Stirring by Microswimmers

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Funding: ERC Advanced Grant

Low Reynolds number swimming

(The Scallop theorem)

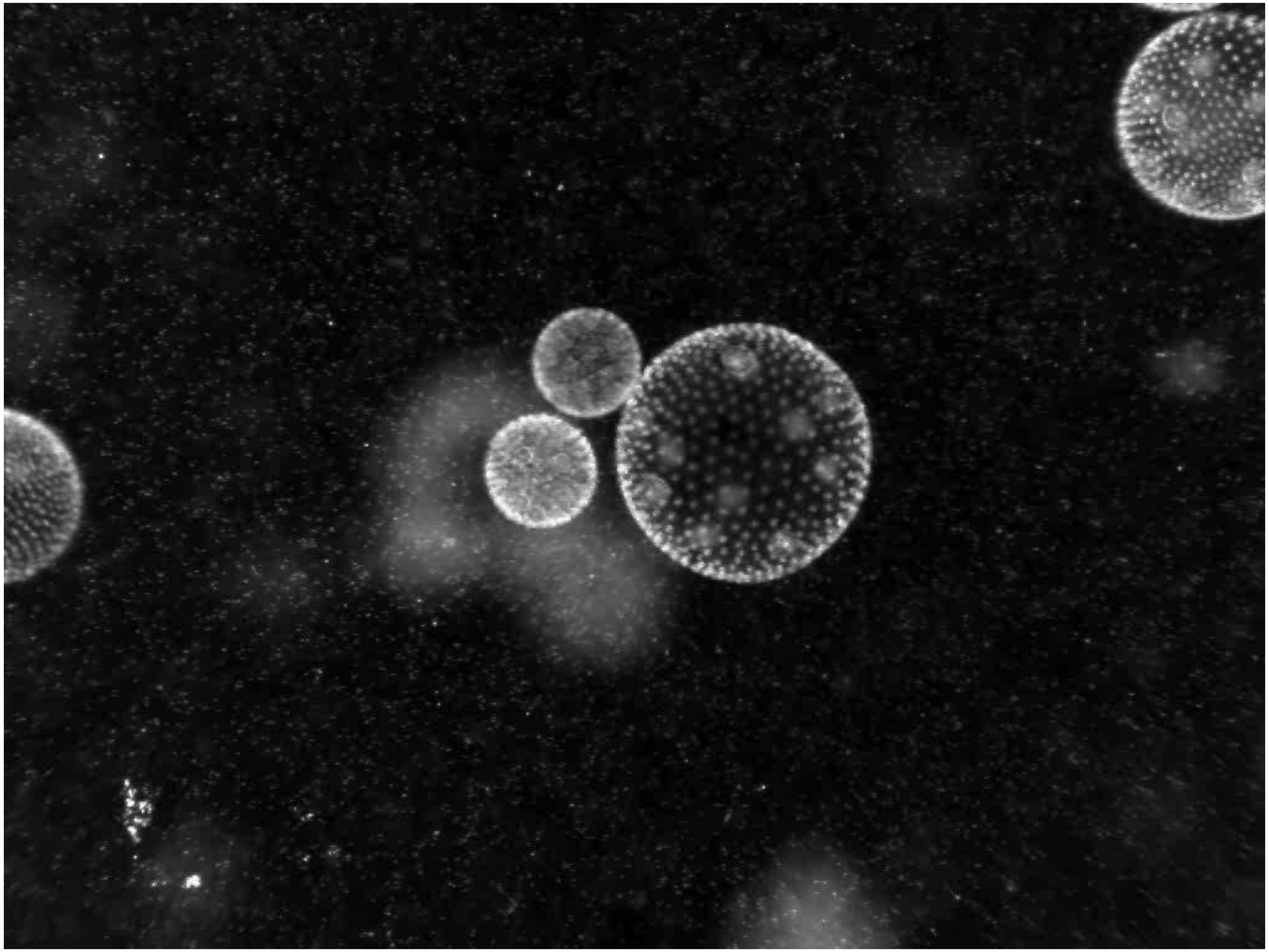
Dipolar flow fields

Stirring by microswimmers

Loops

Entrainment

Random re-orientations



Volvox Goldstein group, Cambridge

Stokes equations

$$\nabla p = \mu \nabla^2 \mathbf{v} + \mathbf{f} \qquad\qquad \nabla \cdot \mathbf{v} = 0$$

Purcell's Scallop Theorem

$$\nabla p = \mu \nabla^2 \mathbf{v} + \mathbf{f} \qquad \nabla \cdot \mathbf{v} = 0$$

No time dependence implies the Scallop Theorem

A swimming stroke must not be invariant under time reversal

Green function of the Stokes equation

$$\nabla p = \mu \nabla^2 \mathbf{v} + \mathbf{f}\delta(\mathbf{r}) \qquad \nabla \cdot \mathbf{v} = 0$$

$$\mathbf{v} = \frac{\mathbf{f}}{8\pi\mu} \cdot \left(\frac{\mathbf{I}}{r} + \frac{\mathbf{rr}}{r^3} \right)$$

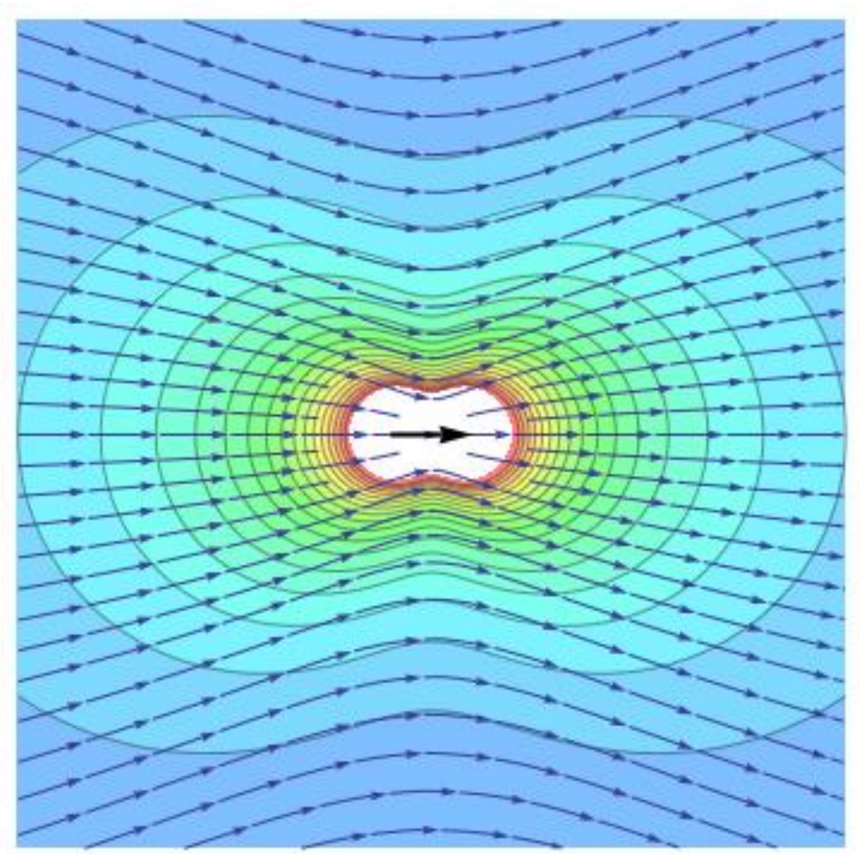
Stokeslet

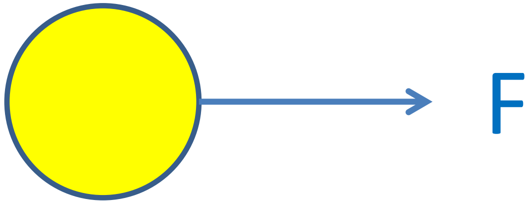
$$p = p_0 + \frac{\mathbf{f} \cdot \mathbf{r}}{4\pi r^3}$$

Maciej Lisicki http://www.fuw.edu.pl/~mklis/publications/Hydro/oseen.pdf

Green function of the Stokes equation

$$\mathbf{v} = \frac{\mathbf{f}}{8\pi\mu} \cdot \left(\frac{\mathbf{I}}{r} + \frac{\mathbf{rr}}{r^3} \right)$$



