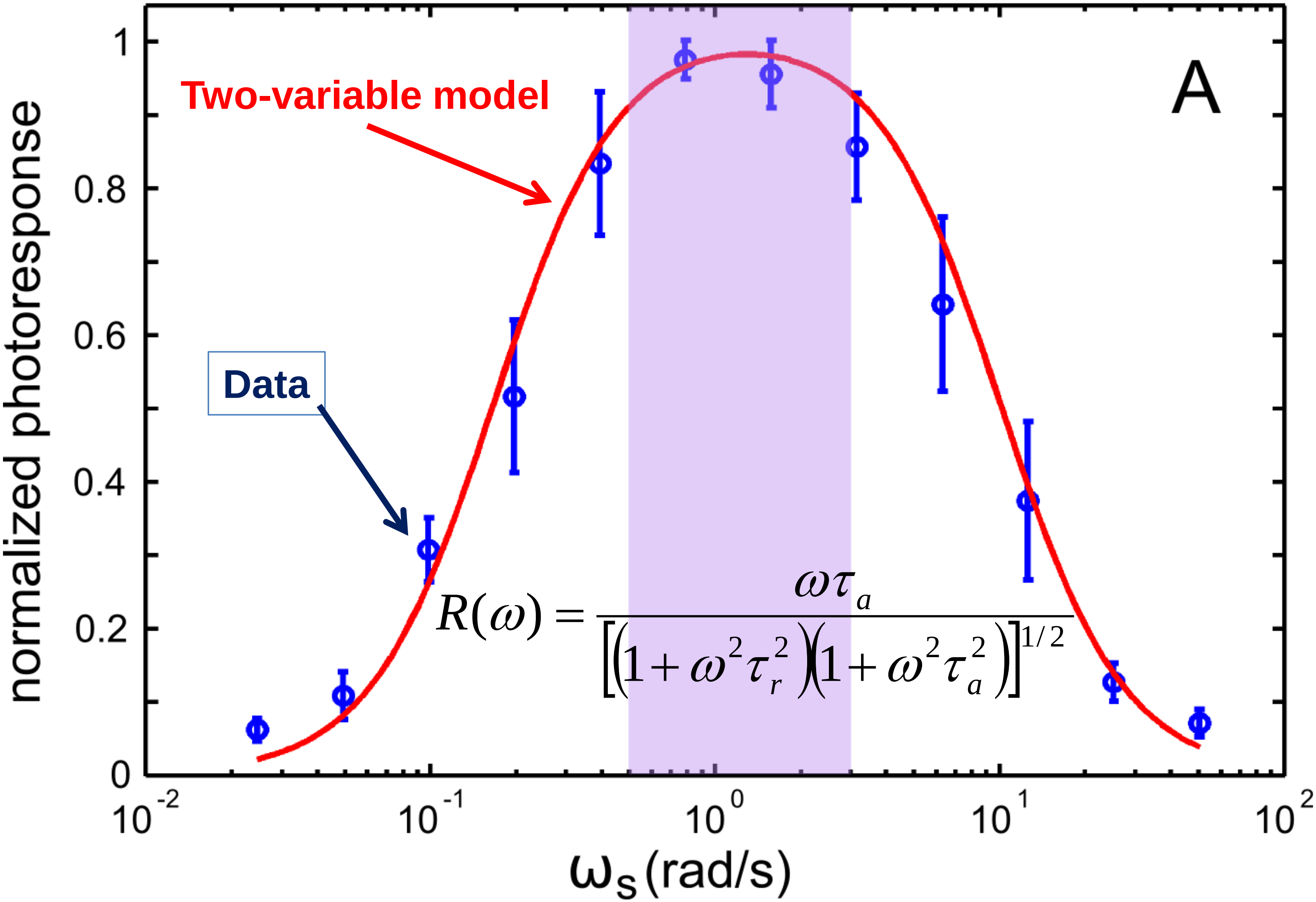
Simple modulation of flow

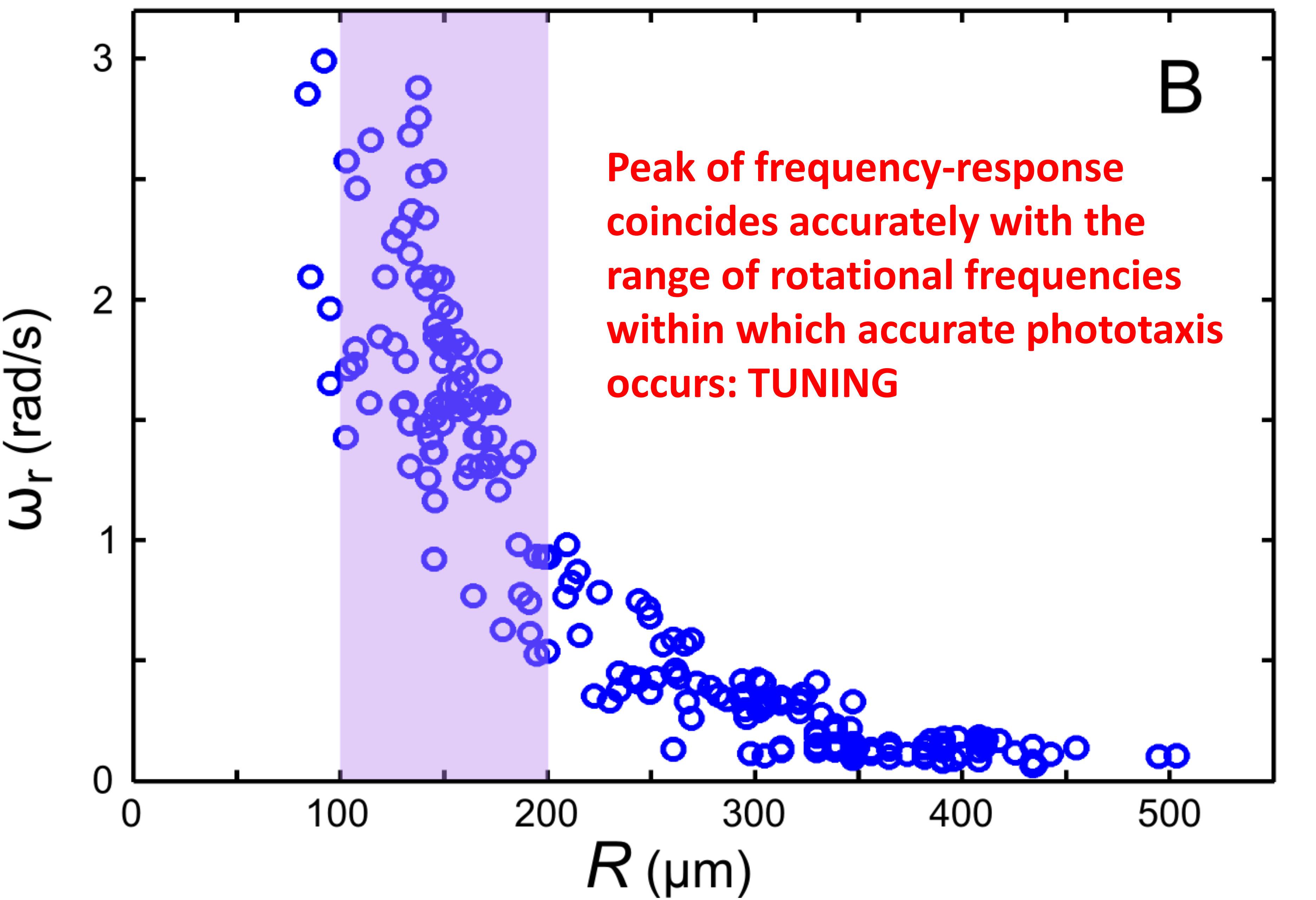
Adaptive dynamics also play
a role in sperm chemotaxis:
Friedrich and Jülicher (2007,09)

