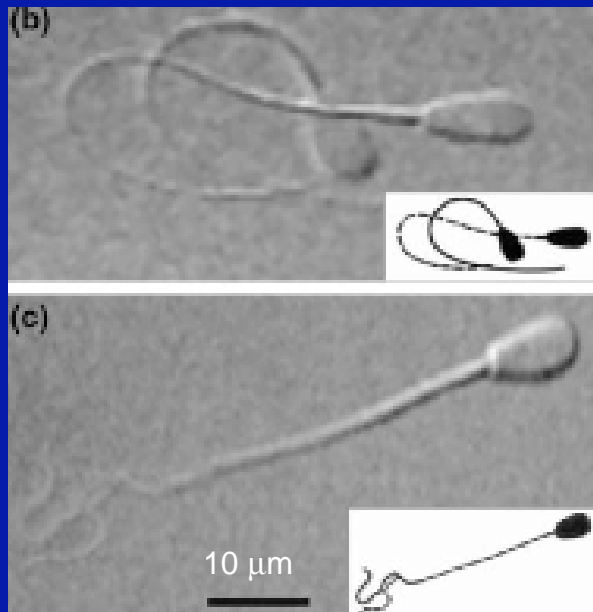


“Life at low Reynolds number” revisited

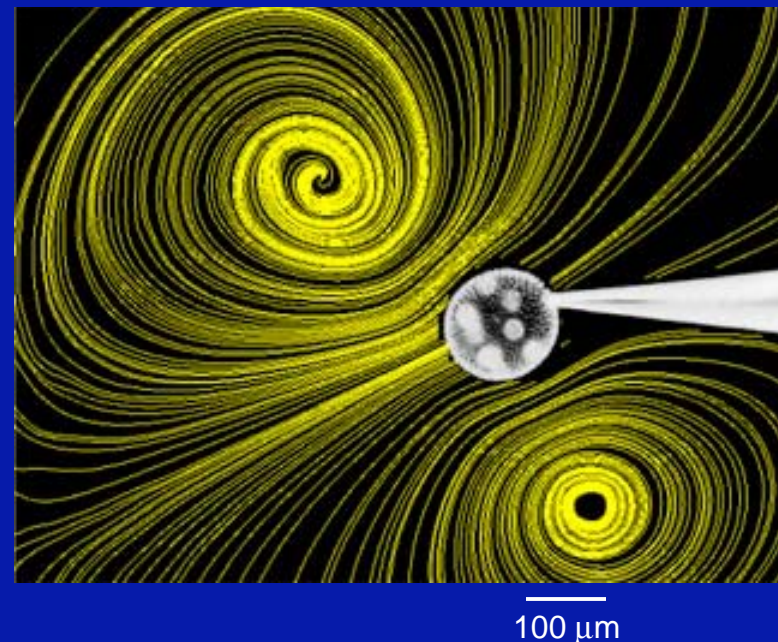
T.R. Powers, Brown University

- Purcell’s 1977 *Am. J. Phys.* paper
- Swimming in a viscoelastic medium (with H. Fu, C. Wolgemuth)
- Nutrient uptake in *Volvox* (with M. Short, C. Solari, S. Ganguly, J. Kessler, & R. Goldstein; PNAS, May 2006)

Ho & Suarez, 2001



Short et al., 2006



Support: NSF grants DMS-0615919, NIRT-0404031, & CMS-0093658 (TRP); NSF grant CTS-0623870 and NIH grant GM072004 (CWW); NSF grants DEB-0075296 (CAS) & PHY-0551742 (MBS, SG, JOK, REG)



American Journal of Physics, Vol. 45, No. 1, January 1977

Life at low Reynolds number

E. M. Purcell

Lyman Laboratory, Harvard University, Cambridge, Massachusetts 02138

(Received 12 June 1976)

$$\mathcal{R} = \text{Re} = \frac{\tau_{\text{vis}}}{\tau_{\text{conv}}} = \frac{LV}{\nu}$$

Kinematic reversibility of Stokes flow

If $Q \ll 1$:

Navier - Stokes:

$$-\nabla p + \eta \nabla^2 \vec{v} = \cancel{\rho \frac{\partial \vec{v}}{\partial t}} + \cancel{\rho (\vec{v} \cdot \nabla) \vec{v}}$$

Ludwig, 1930

If $Q \ll 1$:

Time doesn't matter. The pattern of motion is the same, whether slow or fast, whether forward or backward in time.