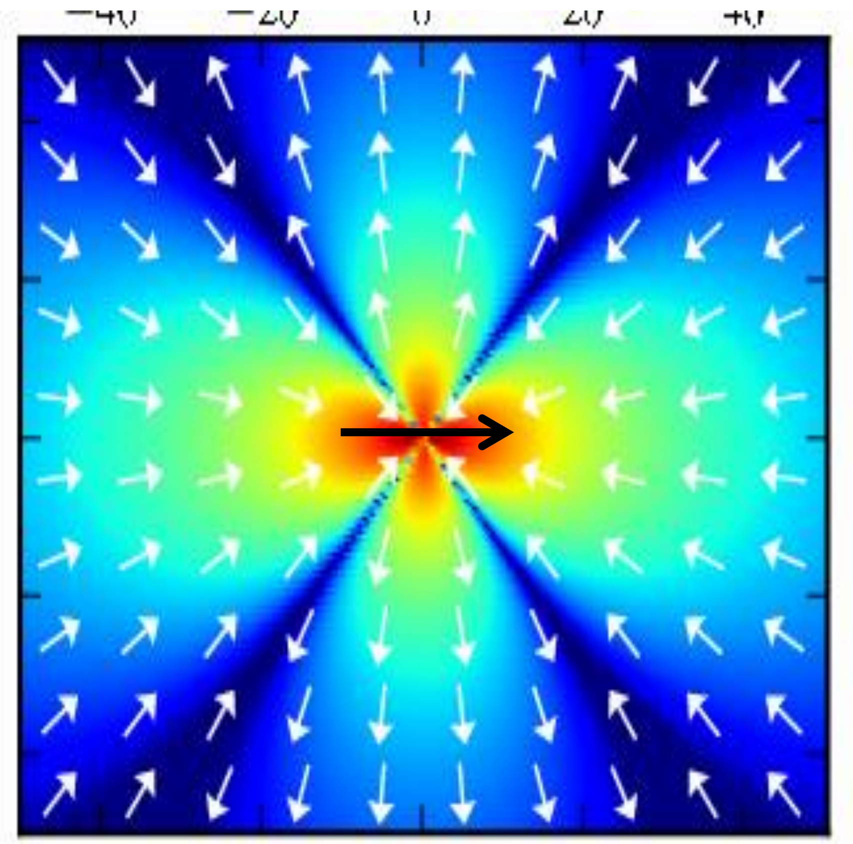


Far flow field of a swimmer

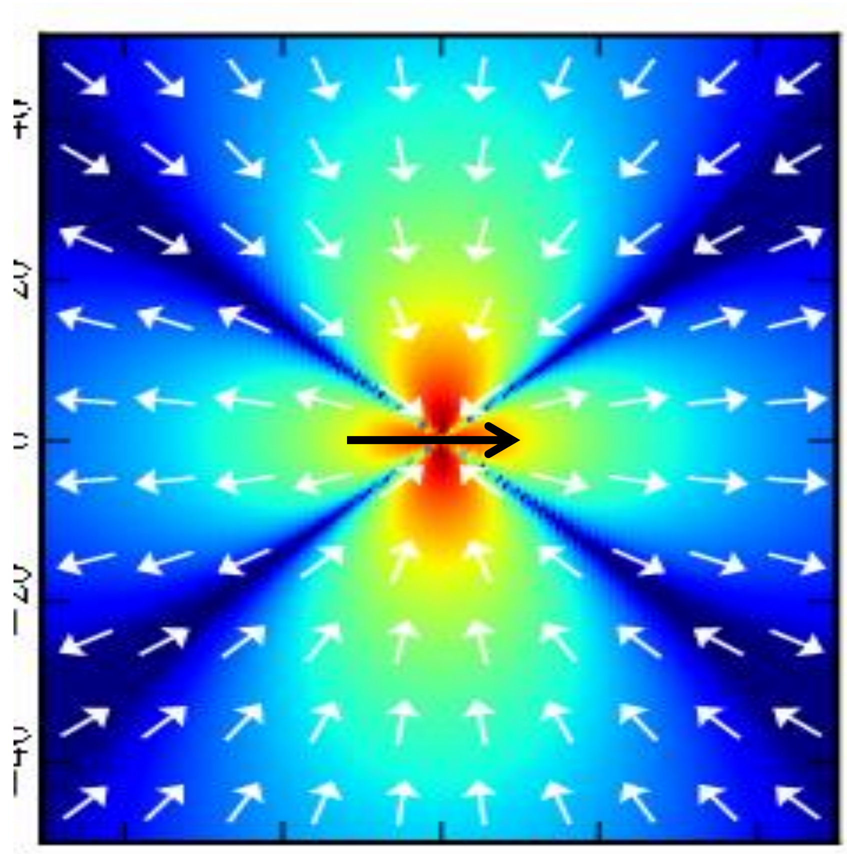
$$v_r = \frac{f}{4\pi\mu} \; \frac{L}{r^2} \; \left(3\cos^2\theta - 1\right)$$

Swimmers have dipolar far flow fields because they have no net force acting on them

Dipolar flow field



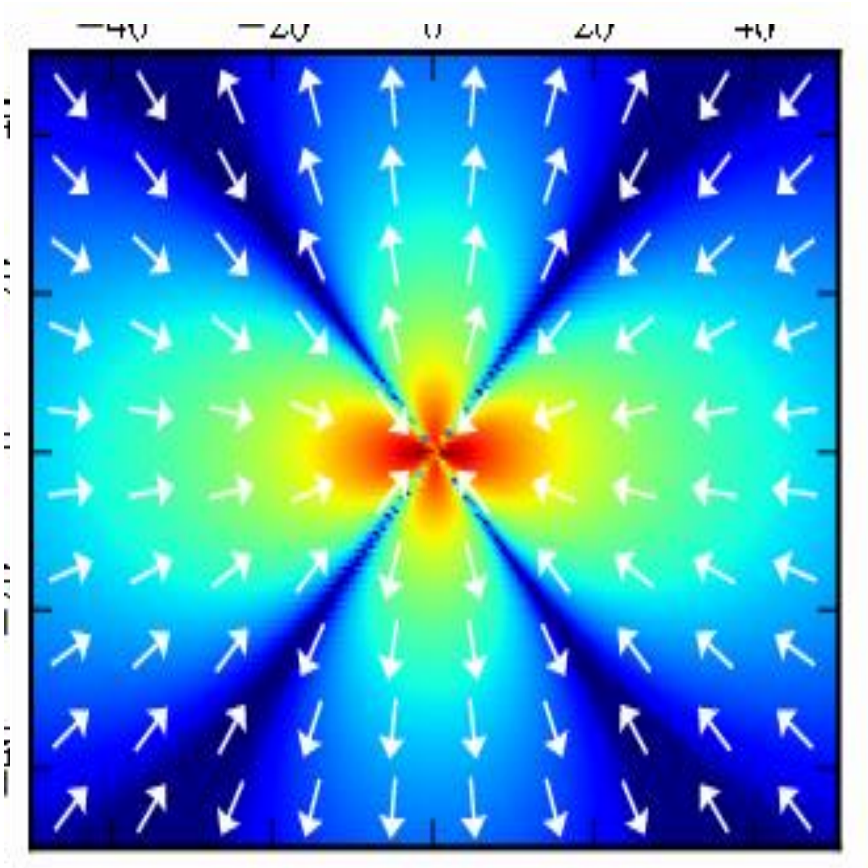
puller (contractile)

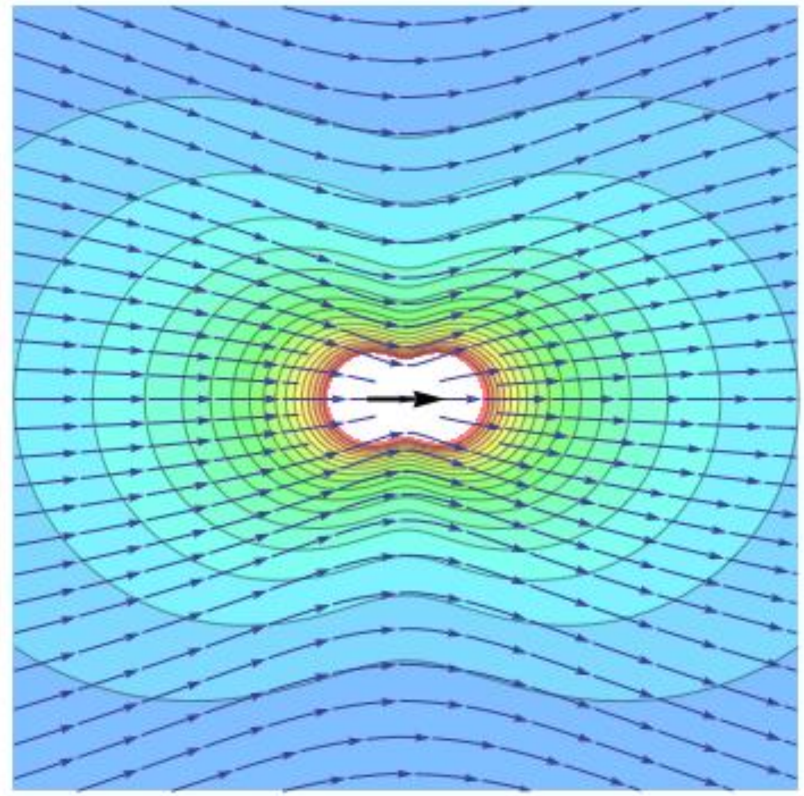


pusher (extensile)

$$v_r = \frac{f}{4\pi\mu} \; \frac{L}{r^2} \; \left(3\cos^2\theta - 1\right)$$

Swimmer and colloidal flow fields





$$v \sim \frac{1}{r^2}$$

$$v \sim \frac{1}{r}$$

Multipole expansion

Stokeslet:

$$\mathbf{u}^{\mathbf{S}}(\mathbf{r},\mathbf{k}) = \mathbf{k}\cdot\mathbf{J}, \quad \mathbf{J} = \frac{\mathbf{I}}{r} + \frac{\mathbf{r}\mathbf{r}}{r^3}$$

Dipole term:

$$\mathbf{u}^{\mathbf{D}}(\mathbf{r},\mathbf{k}) = -\kappa(\mathbf{k}\cdot\nabla)\,\mathbf{u}^{\mathbf{S}}(\mathbf{r},\mathbf{k})$$

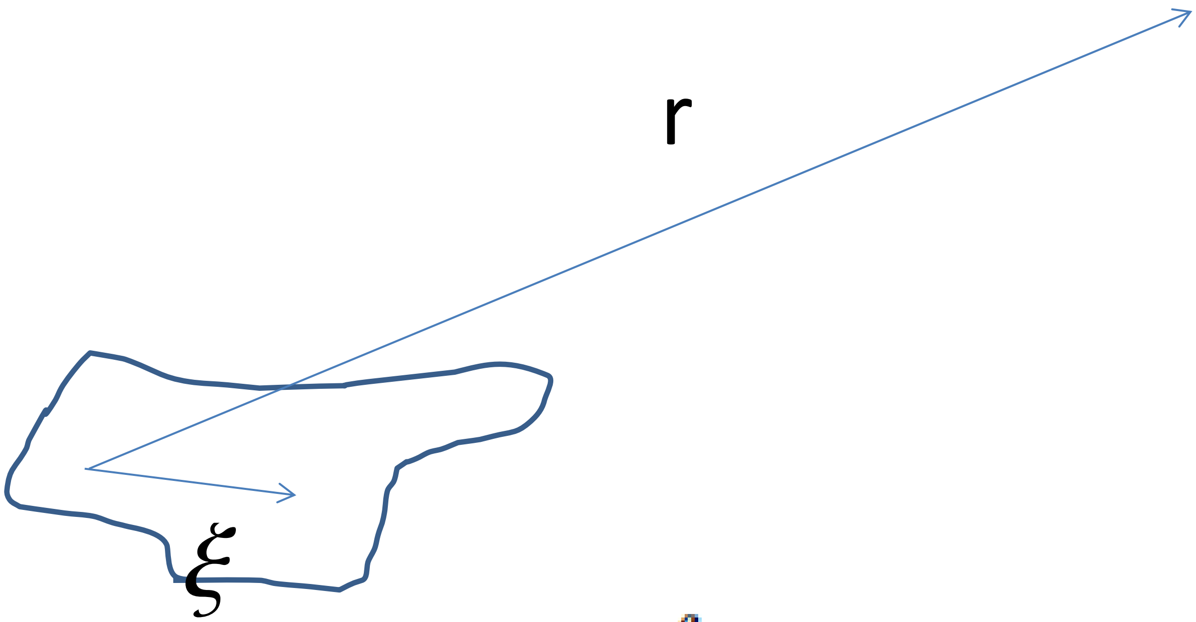
Quadrupole term:

$$\mathbf{u}^{\mathbf{Q}}(\mathbf{r},\mathbf{k}) = -\frac{1}{2}\left(Q_{\|}(\mathbf{k}\cdot\nabla)^2 + Q_{\perp}\nabla_{\perp}^2\right)\mathbf{u}^{\mathbf{S}}(\mathbf{r},\mathbf{k})$$

$$Q_{\perp} = -\frac{1}{2}\int_S f_z\rho^2 dS$$

$$\mathbf{u}(\mathbf{r},\mathbf{k}) = (\mathbf{k}\cdot\nabla)\,\mathbf{U}_0(\mathbf{r},\mathbf{k}) + O(r^{-4})$$