Angular Dependence of the Transient Response



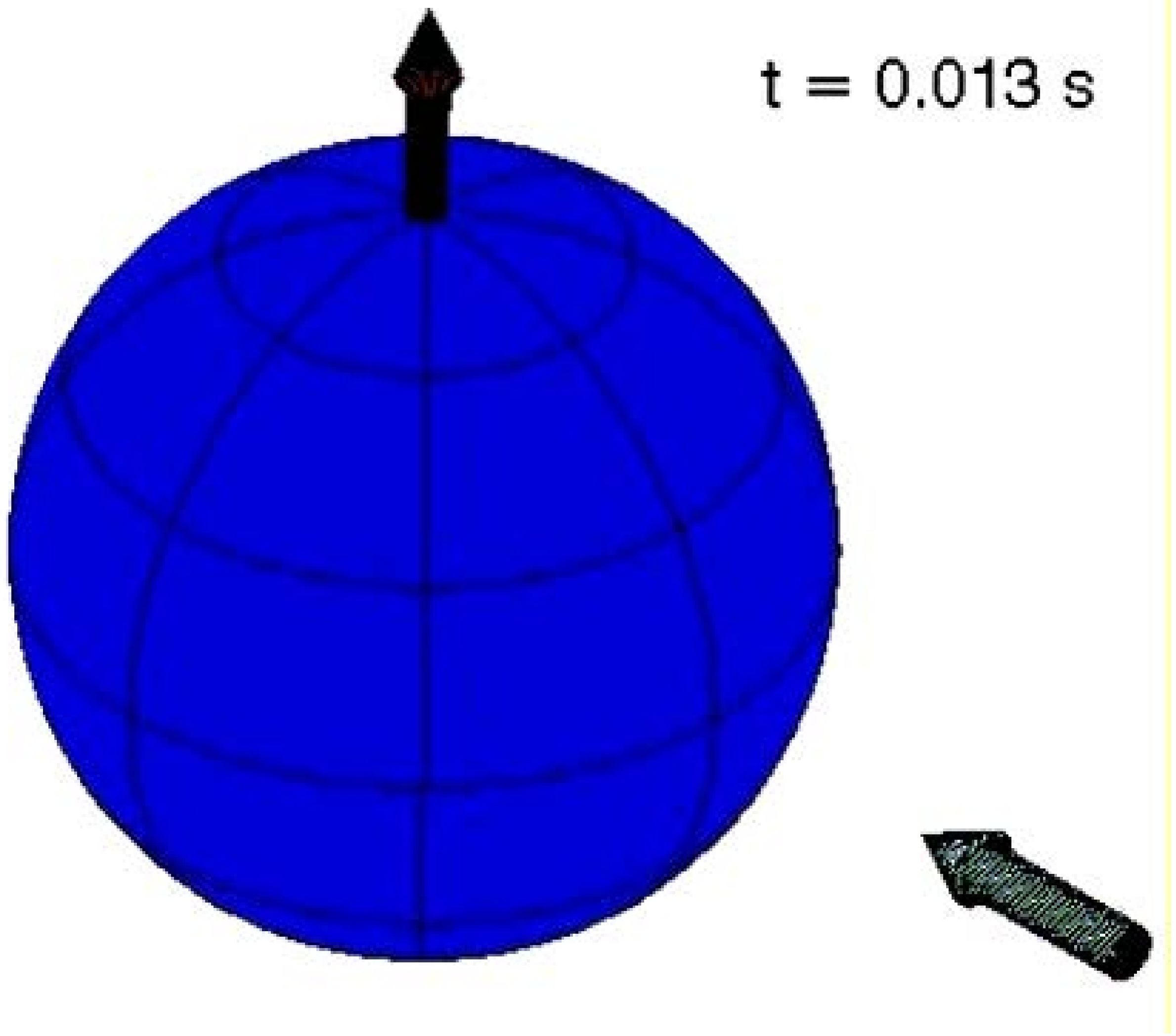
Frequency-Dependent Response





B
Peak of frequency-response coincides accurately with the range of rotational frequencies within which accurate phototaxis occurs: TUNING
ωr (rad/s)
R (µm)
0
1
2
3
0
100
200
300
400
500

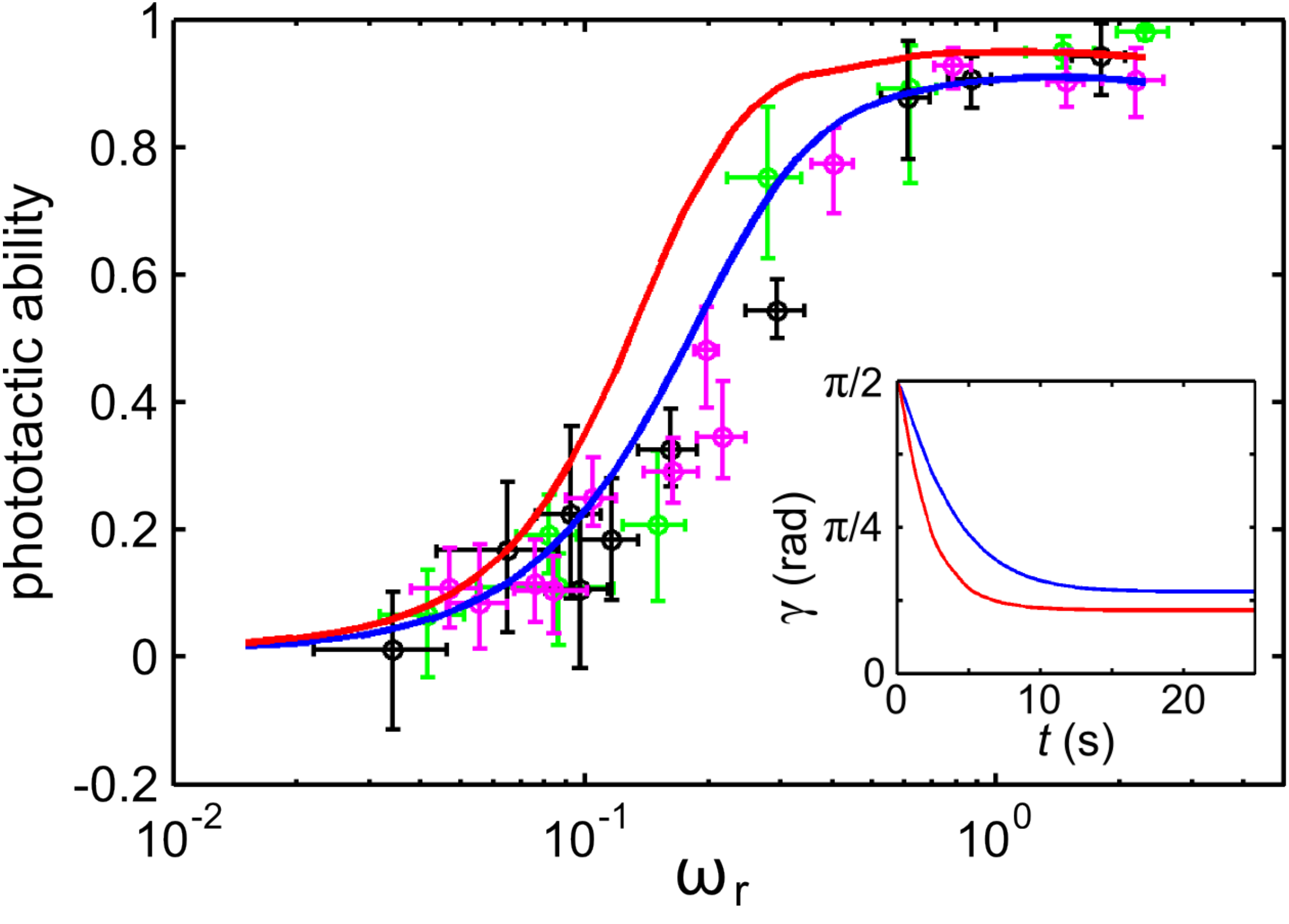
Multicellular Phototaxis as Dynamic Phototropism