The Scallop Theorem



Purcell 1977 American Journal of Physics

Stirring vs. Diffusion

time for transport by stirring: $\frac{l}{v}$

time for transport by diffusion: $\frac{l^2}{D}$

stirring works if $\frac{lv}{D} > 1$

$$S \equiv \frac{lv}{D}$$

$\leftarrow 10^{-5} \text{ cm}^2/\text{sec}$

$$\left[R \equiv \frac{lv}{v} \right]$$

$\leftarrow 10^{-2} \text{ cm}^2/\text{sec}$



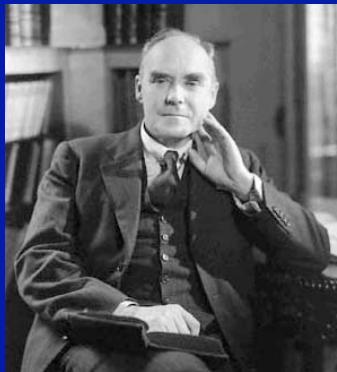
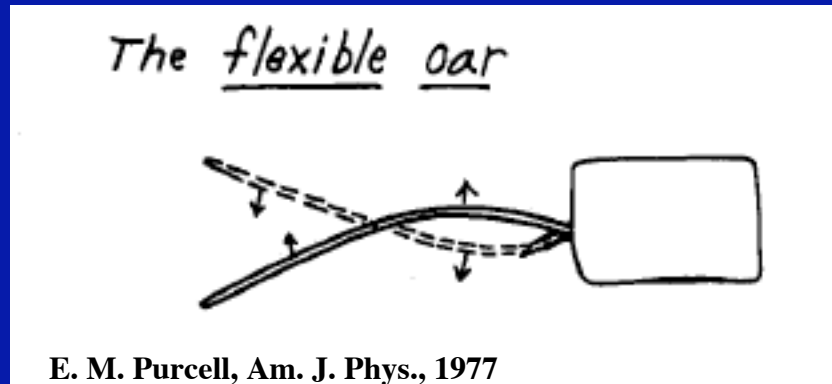
$$S \approx 10^{-2}$$

local stirring accomplishes nothing

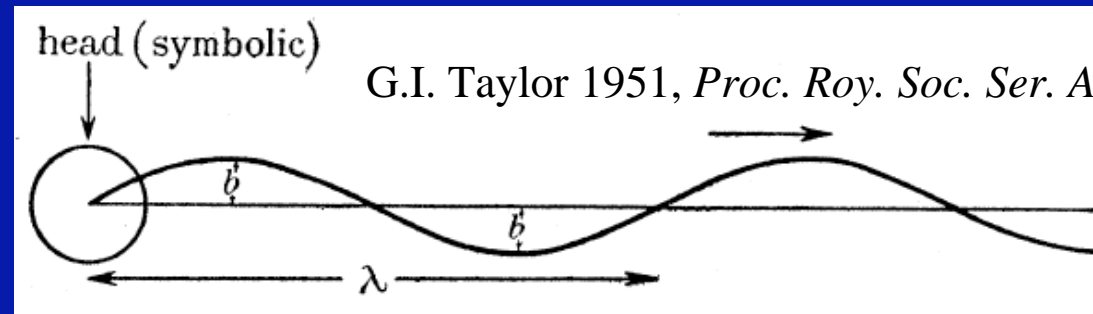
Theory of swimming in a viscoelastic medium (unpublished work)

with Fu & Wolgemuth

One way to elude the “scallop theorem”



www-history.mcs.st-and.ac.uk/history



$$\langle v \rangle = c(qb)^2 / 2 = \omega qb^2 / 2$$

$$q = 2\pi / \lambda \quad c = \omega / q = \text{wave speed}$$

Scallop theorem & Taylor's sheet

- Fix the wavenumber q
- Displacement Δx in one period

$$\Delta x = \langle v \rangle 2\pi / \omega = \pi q b^2$$

- Δx is independent of ω !
- E.g. one period of a fast left-mover followed by a slow right-mover leads to no net motion

Viscoelastic Swimming

- Stress relaxes to viscous stress---linear Maxwell model

$$\sigma_{ij} + \tau \dot{\sigma}_{ij} = \eta \dot{\gamma}_{ij}$$

- Valid for small displacements, but we need to work to 2nd order in the displacement!
- Swimming velocities are *the same* for prescribed shape changes in viscous and linear viscoelastic models (Fulford, Katz, Powell 1998)

Nonlinear viscoelasticity

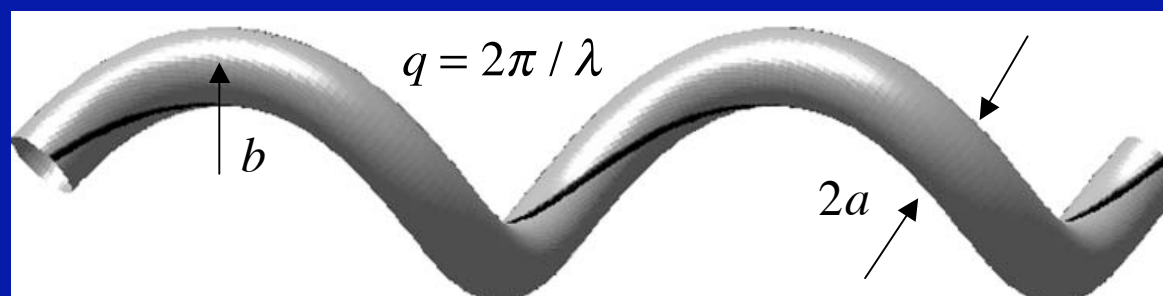
- Continuum version of microscopic elastic dumbbell model---upper-convected Maxwell model

$$\sigma_{ij} + \tau \overset{\nabla}{\sigma}_{ij} = \eta \dot{\gamma}_{ij}$$

$$\overset{\nabla}{\sigma}_{ij} = \frac{\partial \sigma_{ij}}{\partial t} + v^k \frac{\partial \sigma_{ij}}{\partial x^k} - \frac{\partial v_i}{\partial x^k} \sigma_{kj} - \sigma_{ik} \frac{\partial v_j}{\partial x^k}$$