Multipole expansion



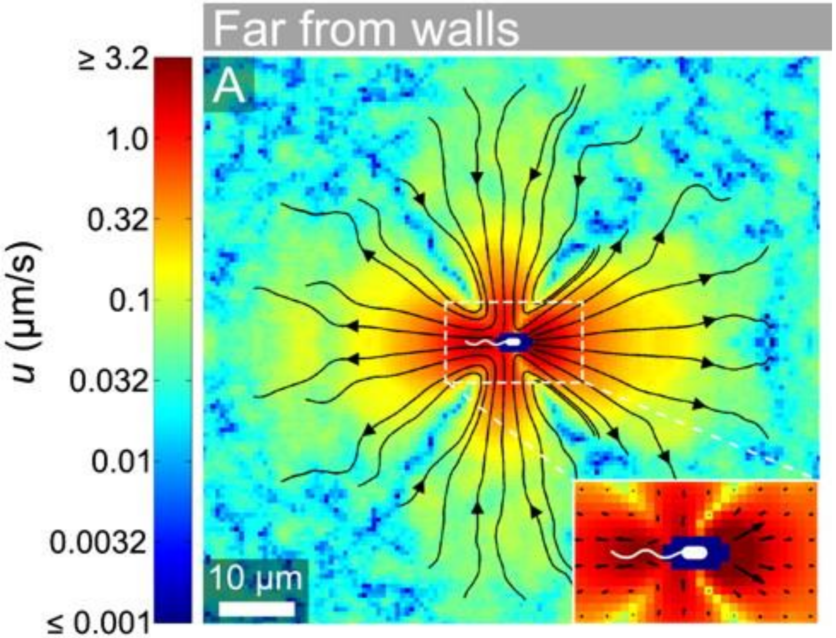
$$v_i(\mathbf{r}) = \int G_{ij}(\mathbf{r}-\xi) f_j(\xi)\, d\xi$$

$$G_{ij}(\mathbf{r}-\xi) = \frac{1}{8\pi\mu}\left(\frac{\delta_{ij}}{|\,\mathbf{r}-\xi\,|} + \frac{(\mathbf{r}-\xi)_i(\mathbf{r}-\xi)_j}{|\,\mathbf{r}-\xi\,|^3}\right).$$

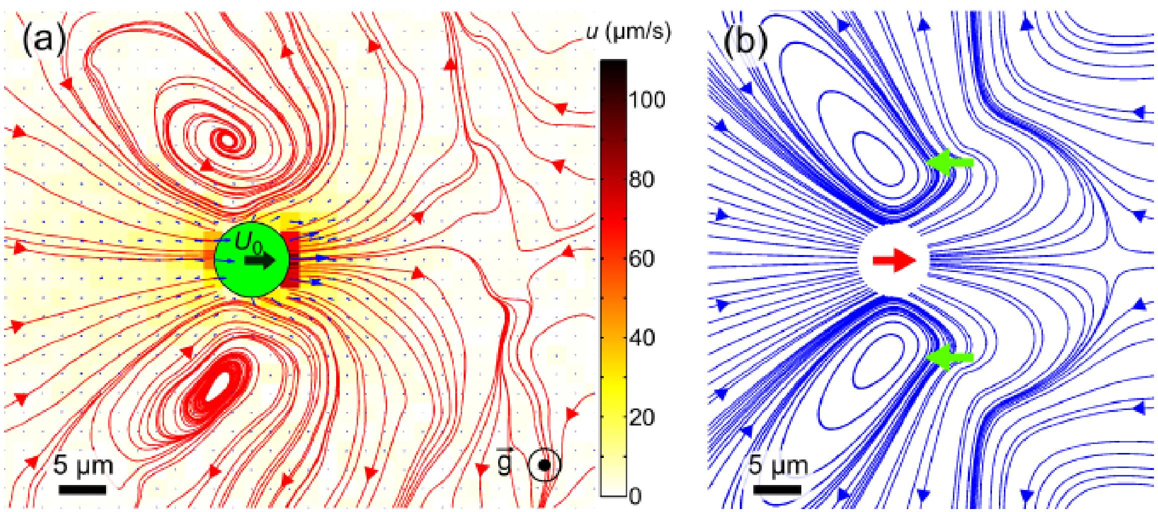
Multipole expansion

$$v_i(\mathbf{r}) = \int G_{ij}(\mathbf{r} - \xi) f_j(\xi)\, d\xi$$

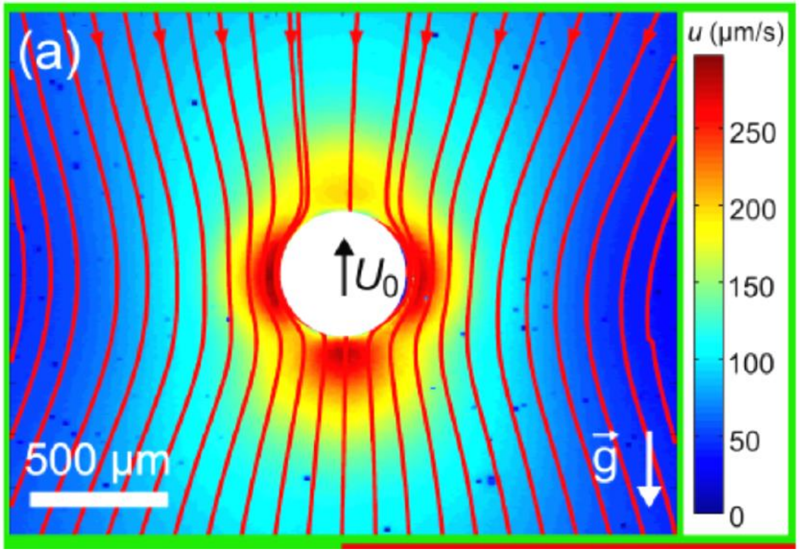
$$\begin{aligned}
v_i(\mathbf{r}) &= \int \left\{ G_{ij}(\mathbf{r}) - \frac{\partial G_{ij}}{\partial \xi_k}(\mathbf{r})\xi_k + \frac{1}{2}\frac{\partial^2 G_{ij}}{\partial \xi_k \partial \xi_l}(\mathbf{r})\xi_k\xi_l \ldots \right\} f_j(\xi)\, d\xi \\
&= G_{ij}(\mathbf{r}) \int f_j(\xi)\, d\xi - \frac{\partial G_{ij}}{\partial \xi_k}(\mathbf{r}) \int \xi_k f_j(\xi)\, d\xi \\
&\quad + \frac{1}{2}\frac{\partial^2 G_{ij}}{\partial \xi_k \partial \xi_l}(\mathbf{r}) \int \xi_k \xi_l f_j(\xi)\, d\xi + \ldots \\
&\equiv G_{ij}(\mathbf{r}) F_j + \frac{\partial G_{ij}}{\partial \xi_k}(\mathbf{r}) D_{jk} + \frac{1}{2}\frac{\partial^2 G_{ij}}{\partial \xi_k \partial \xi_l}(\mathbf{r}) Q_{jkl} + \ldots
\end{aligned}$$



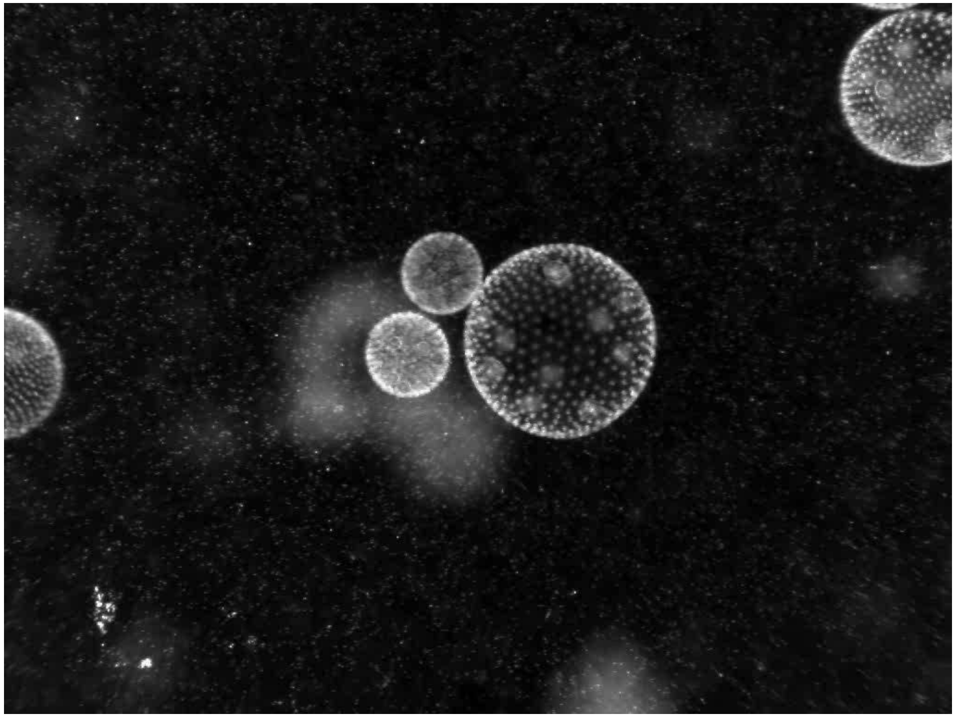
E-coli



Chlamydomonas



Volvox

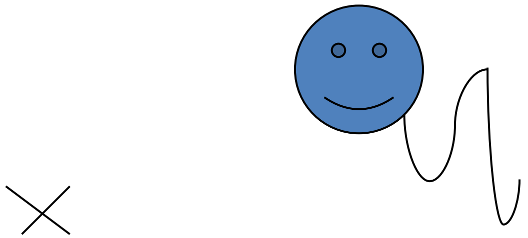


Dresher et al,   PRL 105 (2010)
PNAS 108 (2011)

What is the pdf of the velocity field produced by many swimmers?