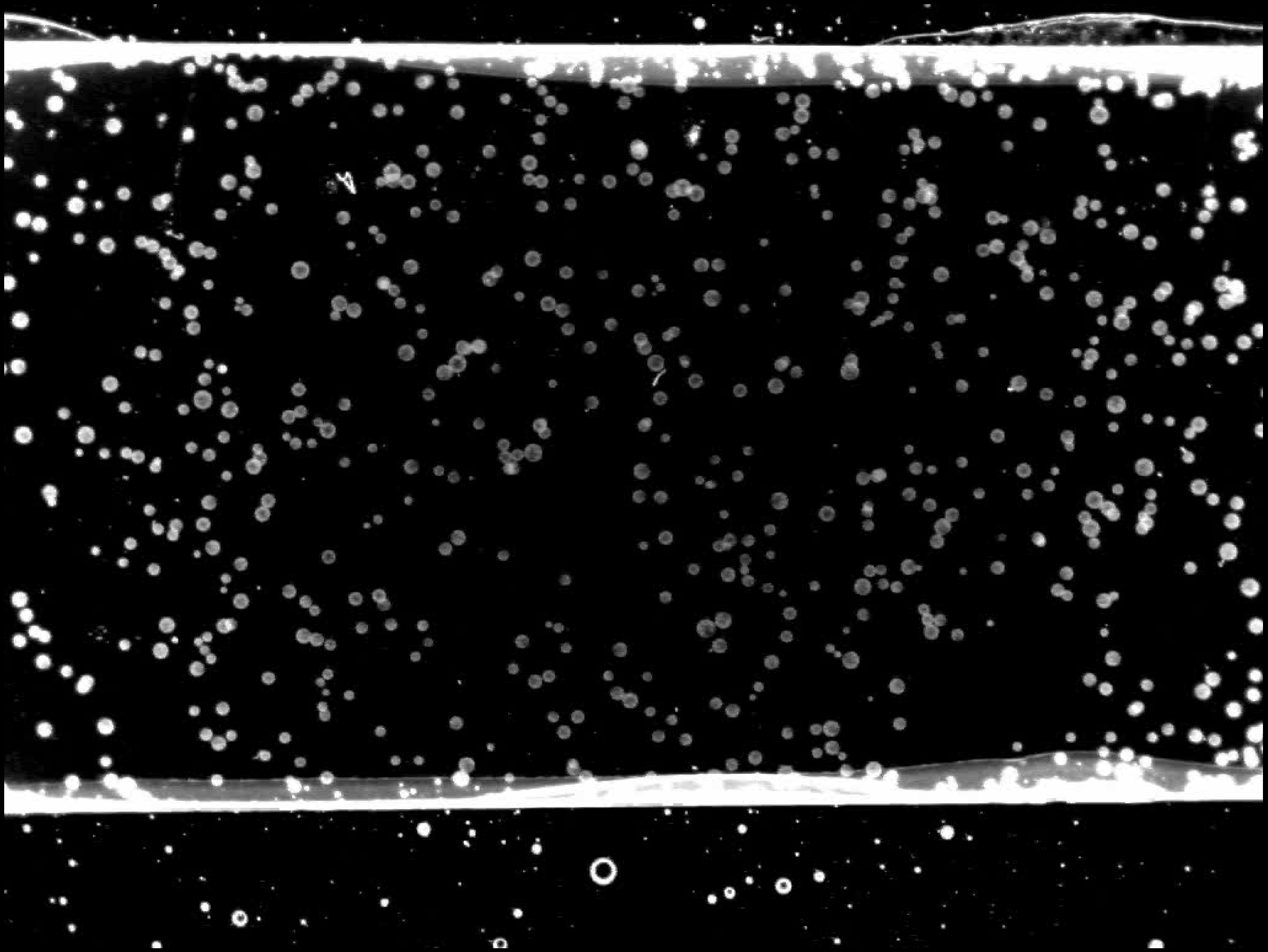
Light direction

Reduced model

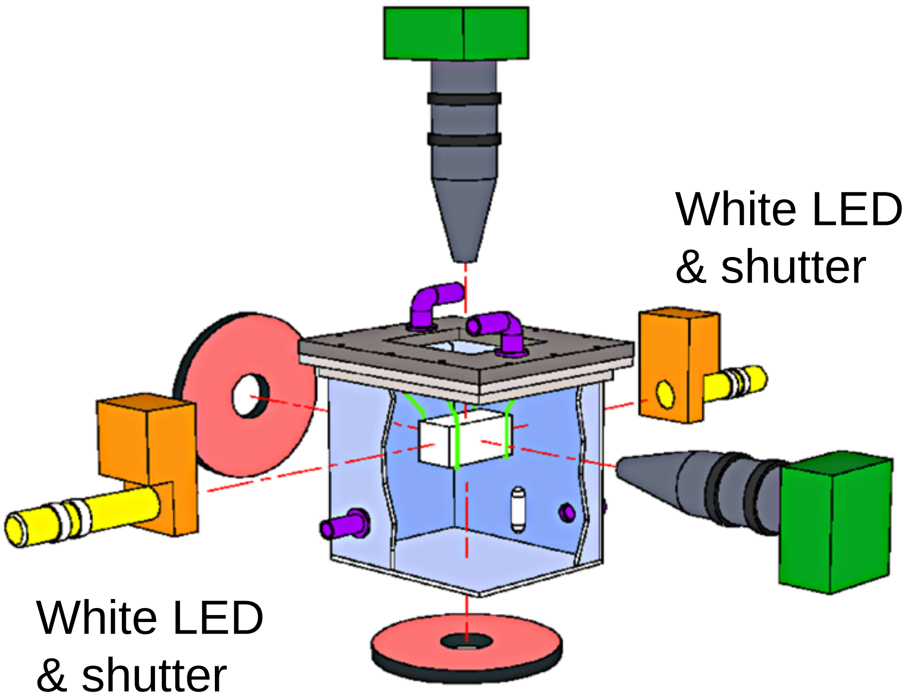
A Test of the Theory

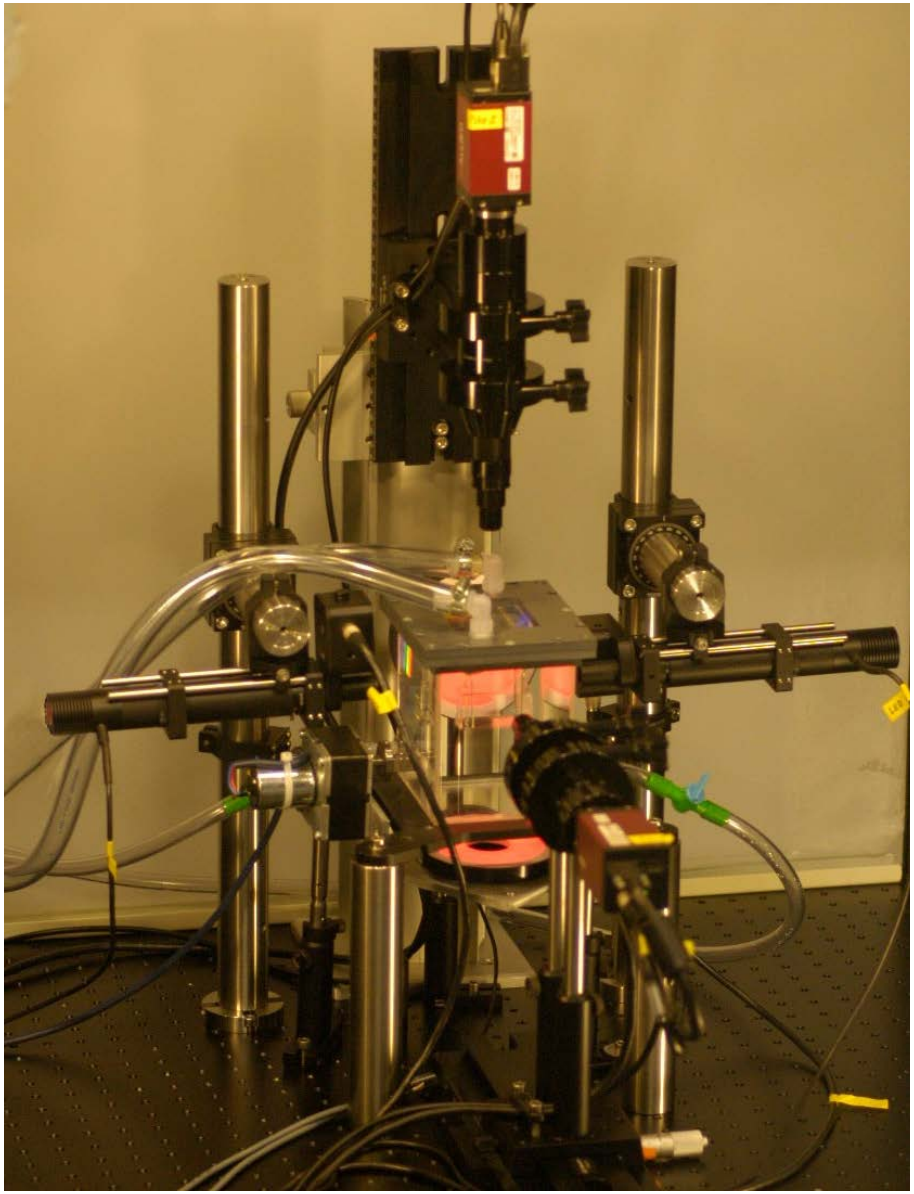


Interacting *Volvox*



Dual-View Apparatus Free of Thermal Convection

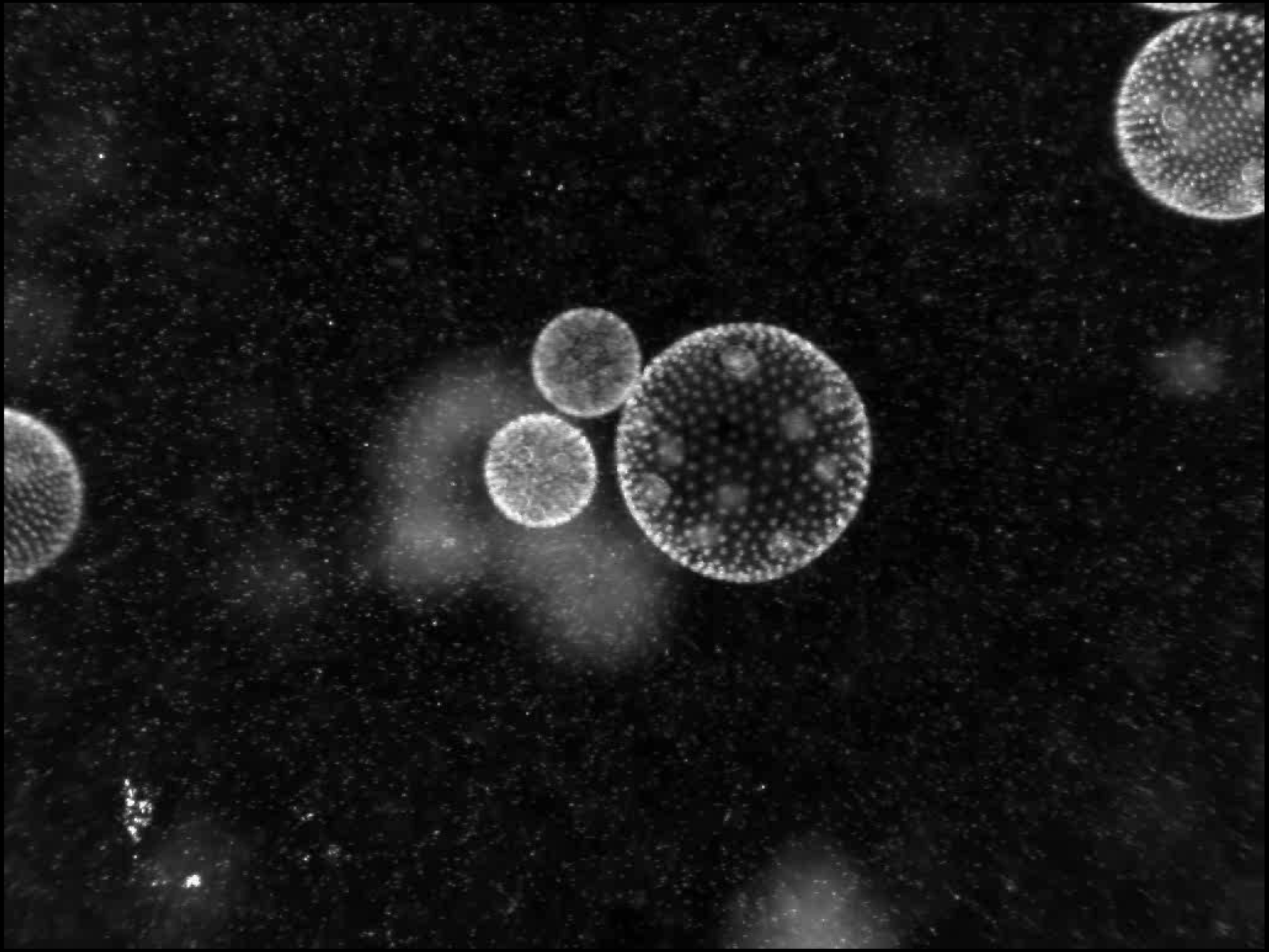




Capable of imaging protists from 10 μm to 1 mm, with tracking precision of ~1 micron, @ 20 fps.

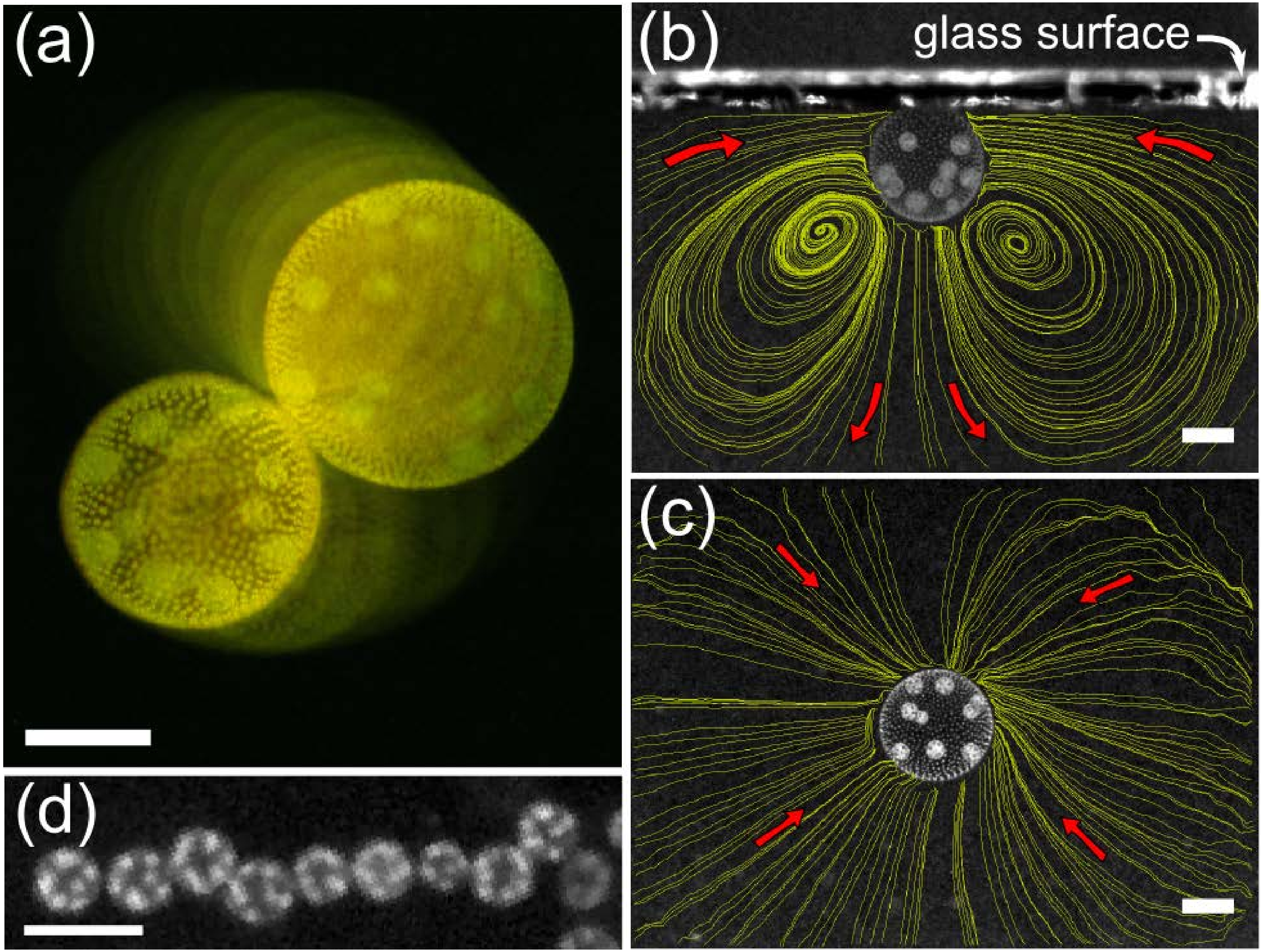
Drescher, Leptos, Goldstein,