- Nonlinear terms lead to normal stress differences
- Oldroyd (1950): constitutive relation cannot depend on motion through space

Fat sinusoidal/helical wave



$$bq \ll aq \ll 1$$

$$\langle v_{\text{sine}} \rangle = \frac{cq^2 b^2}{2} \left(\frac{1}{1 + \omega^2 \tau^2} \right) \left[1 + O\left(\frac{1}{-\log(qa)} \right) \right]$$

$$\langle v_{\text{helix}} \rangle = 2 \langle v_{\text{sine}} \rangle$$

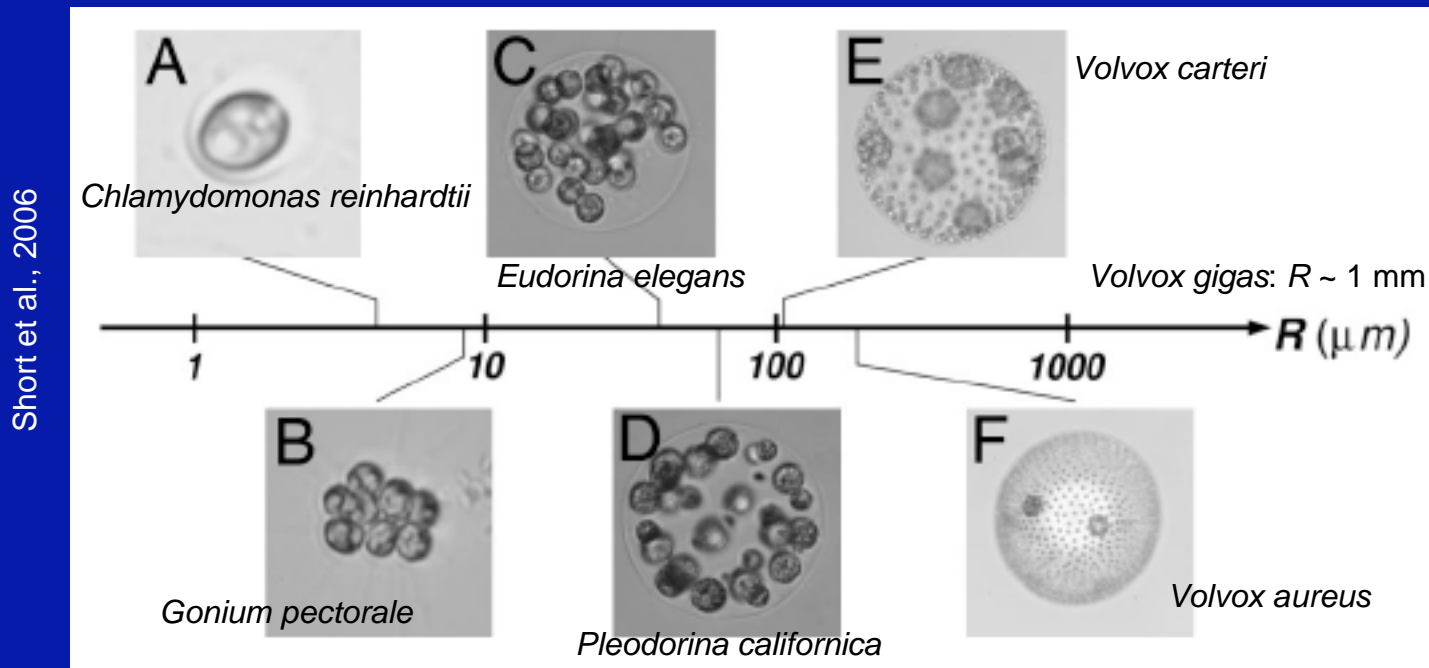
- Nonlinear ω -dependence spoils scallop theorem
- Sine result is the same form as 2d (sheet) calculation of E. Lauga 2007!