$$v \sim 1/r^n$$

n=1 driven swimmer or colloid
n=2 force free swimmer
n=3 quadrupolar swimmer



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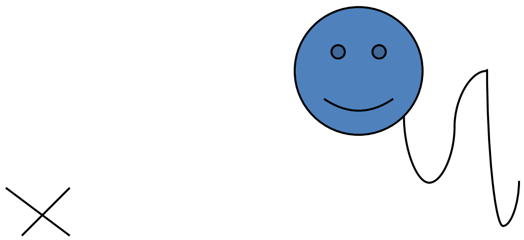
velocity distribution for one swimmer



$$P(r)\,dr \sim r^2\,dr$$

$$P(v)\,dv \sim v^{-(1-3/n)}\,dv$$

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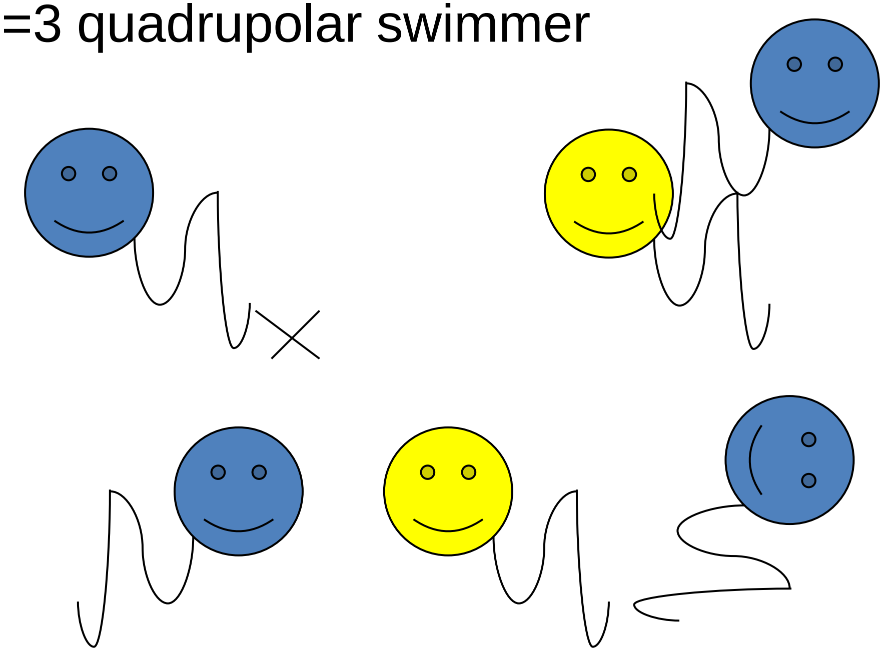

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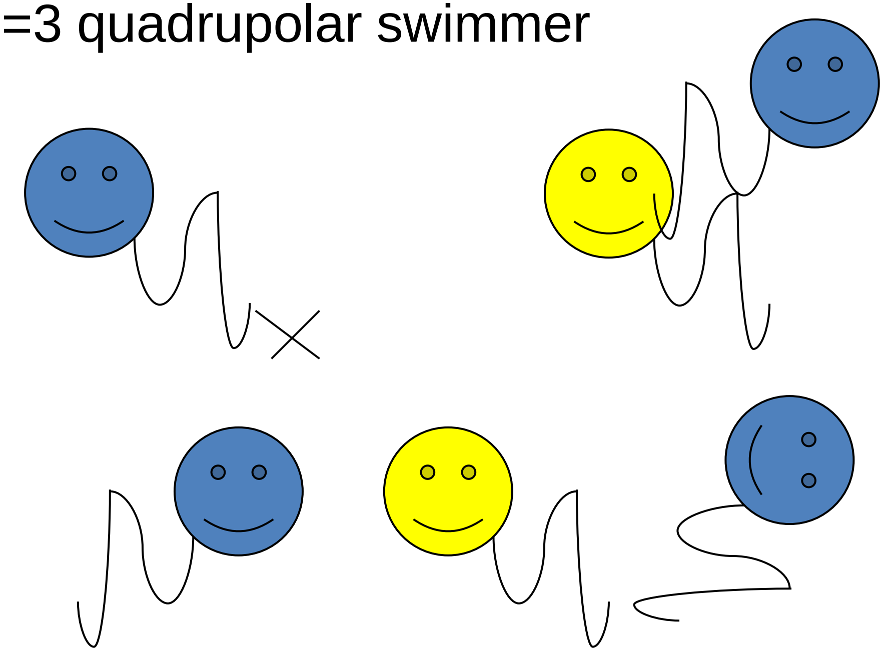

$$P(r)\, dr \sim r^2\, dr$$

$$P(v)\, dv \sim v^{-(1-3/n)}\, dv$$

velocity distribution for many swimmers

Gaussian from the central limit theorem

What is the pdf of the velocity field produced by many swimmers?

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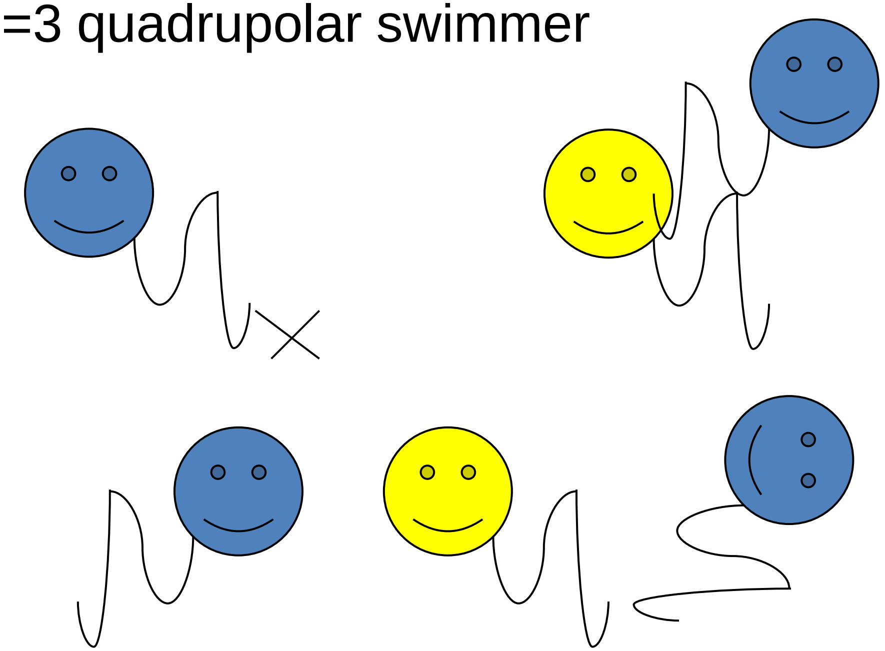

$$P(r)\;dr \sim r^2\;dr$$

$$P(v)\;dv \sim v^{-(1-3/n)}\;dv$$

velocity distribution for many swimmers

Gaussian from the central limit theorem -- **if the variance is finite**

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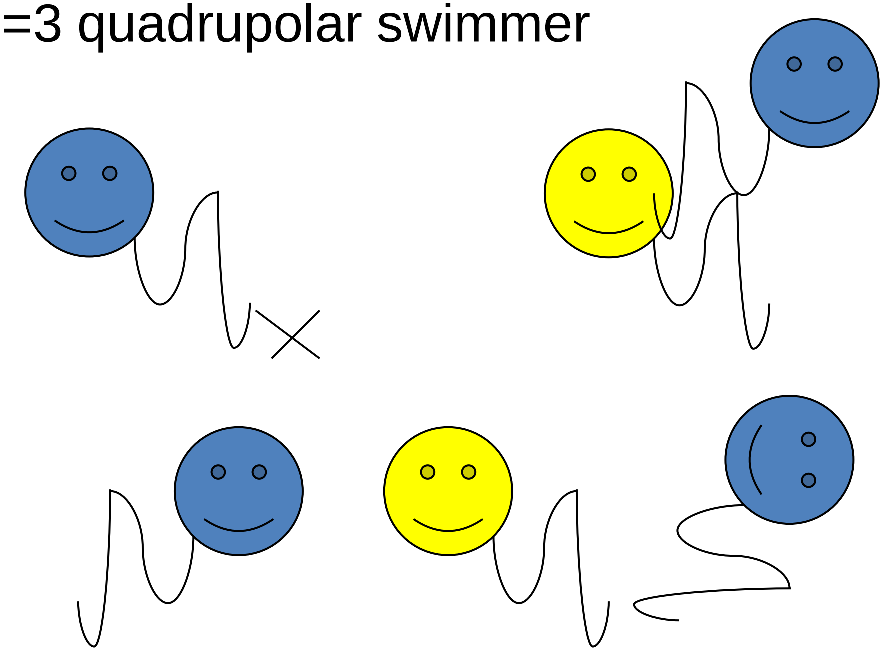
velocity distribution for one swimmer