Review of Scientific Instruments **80**, 014301 (2009)

Walzing *Volvox*: Orbiting "Bound State"



Drescher, *et al*. PRL (2009)

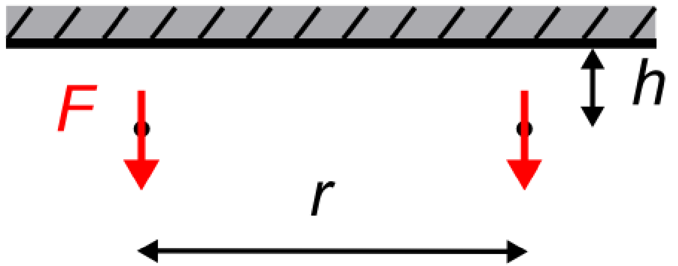
Dual Views with PIV



Model for Mutually-Advected Stokeslets

$$\dot{\mathbf{x}}_i = \mathbf{u}(\mathbf{x}_i) + \mathbf{v}_i$$

$$\dot{\mathbf{p}}_i = \frac{1}{\tau}\mathbf{p}_i \times \left(\hat{\mathbf{z}} \times \mathbf{p}_i\right) + \frac{1}{2}\left(\nabla \times \mathbf{u}\right) \times \mathbf{p}_i$$