Nutrient uptake in *Volvox*

Short, Solari, Ganguly, Powers,
Kessler, Goldstein, *PNAS* 2006

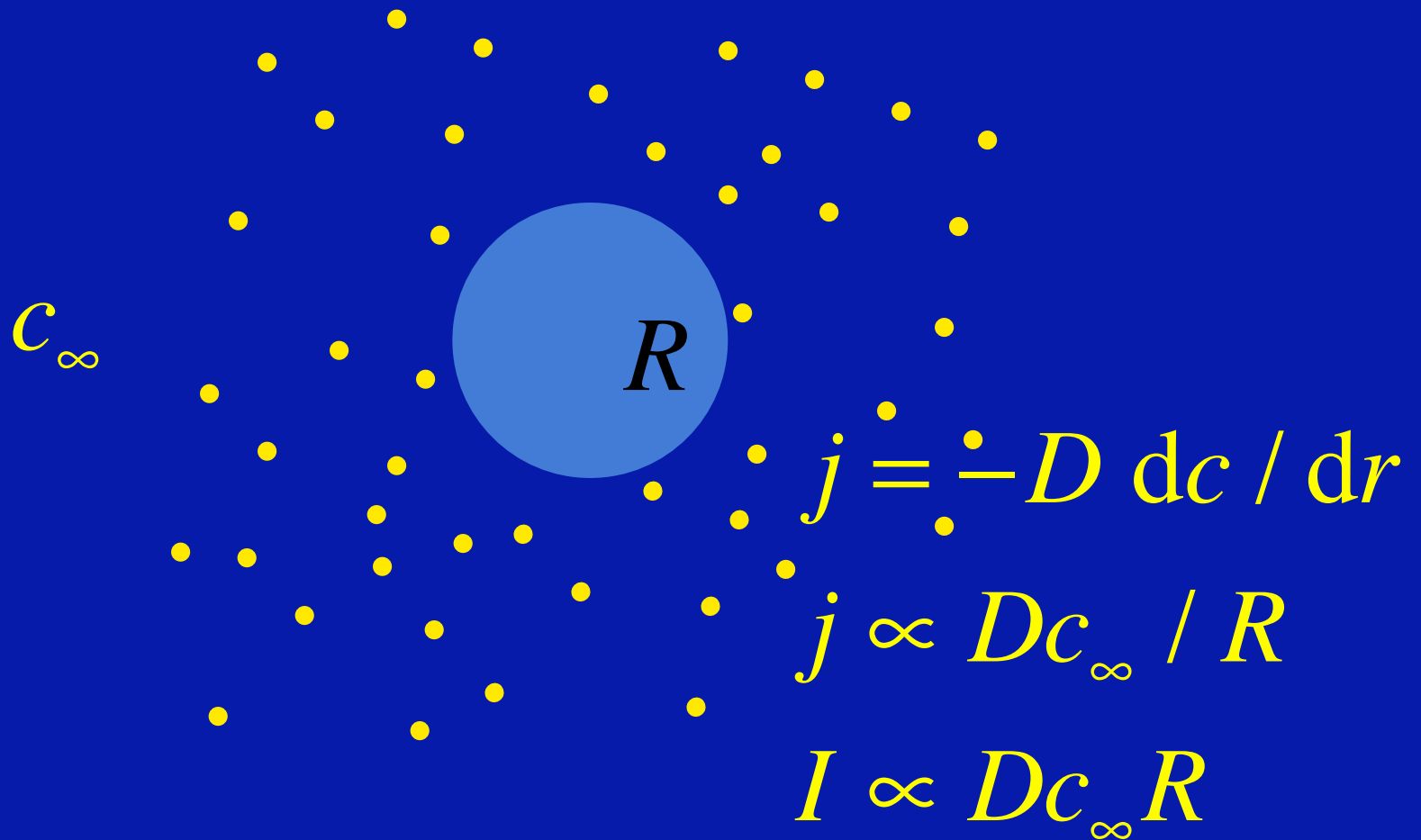
Niklas, 1994: can stirring by flagella increase nutrient uptake in larger organisms?