$$P(r)\, dr \sim r^2\, dr$$

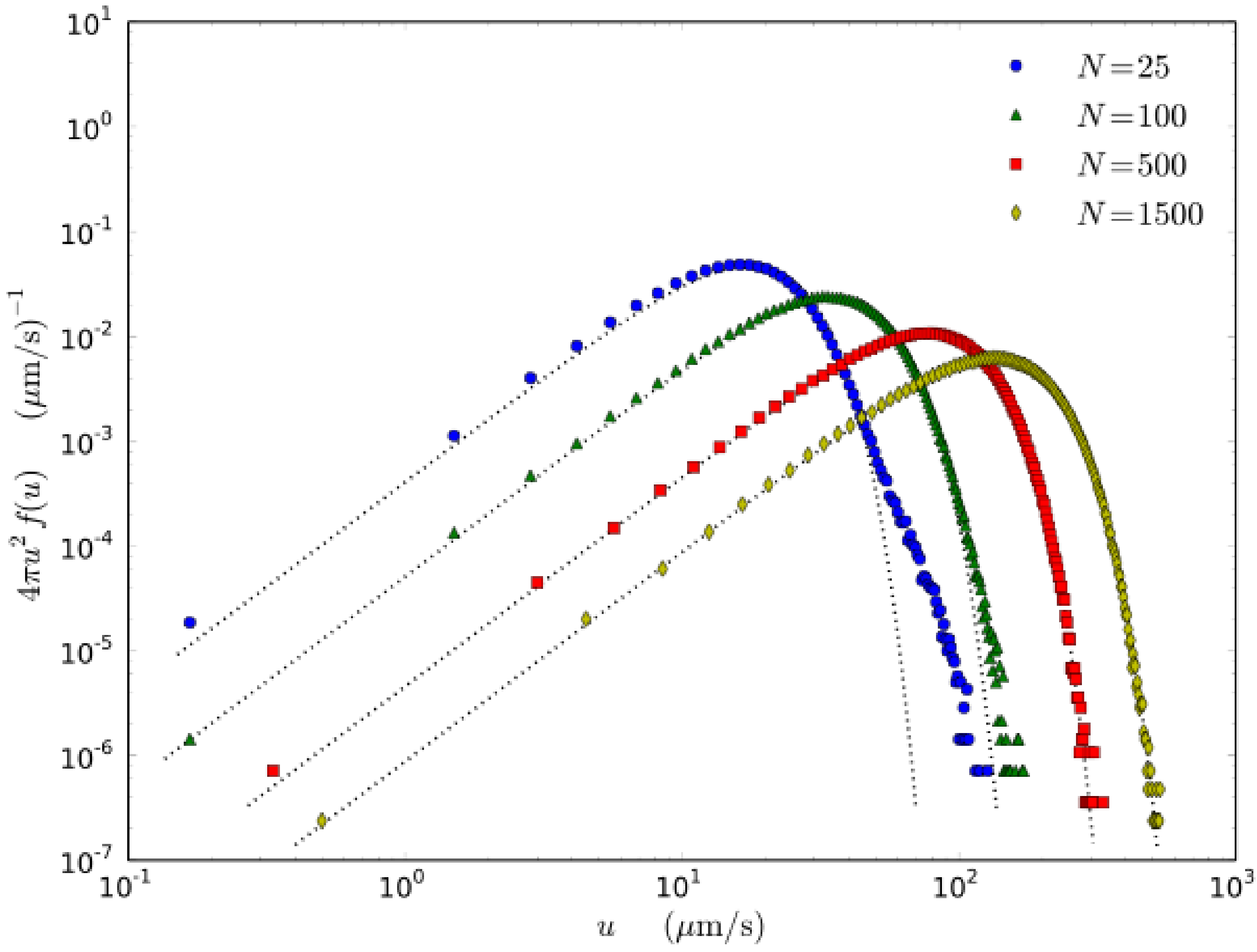
$$P(v)\, dv \sim v^{-(1-3/n)}\, dv$$

velocity distribution for many swimmers

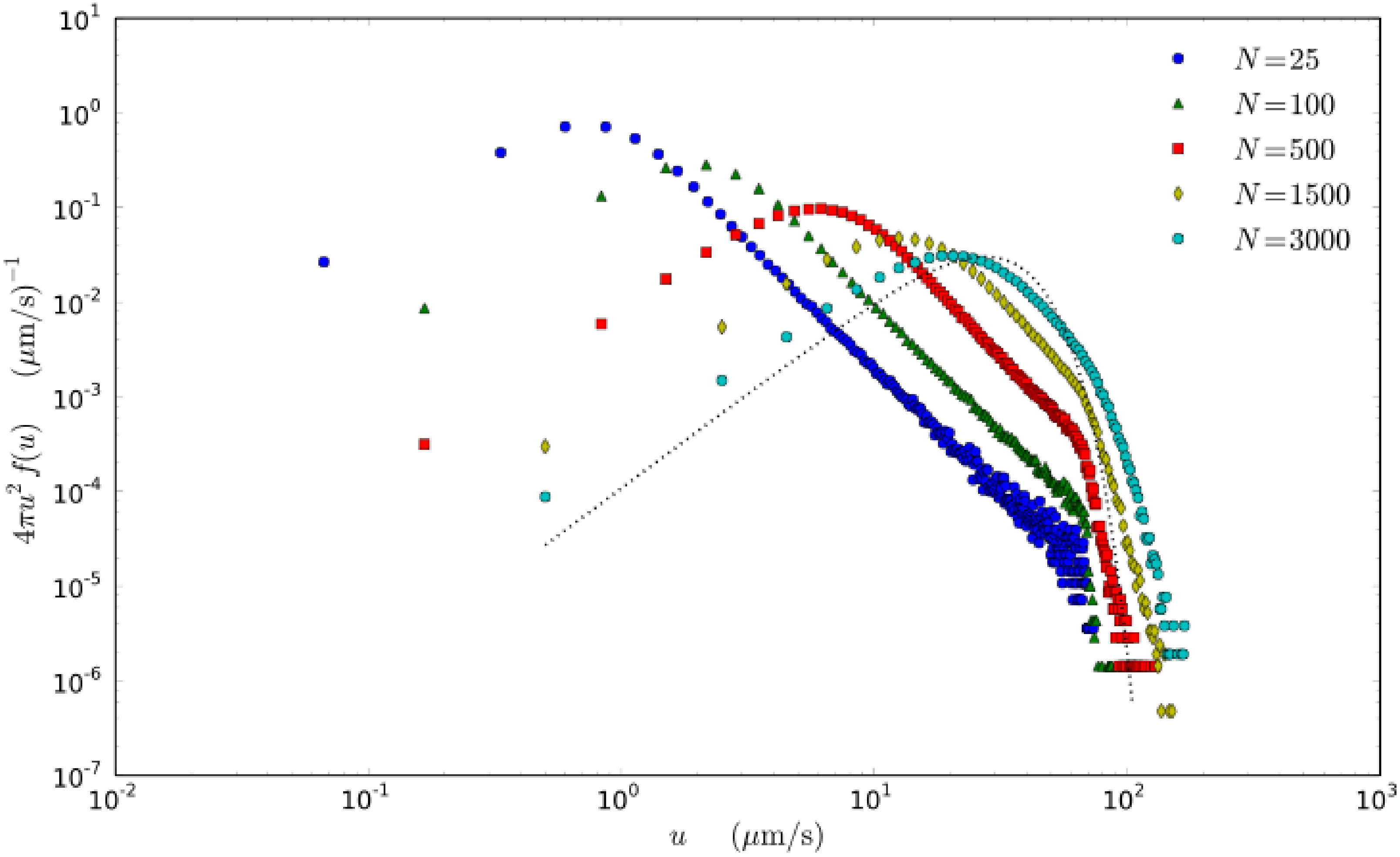
Gaussian from the central limit theorem -- **if the variance is finite**

variance is finite only for n < 3/2

velocity pdf: n=1, concentration dependence



velocity pdf: n=2, concentration dependence



<u>Low Reynolds number swimming</u>

(The Scallop theorem)

Dipolar flow fields

<u>Stirring by microswimmers</u>

Loops

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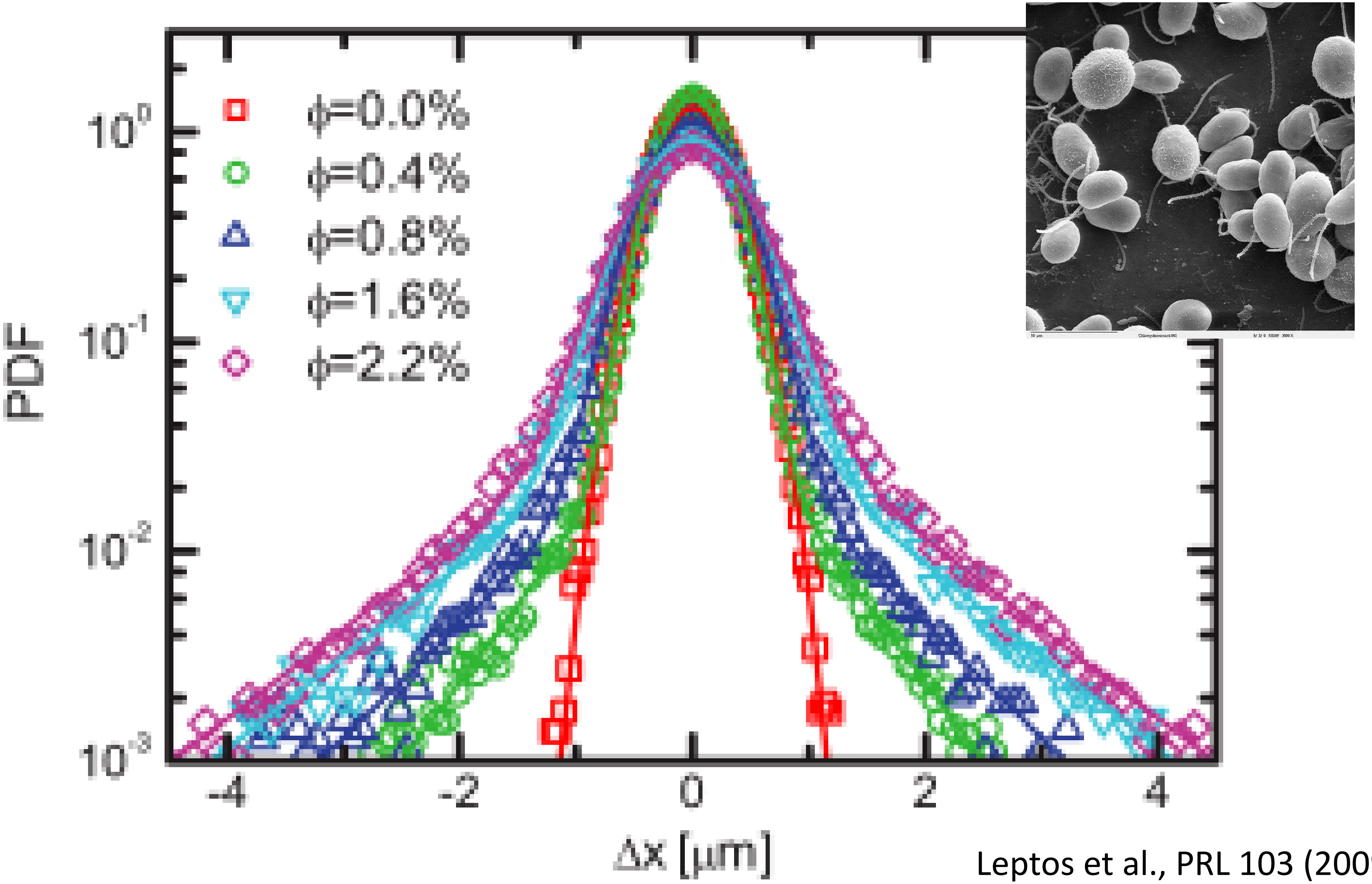
Stirring by microswimmers

(How) do microswimmers stir the fluid they swim in?