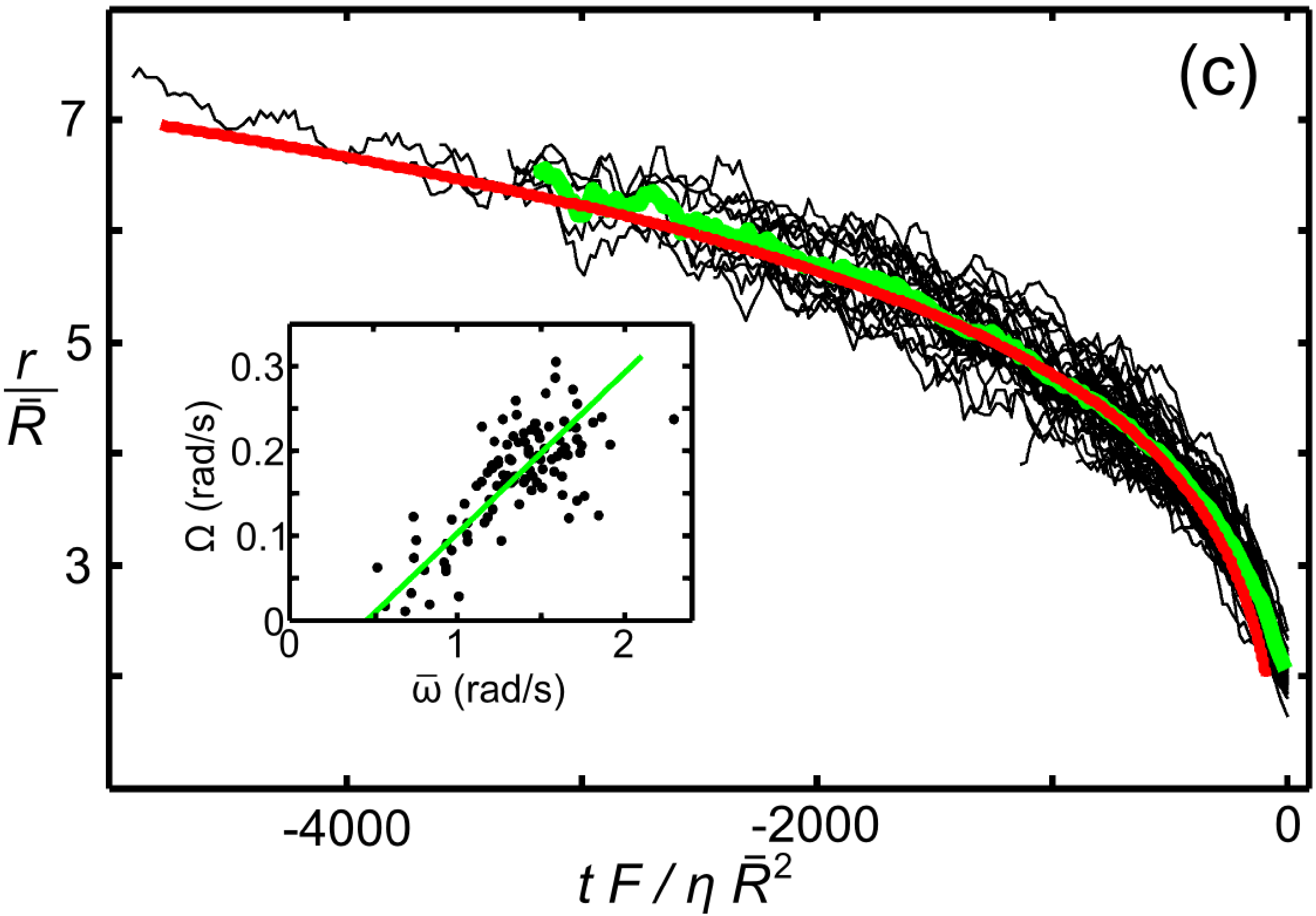


Blake (1971): Flow field of a Stokeslet near a no-slip wall
Squires (2001): Attractive interaction for spheres falling away from a wall

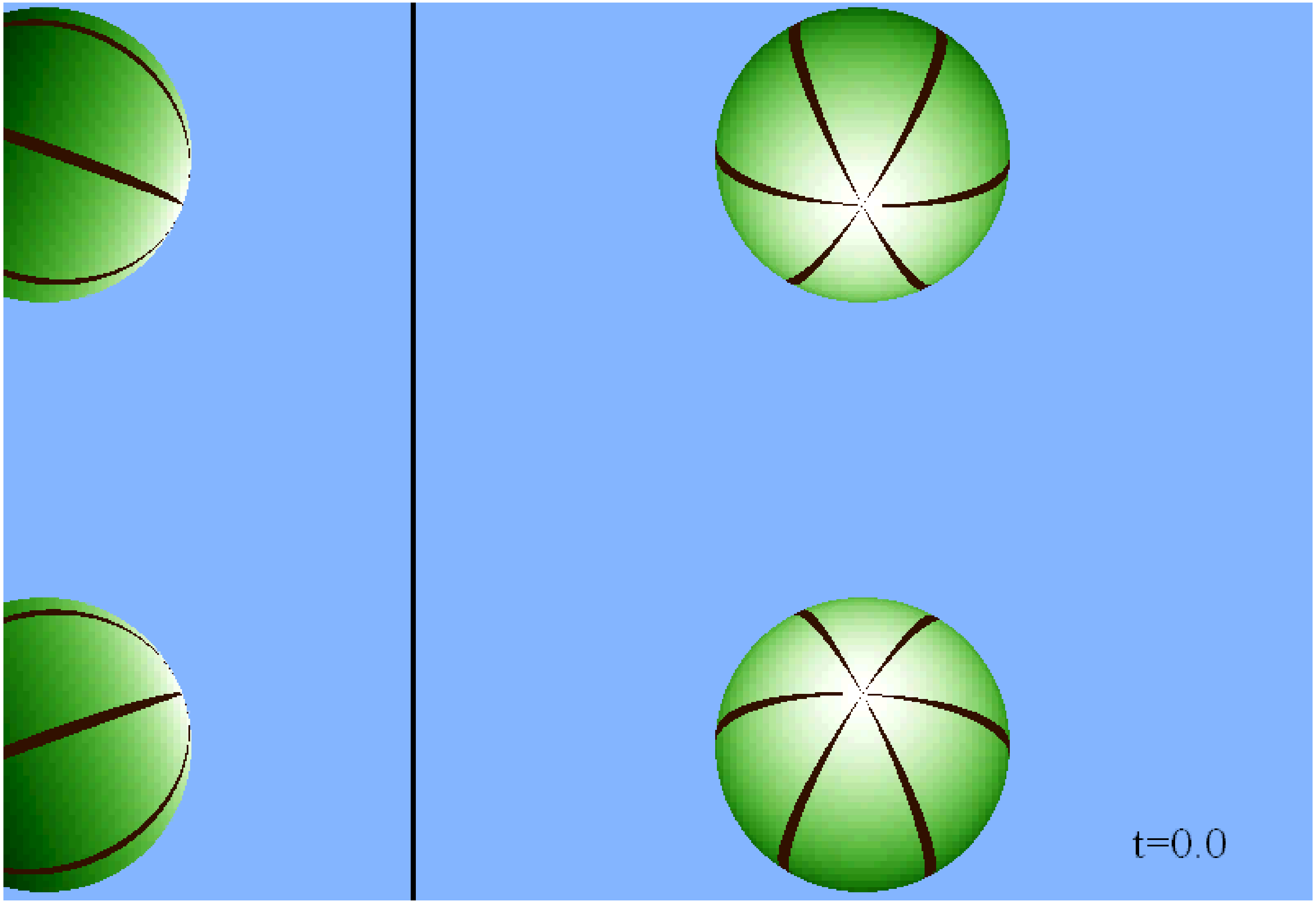
$$\frac{dx}{d\tau} = -\frac{3}{\pi}\frac{x}{\left(x^2+4\right)^{5/2}}$$

$$x = \frac{r}{h}; \quad \tau = \frac{tF}{\eta h^2}; \quad F = 6\pi\eta R\left(U+V\right)$$