Body form of Volvocines is a spherical shell

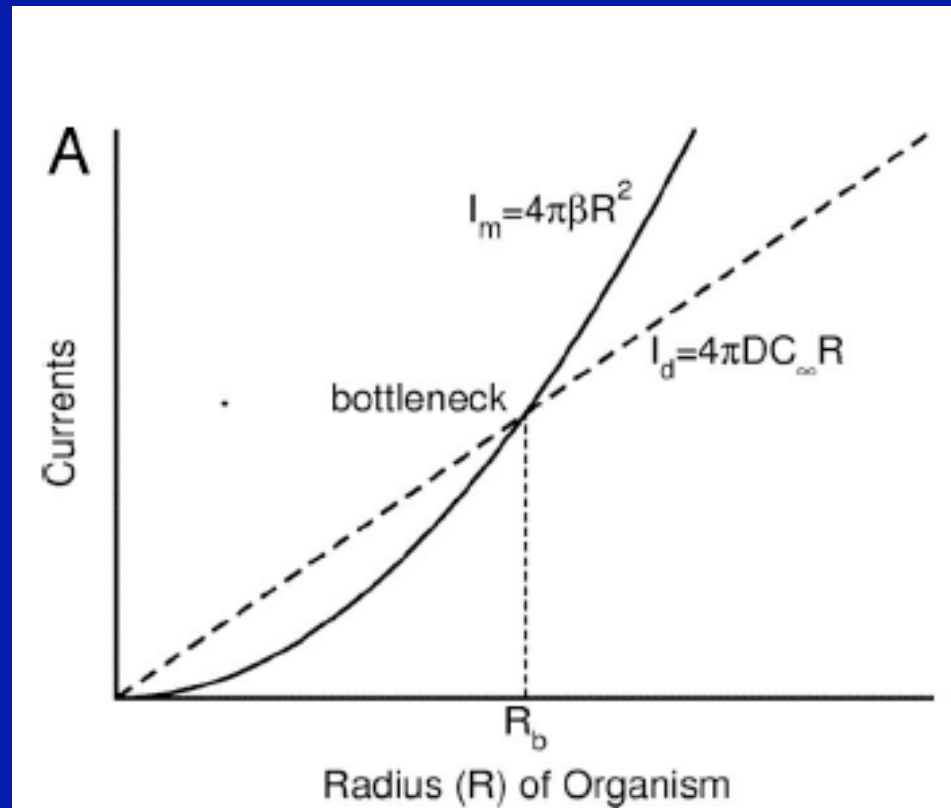


cells is proportional to *surface area*;
therefore, metabolic demands are proportional to
surface area

Uptake rate (current I) of a perfectly absorbing sphere



Bottleneck



Short et al., 2006

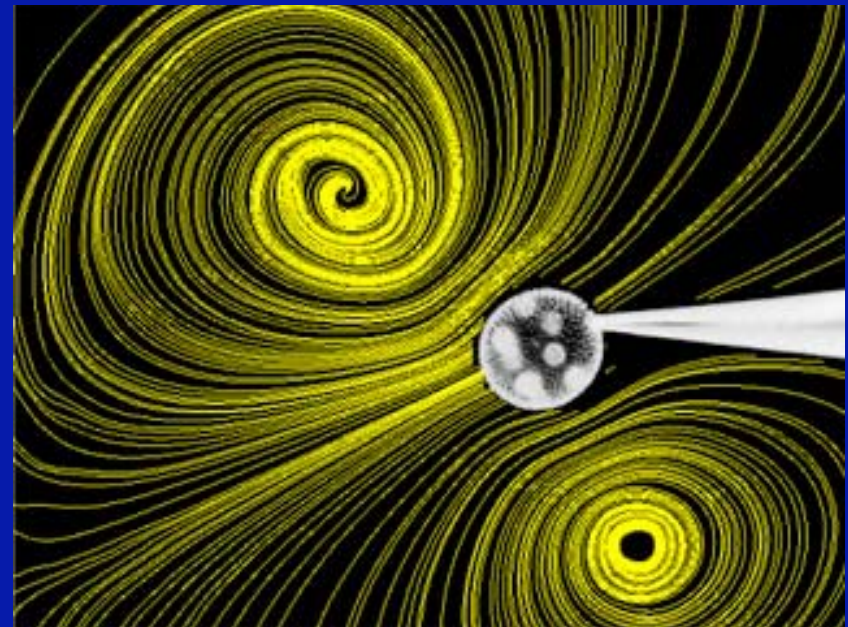
Demands outstrip supply at radius R_b
We estimate $R_b \sim 50 - 200 \mu\text{m}$ (phosphate and O_2)

So far, we've disregarded flow; even a stationary Volvox sets up a flow

See Wim van Egmon's webpage
Micropolitan.org
for the closeup image
of Volvox flagella that
was here

~10 μm

© Wim van Egmon 2003
Micropolitan.org



Short et al., 2006

100 μm

PIV image of flow induced
by stationary Volvox colony

Concentration in presence of flow

Dimensional:

$$\frac{\partial c}{\partial t} + \mathbf{v} \cdot \nabla c = D \nabla^2 c$$

Dimensionless:

$$\frac{\partial c}{\partial t} + \mathbf{v} \cdot \nabla c = \frac{1}{\text{Pe}} \nabla^2 c$$

$\text{Pe} = UL/D$ Peclet number

U = characteristic velocity

L = characteristic length

Small Peclet number

- Diffusion dominates

Large Peclet number

- Flow dominates: c is constant along streamlines of flow

- $c = 0$ at surface implies a boundary layer in c

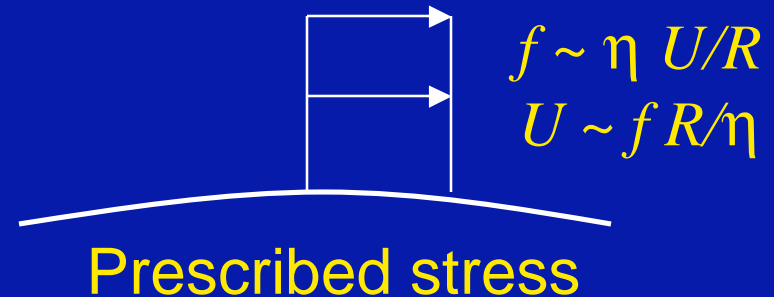
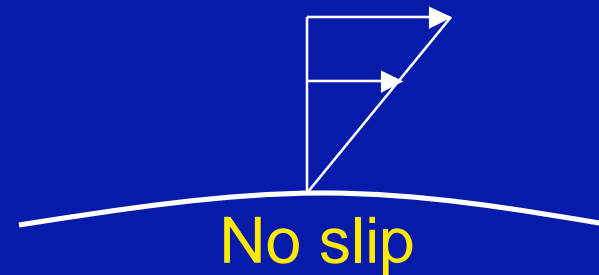
- Details of flow matter in boundary layer