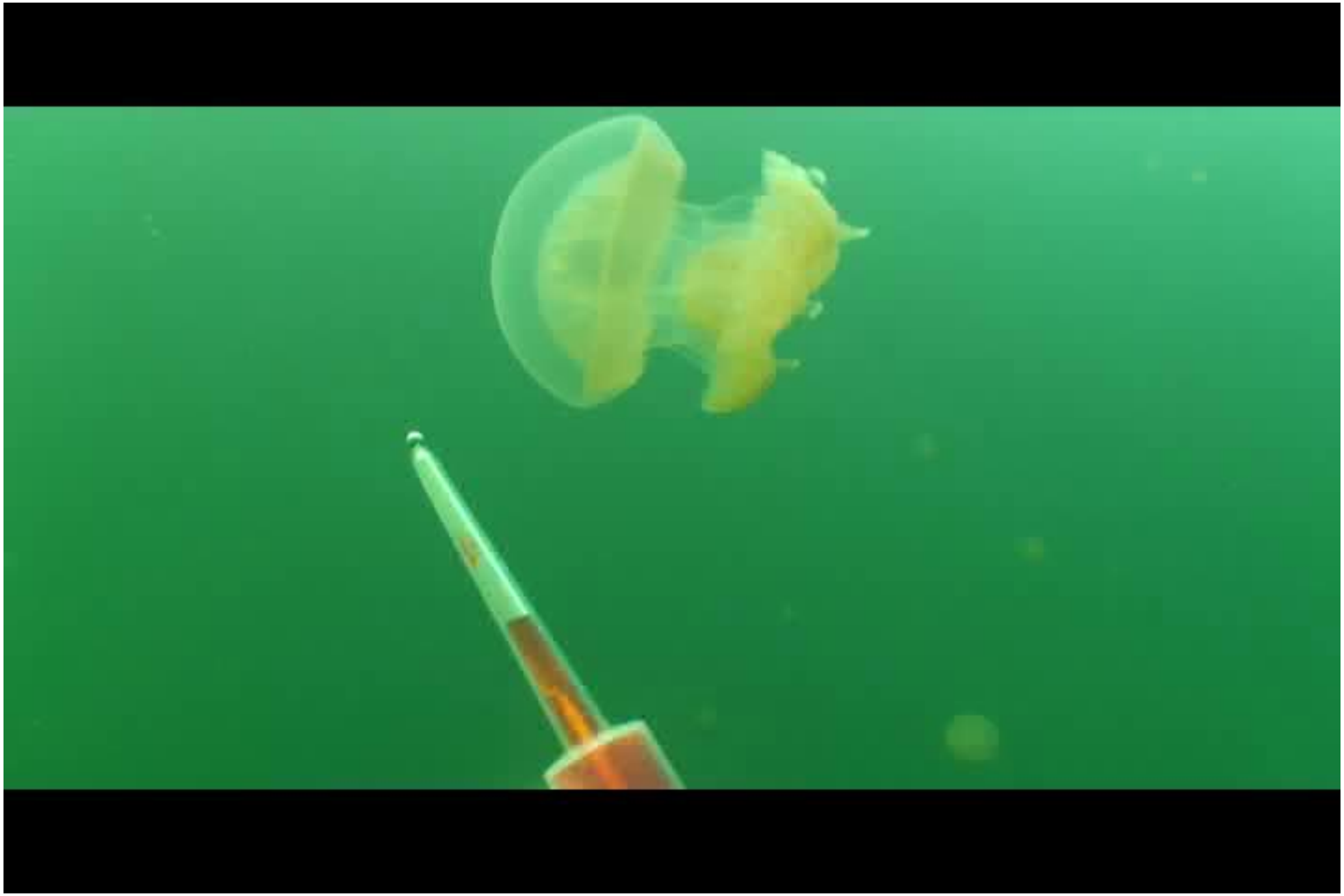
Why do microswimmers stir the fluid they swim in?

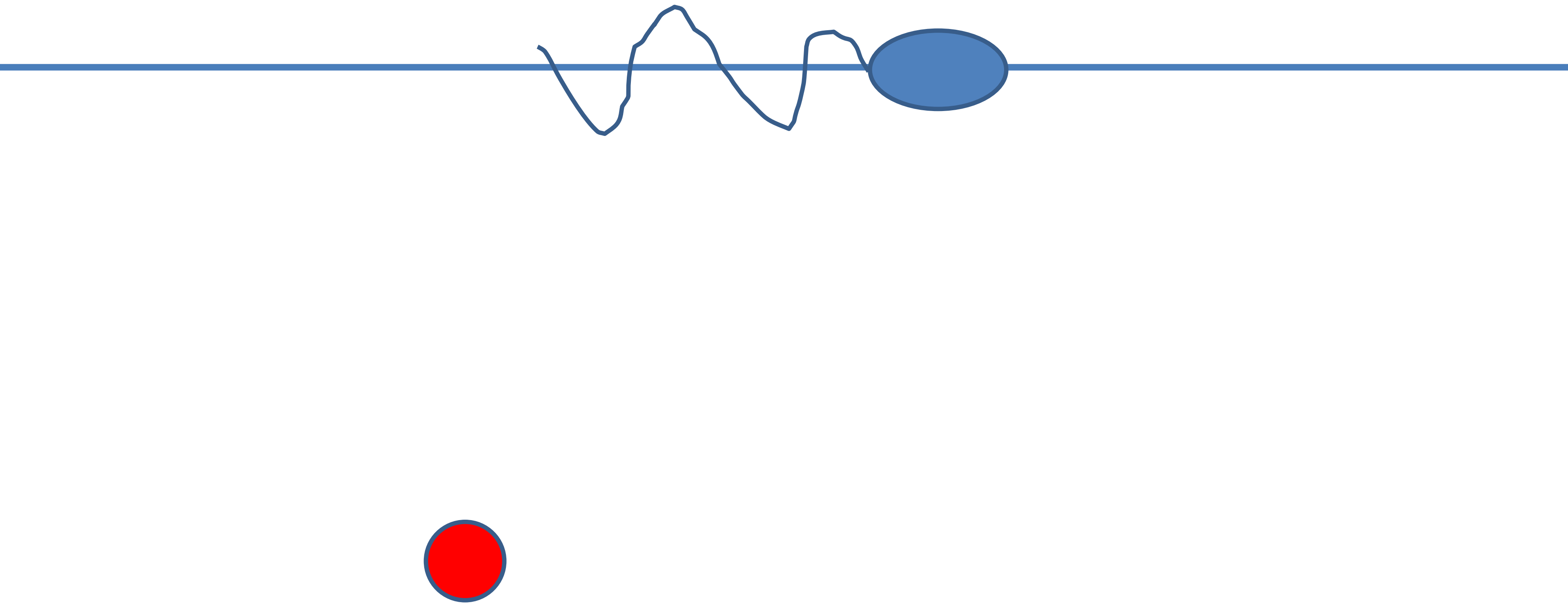
Swimmers enhance diffusion

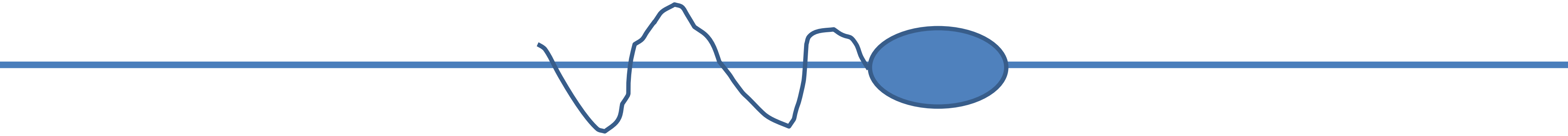


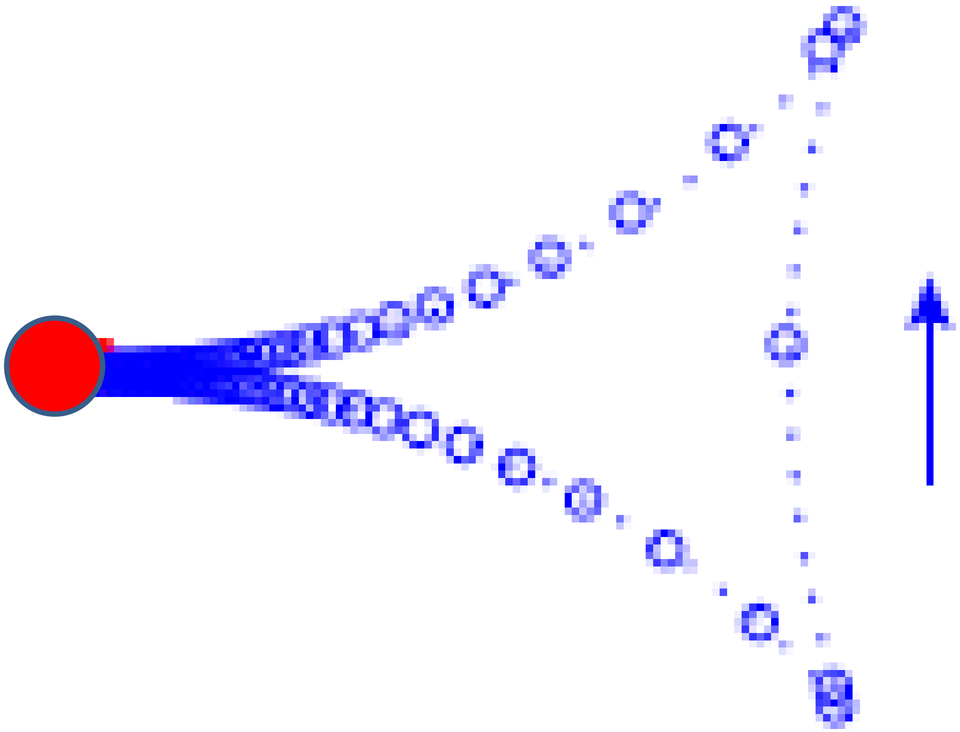
Leptos et al., PRL 103 (2009)

Do small swimmers mix the ocean? K. Katija, J.O. Dabiri, G. Subramanian,
A.M. Leshansky, L.M. Pismen, A.W. Visser