Formation of the Bound State

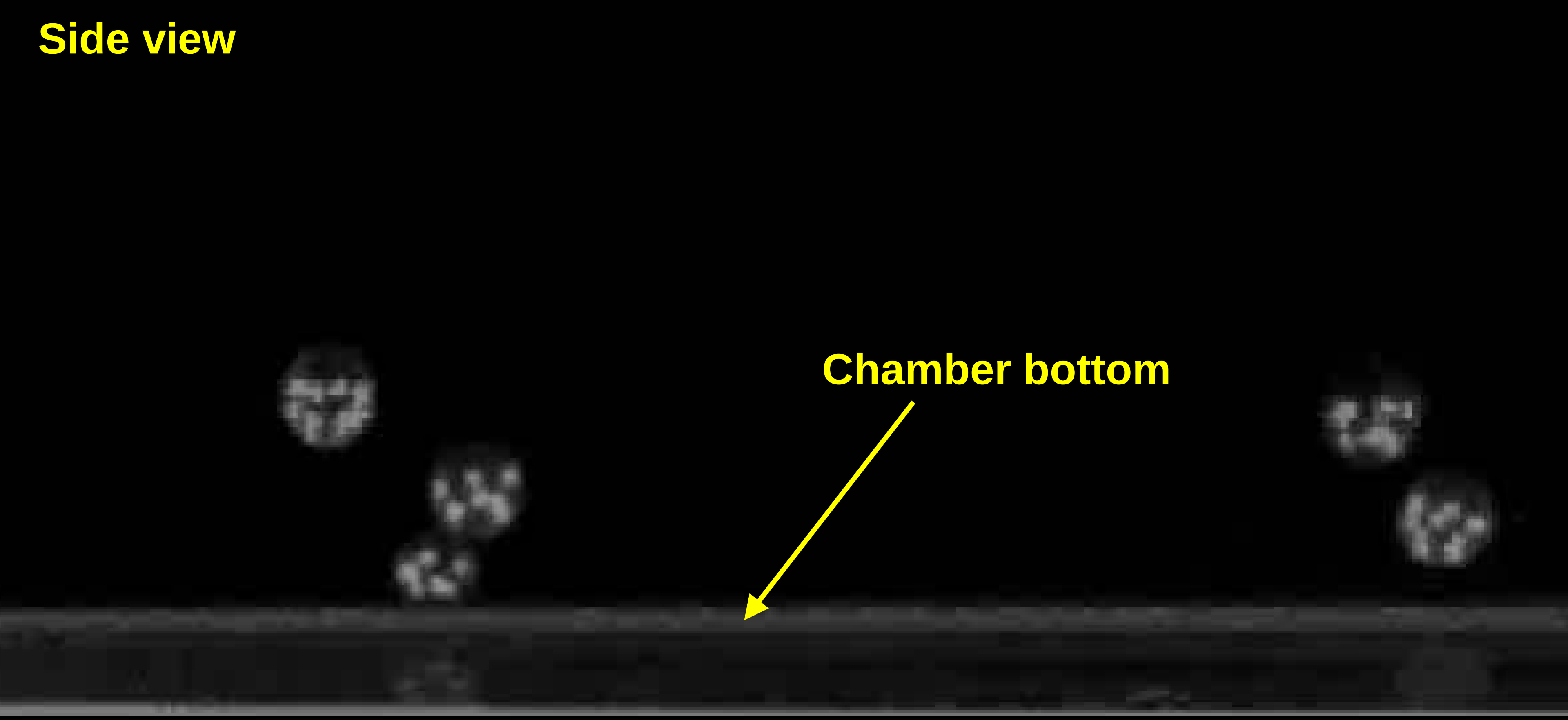


Numerical Studies (Bottom-Heavy Squirmers with Swirl)

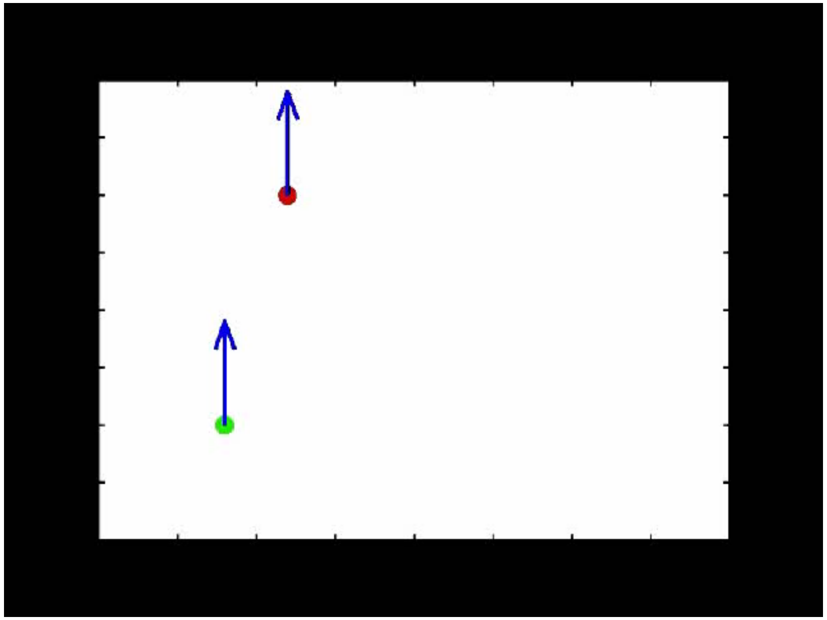


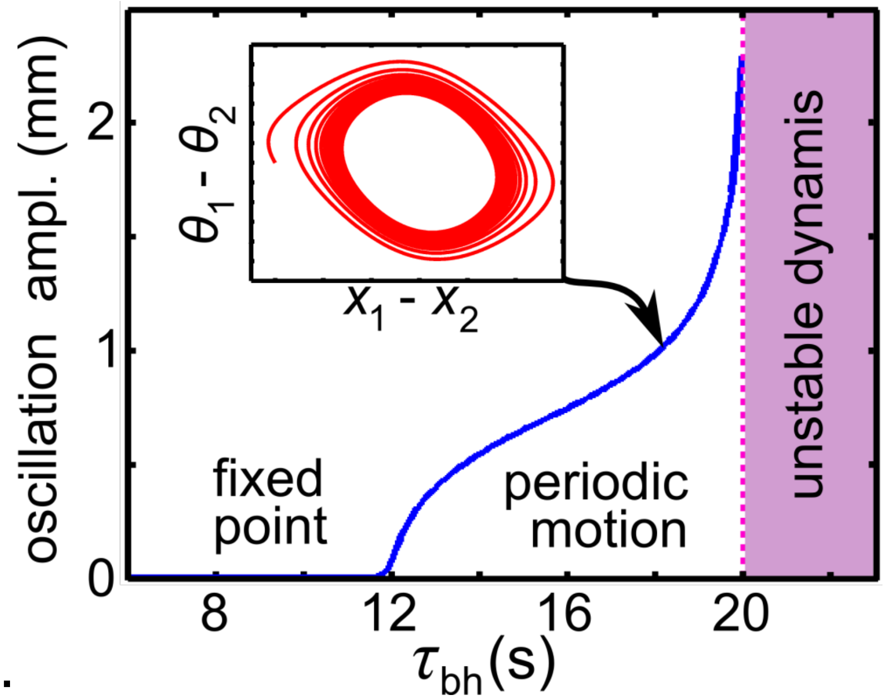
Drescher, *et al*. PRL (2009)

The *Minuet* Bound State



Simplest Model of *Minuet* Bound State



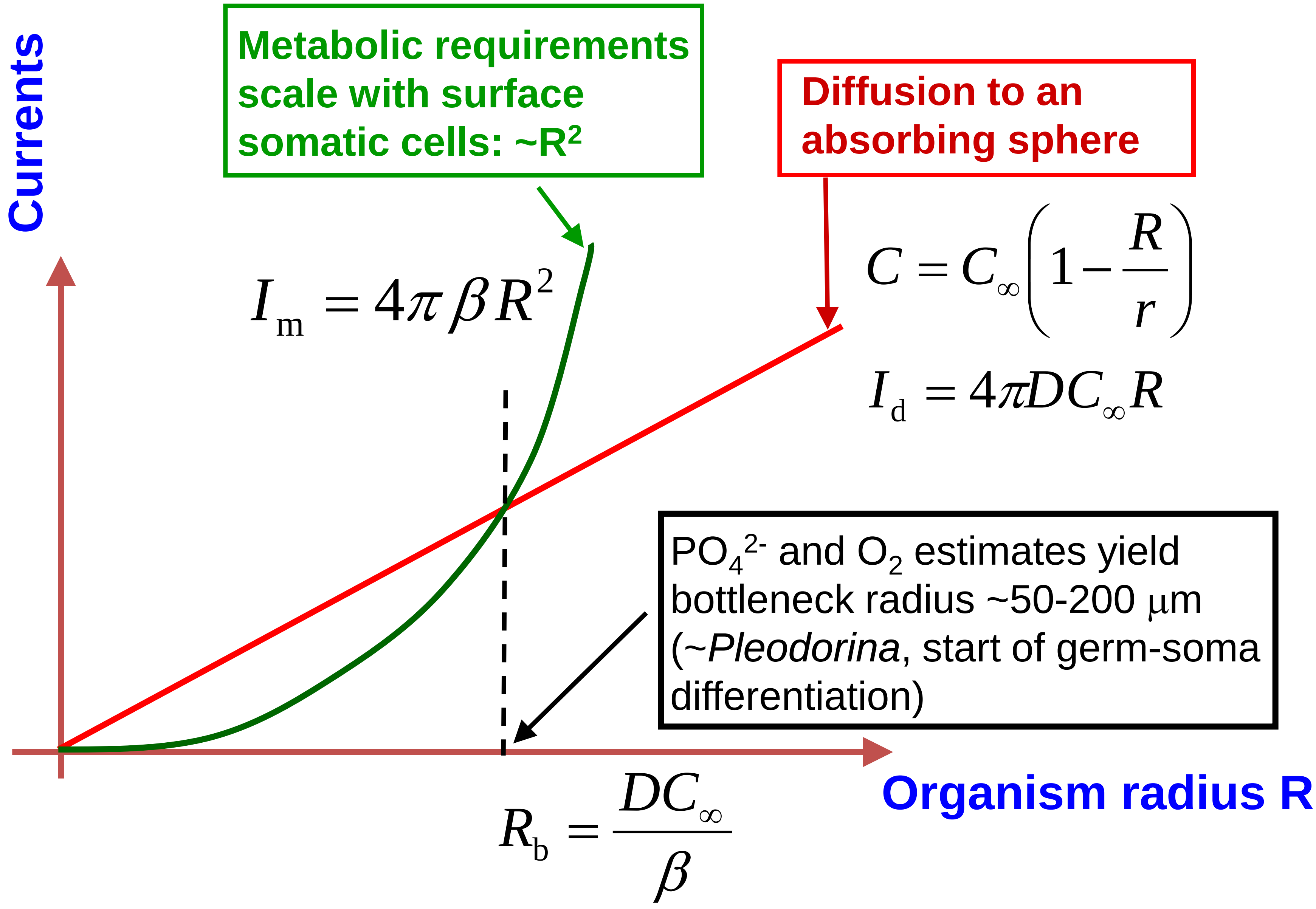


Assumptions of a simple model:

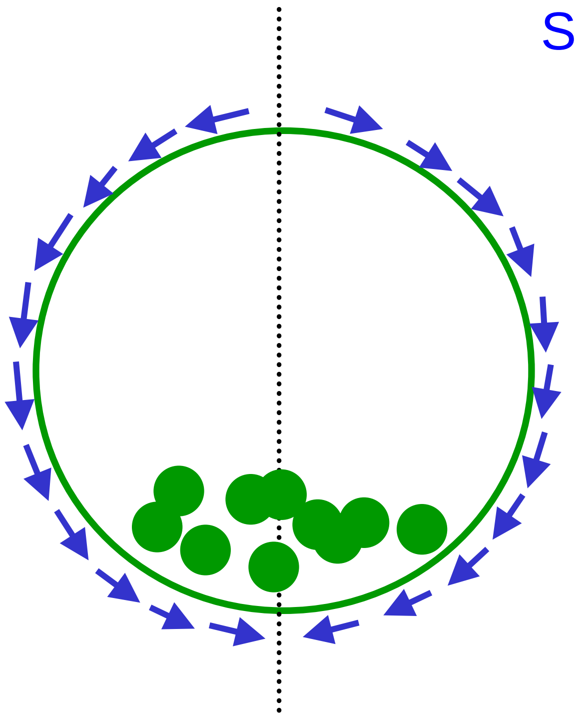
1. *Volvox* hover
2. Each *Volvox* produces a Stokeslet
3. When the *Volvox* axis **k** is tilted from vertical, stokeslets move in horizontal direction
4. Direction of *Volvox* axis changes as given by Pedley & Kessler (1992)

$$\dot{\mathbf{k}} = \frac{1}{\tau_{bh}}\mathbf{k} \times (\mathbf{e}_z \times \mathbf{k}) + \frac{1}{2}\boldsymbol{\omega} \times \mathbf{k}$$

The Diffusional Bottleneck



Flagellar-Driven Flows and Scaling Laws

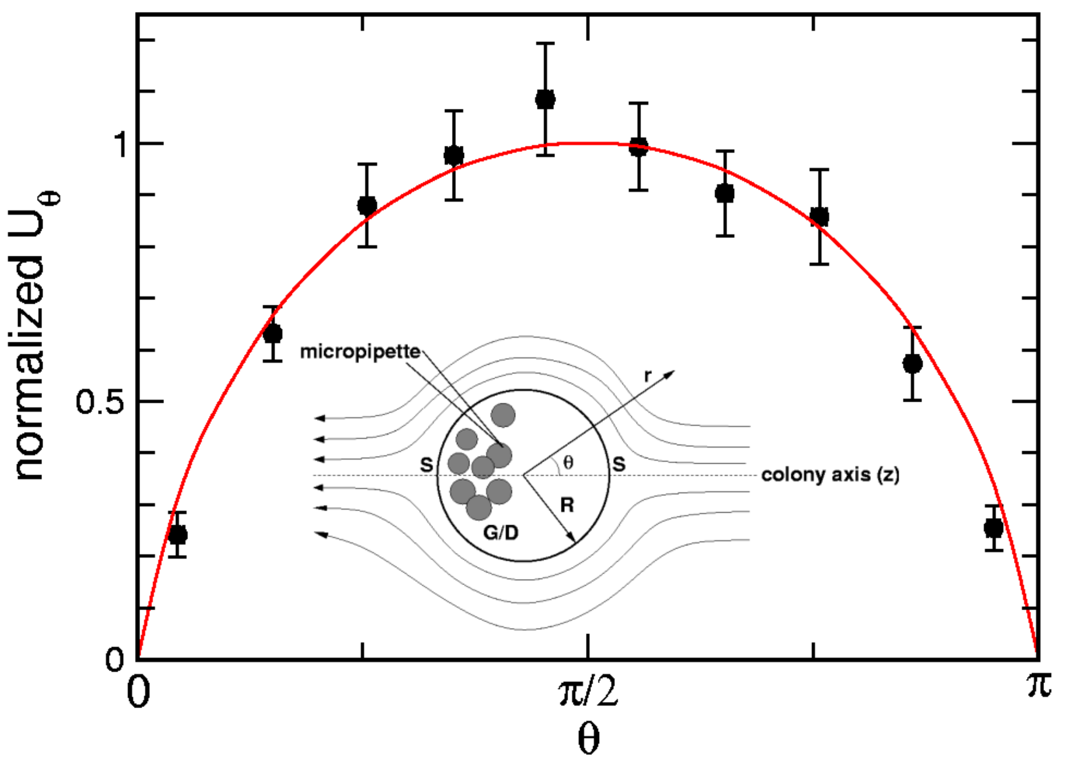


Specified shear stress f at surface

$$u_r = -U\left[\left(c - \frac{R^3}{r^3}\right)P_1(\cos\theta) - \sum_{l=2}^{\infty} A_l(r)P_l(\cos\theta)\right]$$

$$u_\theta = -U\left[\left(d + \frac{R^3}{2r^3}\right)P_1^1(\cos\theta) + \sum_{l=2}^{\infty} B_l(r)P_l^1(\cos\theta)\right]$$

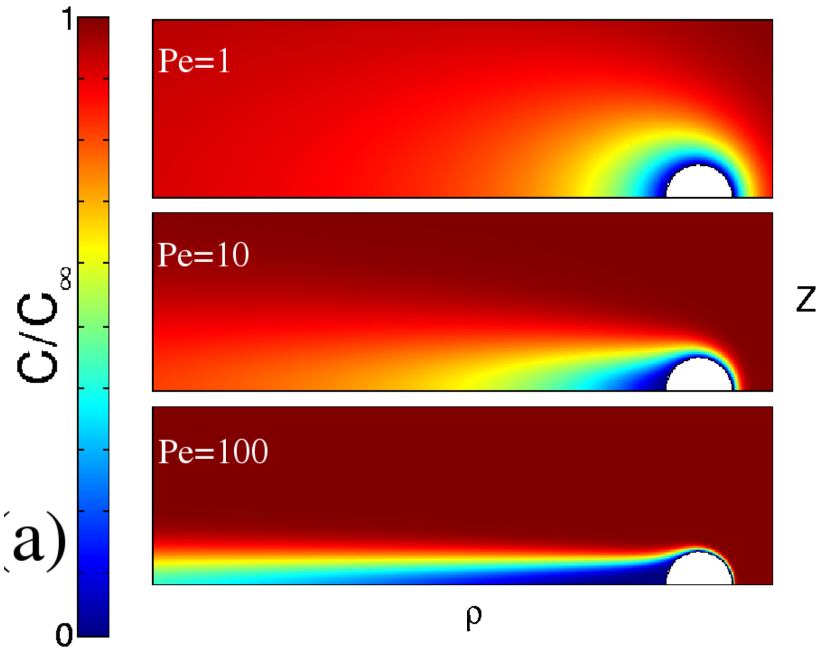
$$U = \frac{\pi f R}{8\eta}$$



Short, Solari, Ganguly, Powers, Kessler & Goldstein, *PNAS* (2006)

Metabolite Exchange

$$\vec{u} \cdot \vec{\nabla} c = D \nabla^2 c$$



Acrivos & Taylor (1962)
heat transport from a solid sphere:

$$current \sim RPe^{1/3}$$

Magar, Goto & Pedley (2003)
prescribed tangential velocity in a model of "squirmers"

$$current \sim RPe^{1/2}$$

$$u_r \frac{\partial C}{\partial y} \approx D \frac{\partial^2 C}{\partial y^2}$$

$$U \frac{\varepsilon}{R} \frac{C}{\varepsilon} \approx D \frac{C}{\varepsilon^2}$$