Model for flow field

Observations

- Flow near flagella is complex
- Bigger colonies swim faster

Model: prescribe tangential stress f at surface of sphere; solve Stokes equations for flow

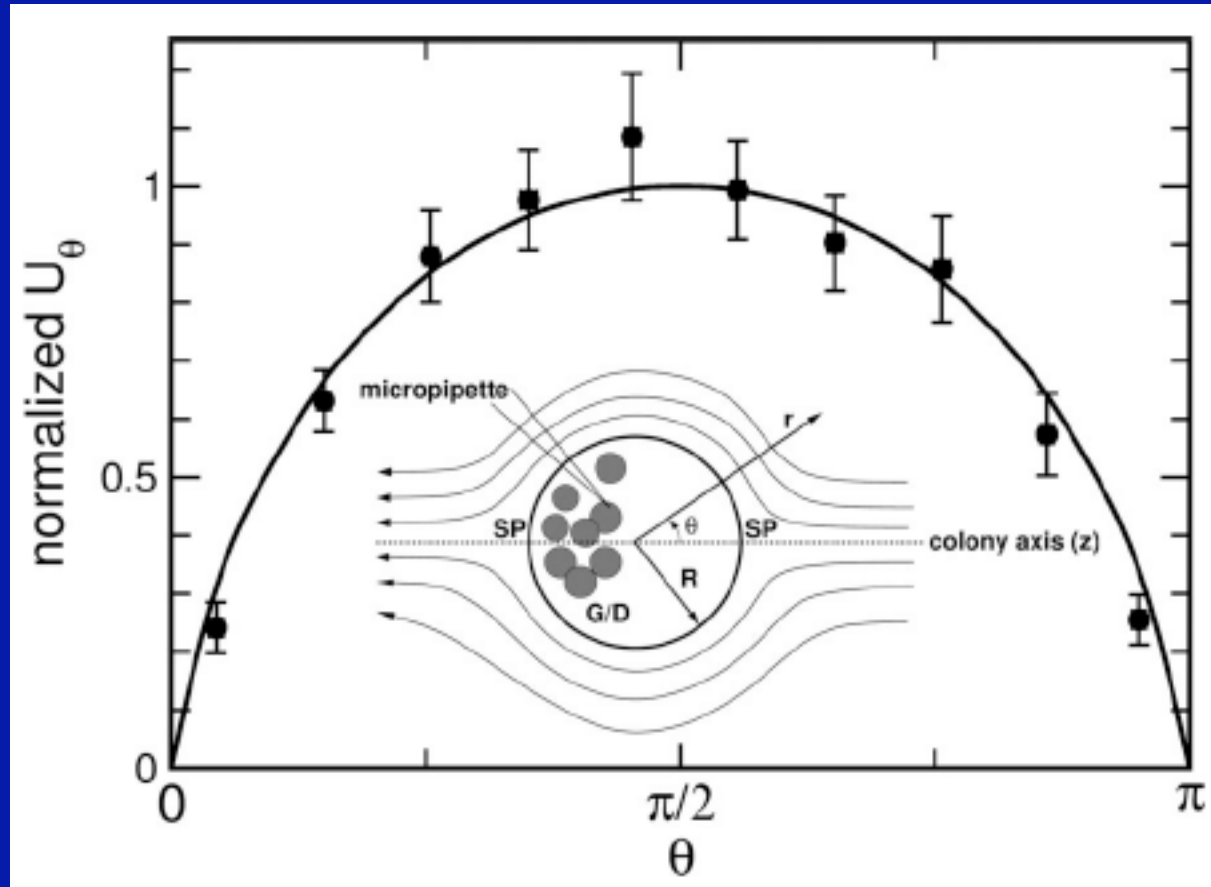


$$P \sim f UR^2 \sim f^2 R^3/\eta$$

Cubic dependence on R!