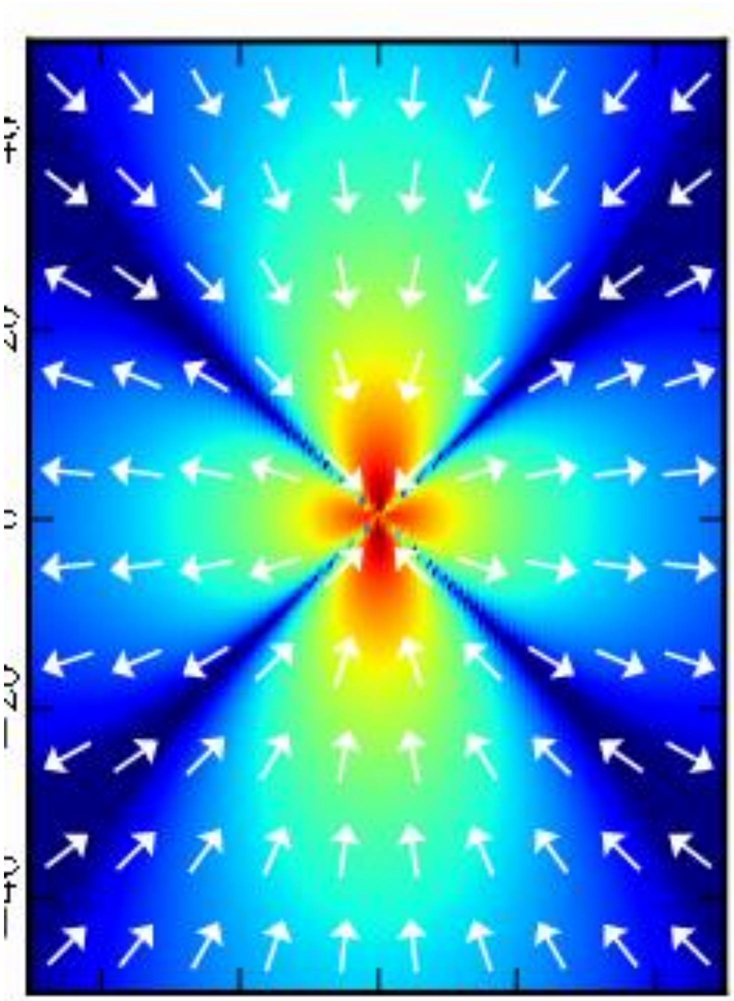






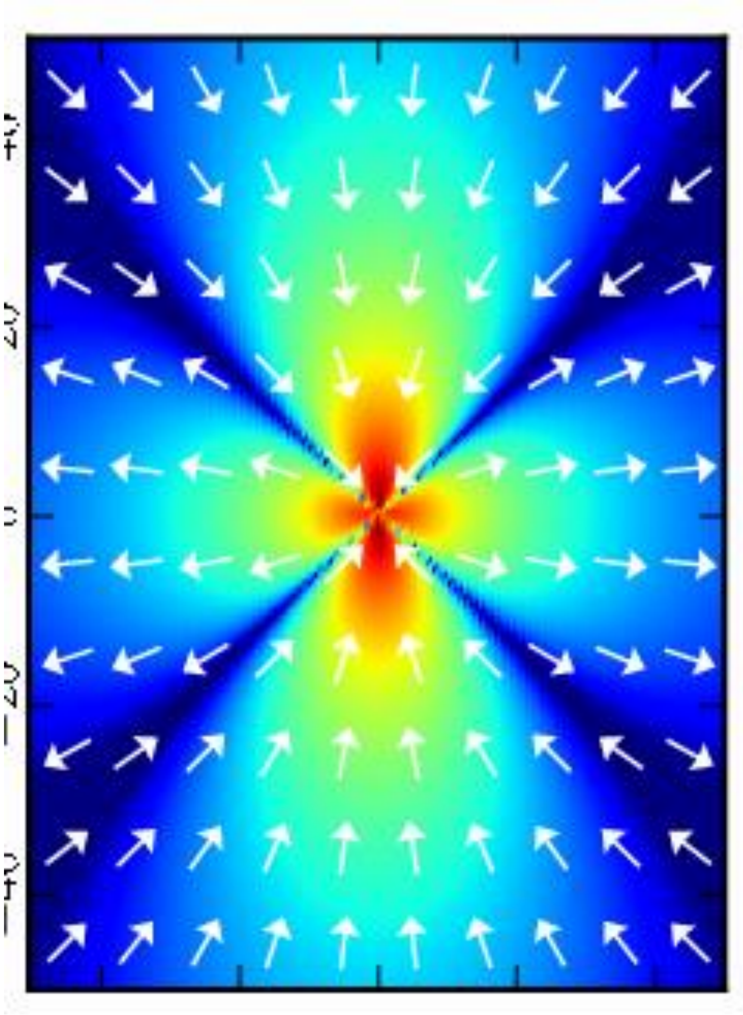


Multipole flow fields

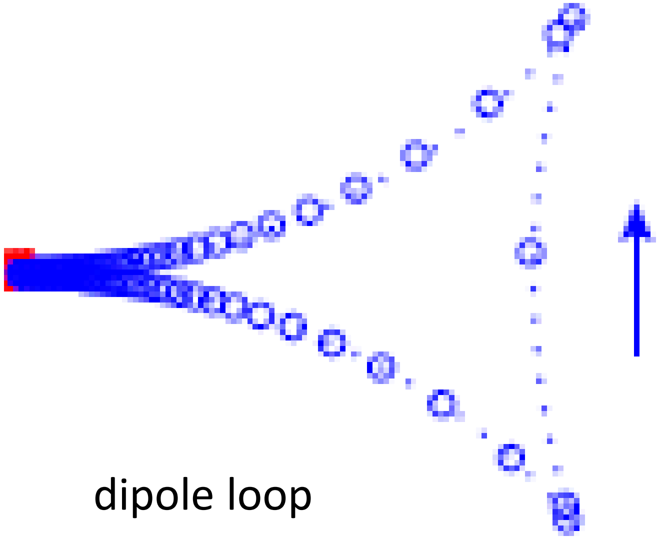


Dipole flow field

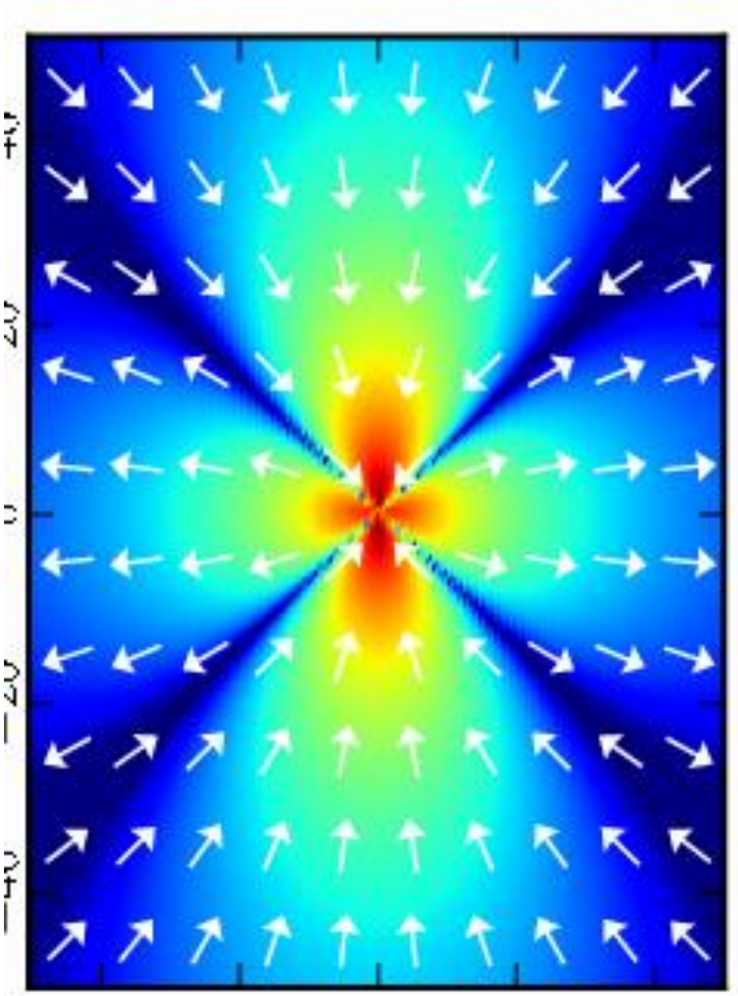
Multipole flow fields



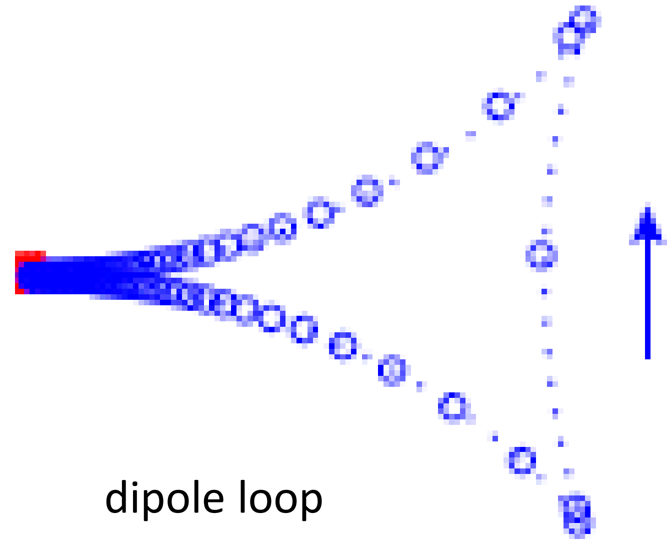
Dipole flow field



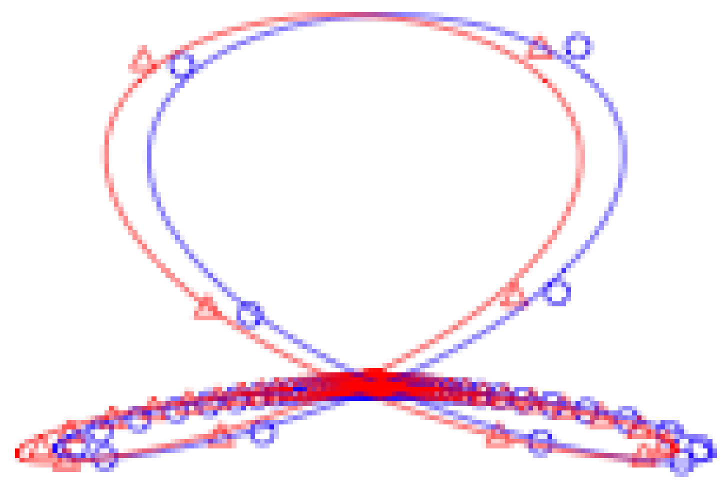
Multipole flow fields



Dipole flow field



dipole loop



quadrupole loop

?? enhanced diffusion and loops ??