Boundary layer scale:

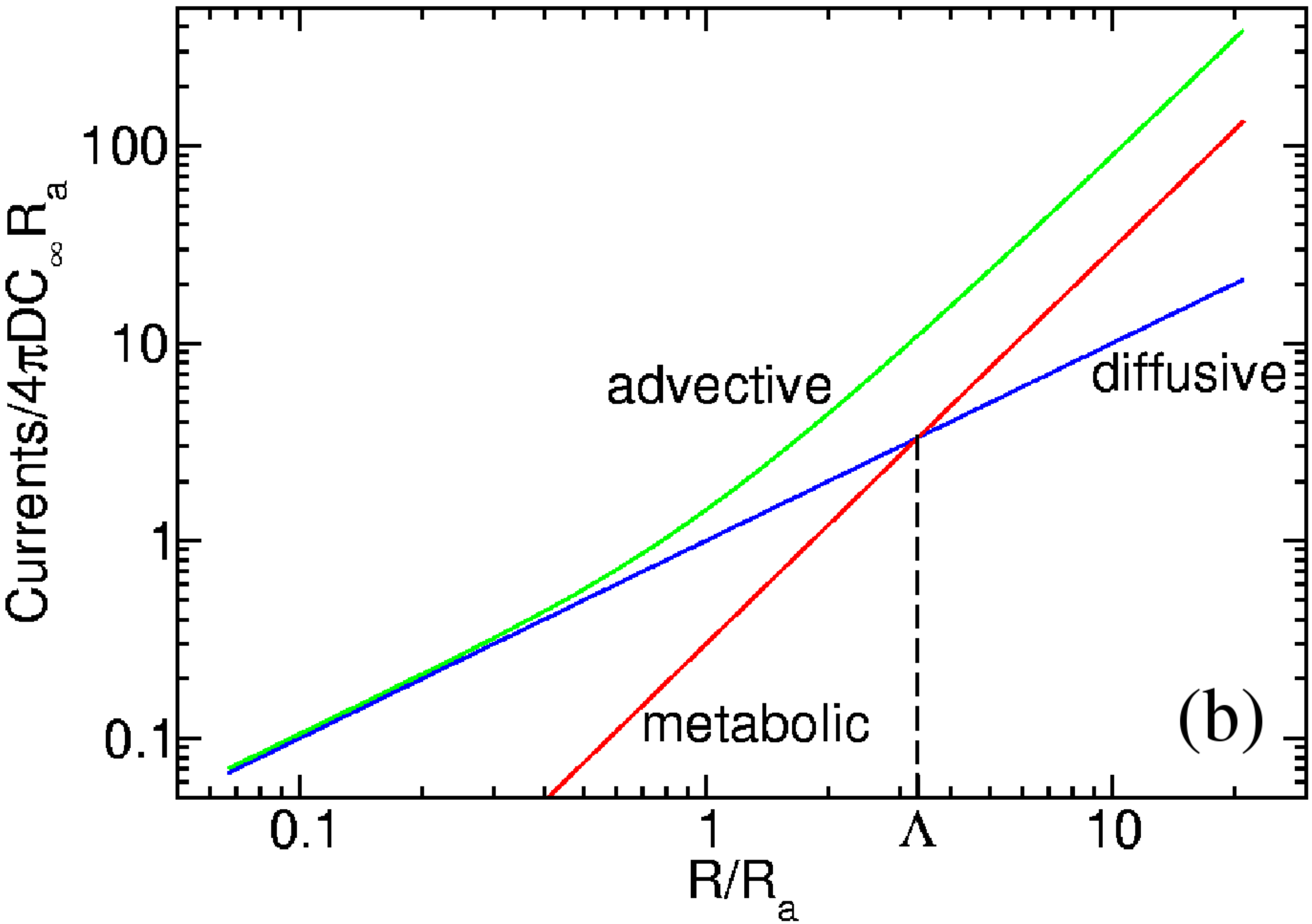
$$\frac{\varepsilon}{R} \sim \left(\frac{UR}{D} \right)^{-1/2} \sim Pe^{-1/2}$$

The Peclet number scales as:

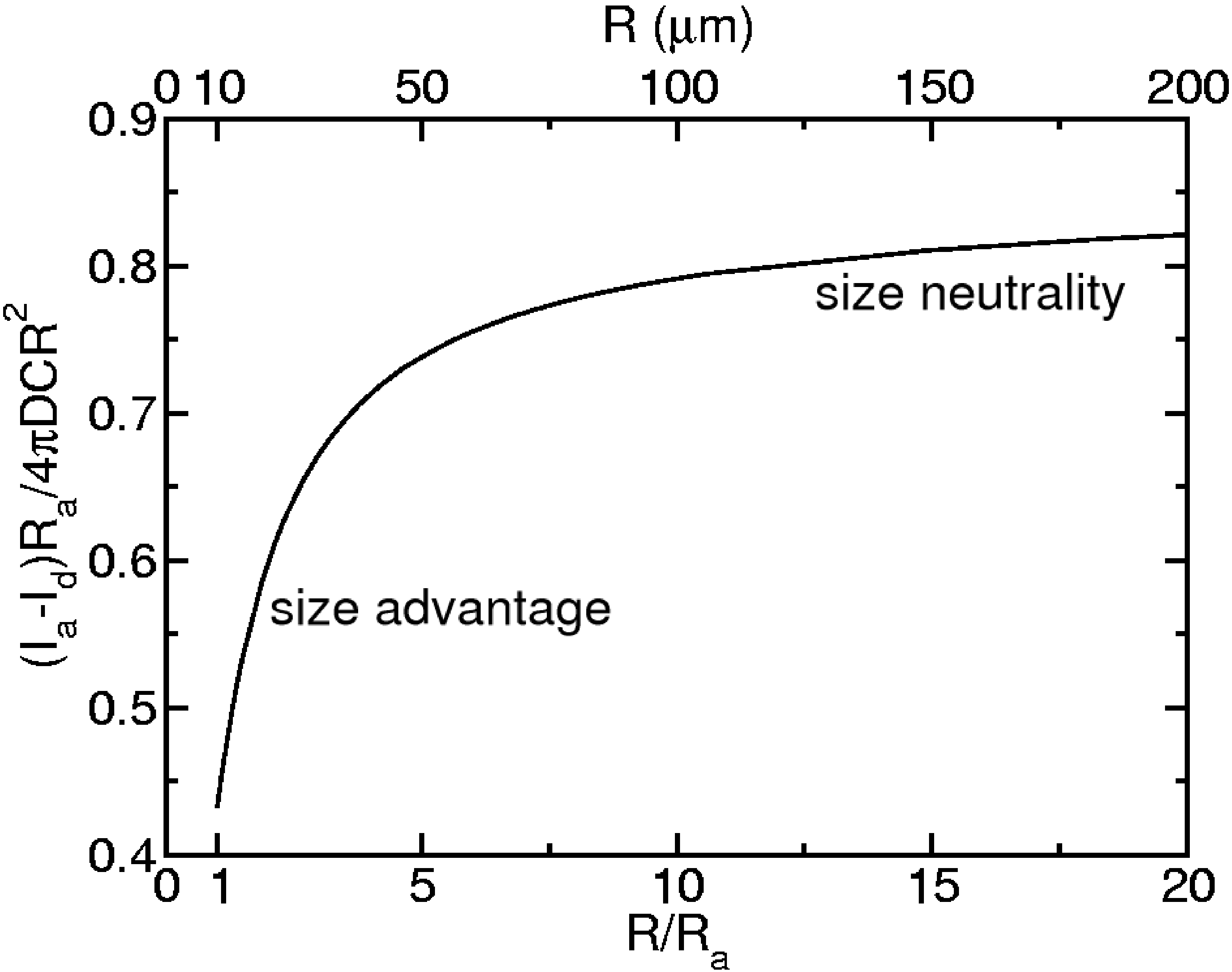
$$Pe = \frac{2Ru_\theta}{D} \approx \left(\frac{R}{R_a} \right)^2 ; \quad R_a = \left(\frac{4\eta D}{\pi f} \right)^{1/2} \approx 10\,\mu m < R_b$$

Bottleneck Bypassed (!)

$$I_a = -DR^2 \int d\Omega \frac{\partial C}{\partial r} \approx 4\pi DR^2 \frac{C_\infty}{R_a} \approx 4\pi DC_\infty RPe^{1/2} \sim R^2 \text{ (!)}$$



Advantage of Size



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Timothy J. Pedley - DAMTP
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Rick Michod – Arizona
Jerry P. Gollub – Haverford/Cambridge
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Schlumberger EPSRC
BBSRC bioscience for the future
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wellcome trust Investigator