Volvox C.: $P/\text{cell} \sim 4P/(E. coli)$

Measure the flow



Model: prescribing force/area f (instead of flow velocity) at colony surface leads to swimming velocity $U \sim f R/\eta$

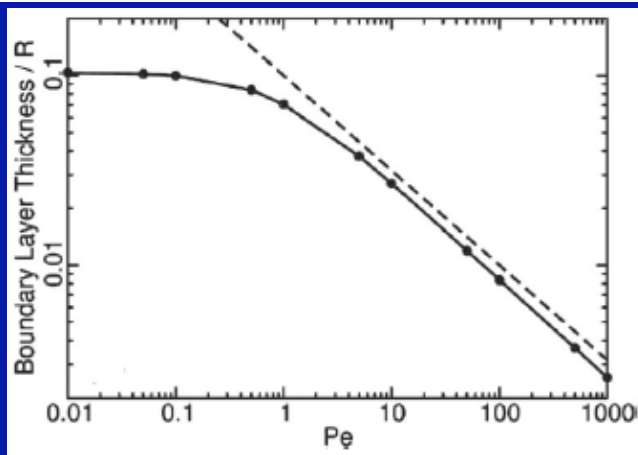
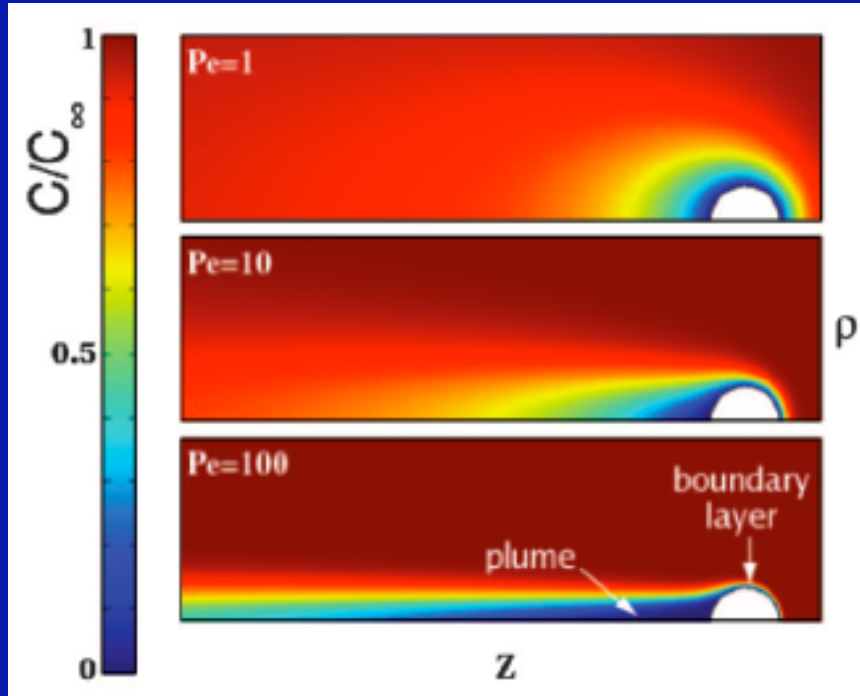
$$Pe = UR/D$$

$$Pe = R^2/R_a^2$$

$$R_a = \sqrt{\frac{4\eta D}{\pi f}}$$

Calculate the concentration field

Short et al., 2006



Short et al., 2006

$$j \propto Dc_{\infty} / R_a; \quad Pe \gg 1$$

$$I \propto Dc_{\infty} R^2 / R_a$$

$$I \propto c_{\infty} DR (Pe)^{1/2}; \quad Pe \gg 1$$

$$Pe = UR / D$$

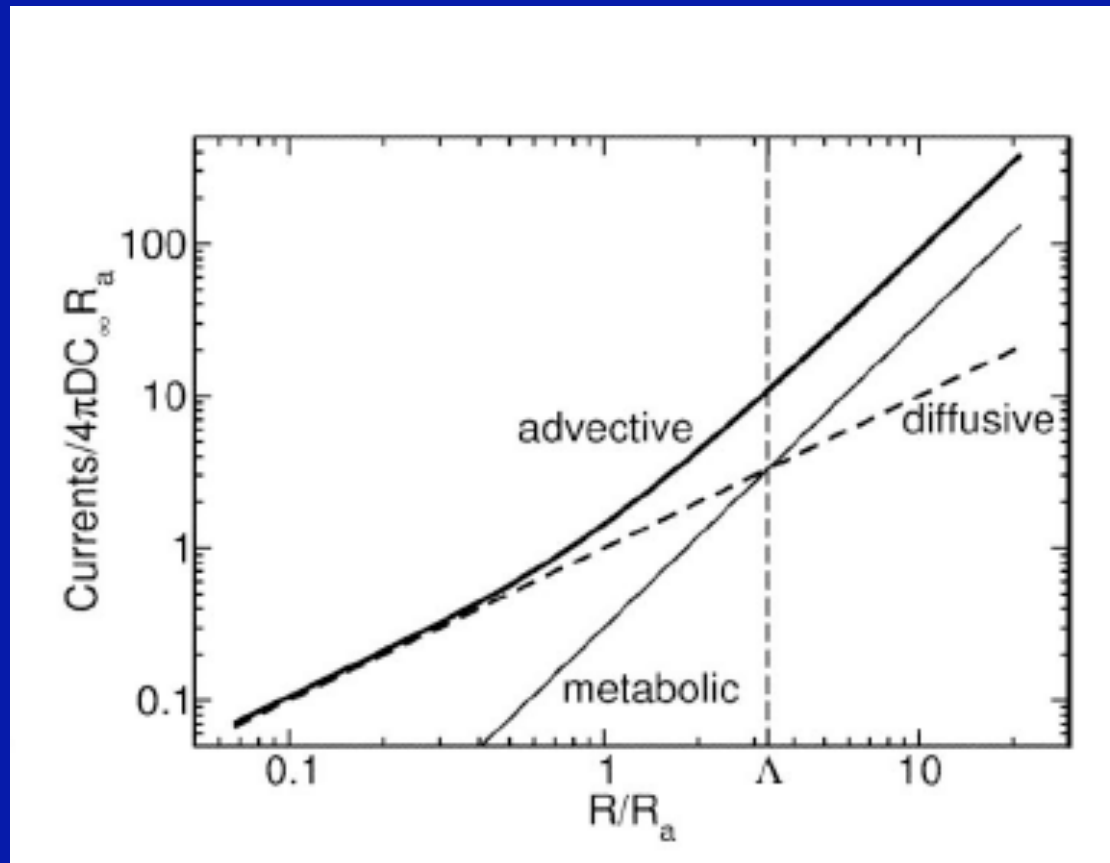
$$U \propto Rf / \eta$$

$$\therefore I \propto R^2$$

Cf. current scaling with Magar, Goto, & Pedley (2003) Q. J. Mech. Appl. Math. **56**, 65-91.

Bottleneck circumvented

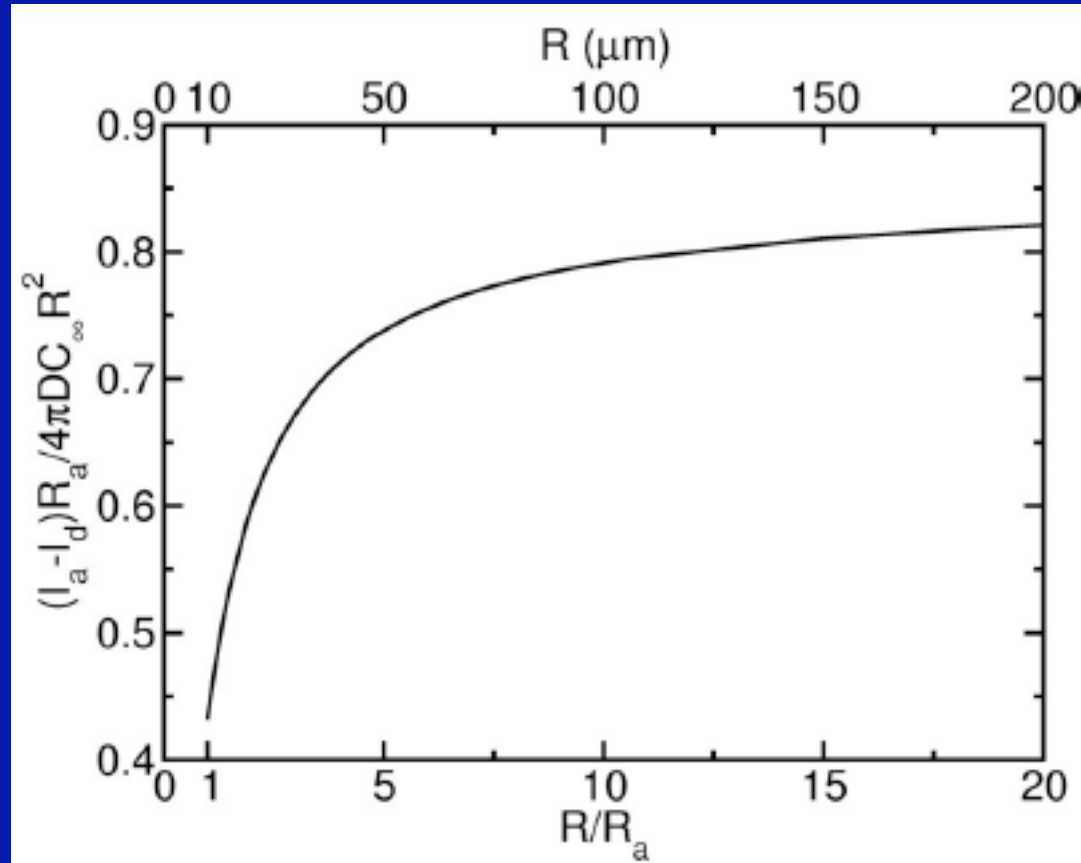
Short et al., 2006



Transport by the collective beating of flagella eliminates the diffusion-only inhibition to growth and thus facilitates the transition to enlargement and multicellularity

Diminishing returns

Short et al., 2006



Conclusions

- Swimmers in a viscoelastic material
 - Elasticity/fading memory slows the swimmer
 - Scallop theorem inapplicable
 - Next: resistive force theory, finite length swimmers (end effects are crucial!)....
- Advantage of increased size = greater rate of nutrient uptake per unit area