Multipole expansion

Stokeslet:

$$\mathbf{u}^{\mathbf{S}}(\mathbf{r},\mathbf{k}) = \mathbf{k}\cdot\mathbf{J}, \quad \mathbf{J} = \frac{\mathbf{I}}{r} + \frac{\mathbf{r}\mathbf{r}}{r^3}$$

Dipole term:

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Quadrupole term:

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$$Q_{\perp} = -\frac{1}{2}\int_S f_z\rho^2 dS$$

$$\mathbf{u}(\mathbf{r},\mathbf{k}) = (\mathbf{k}\cdot\nabla)\,\mathbf{U}_0(\mathbf{r},\mathbf{k}) + O(r^{-4})$$

$$\frac{d\mathbf{r}_T}{dt} = \mathbf{u}\left(\mathbf{r},\mathbf{k}\right) = \left(\mathbf{k}\cdot\nabla\right)\mathbf{U}_0\left(\mathbf{r},\mathbf{k}\right)$$

Lagrangian derivative at the position of the tracer $\mathbf{r}_T$:

$$\frac{d\mathbf{U}_0}{dt} = \left(\mathbf{V}\cdot\nabla\right)\mathbf{U}_0 - \left(\frac{d\mathbf{r}_T}{dt}\cdot\nabla\right)\mathbf{U}_0, \quad \mathbf{V} = V\mathbf{k}$$

Eulerian derivative:

$$\frac{d\mathbf{U}_0}{dt} \approx V\left(\mathbf{k}\cdot\nabla\right)\mathbf{U}_0$$

tracer velocity:

$$\frac{1}{V}\frac{d\mathbf{U}_0}{dt} \approx \frac{d\mathbf{r}_T}{dt}$$

total tracer displacement:

$$\Delta\mathbf{r}_T = \int_{-\infty}^{+\infty}\frac{d\mathbf{r}_T}{dt}dt = -\frac{\kappa}{V}\left(\mathbf{U}_0(+\infty) - \mathbf{U}_0(-\infty)\right) = \mathbf{0}$$

$$\mathbf{u}\left(\mathbf{r},\mathbf{k}\right)=\left(\mathbf{k}\cdot\nabla\right)\mathbf{U}_0\left(\mathbf{r},\mathbf{k}\right)+O(r^{-4})$$

entrainment

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infinite swimmer path

Low Reynolds number swimming

The Scallop theorem

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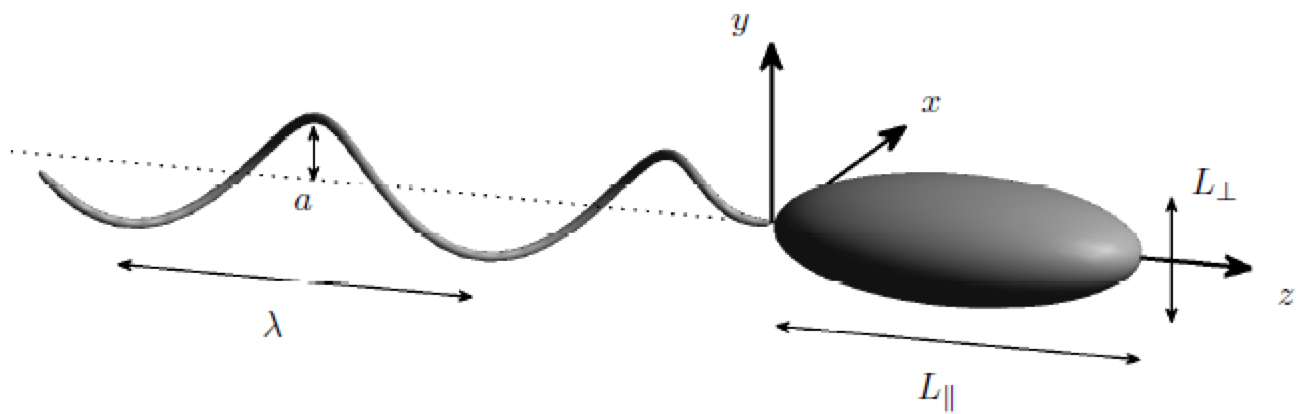
Rhodobacter sphaeroides



Boundary element simulations

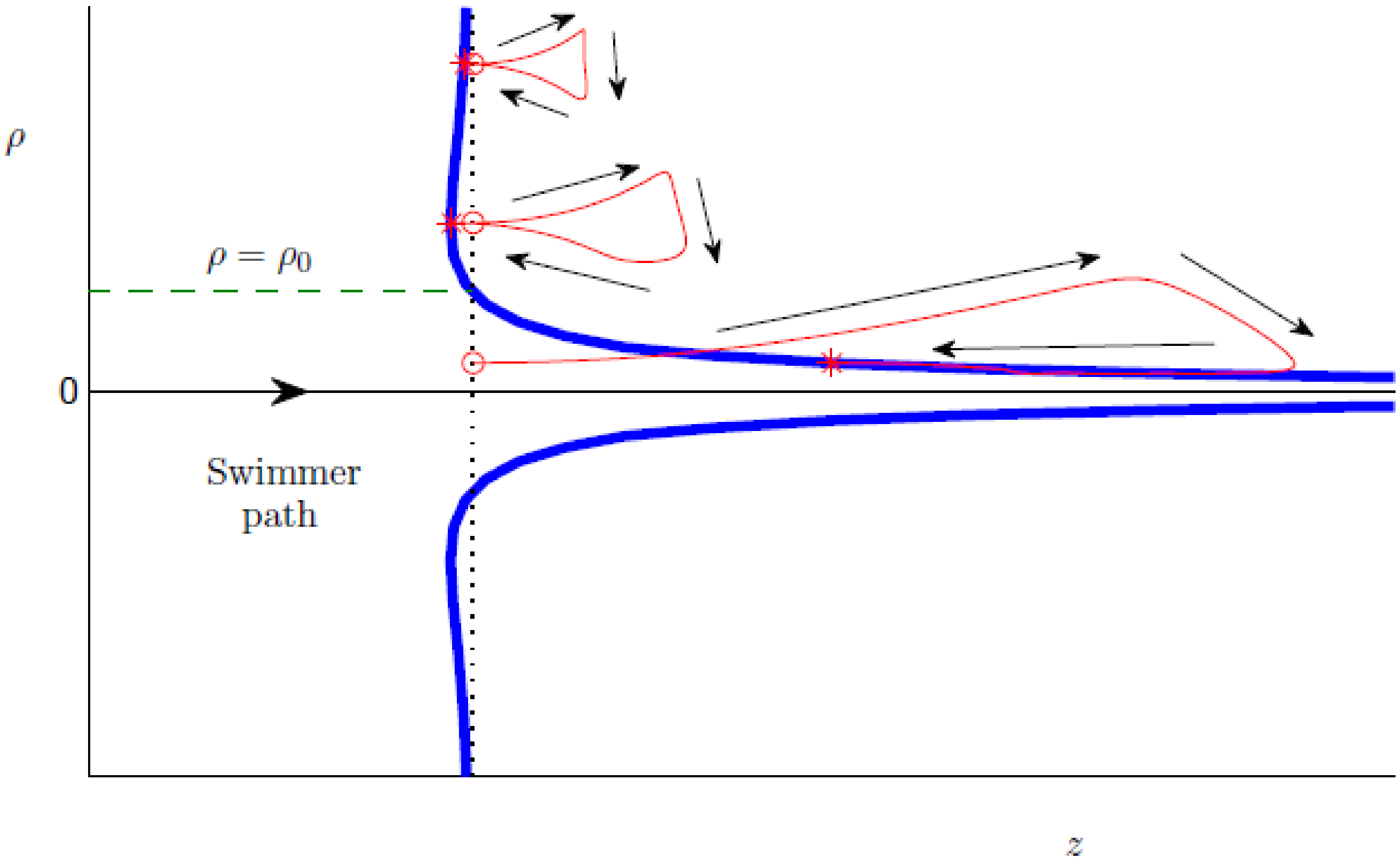
Solve Stokes equations, no slip on swimmer surface, swimmer force and torque free

Swimmer radius 1; swimmer velocity 1; ~ 10 rotations of tail to advance one body length

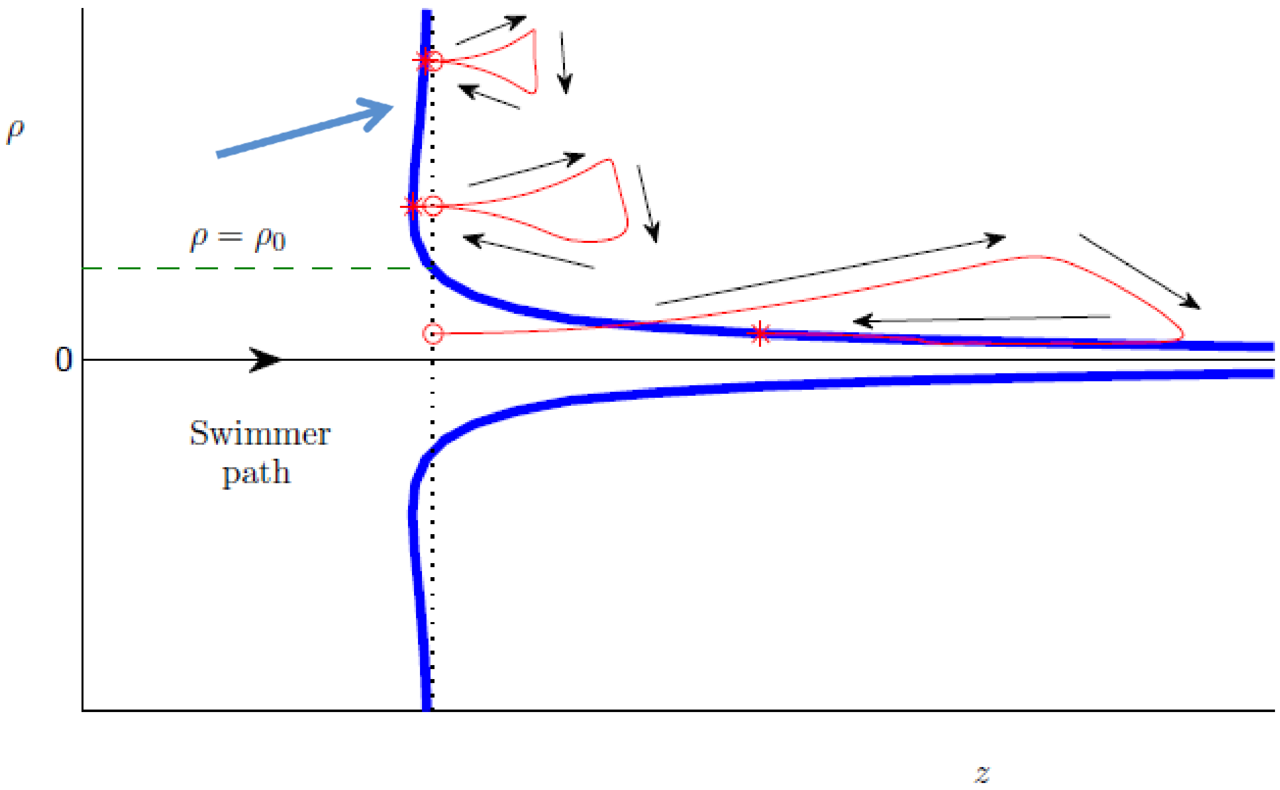
Net tracer displacement along z – deviations from the z-direction very small

Swimmer moves from z= -1000 to z= +1000, and extrapolate to infinite swimmer path

Entrainment



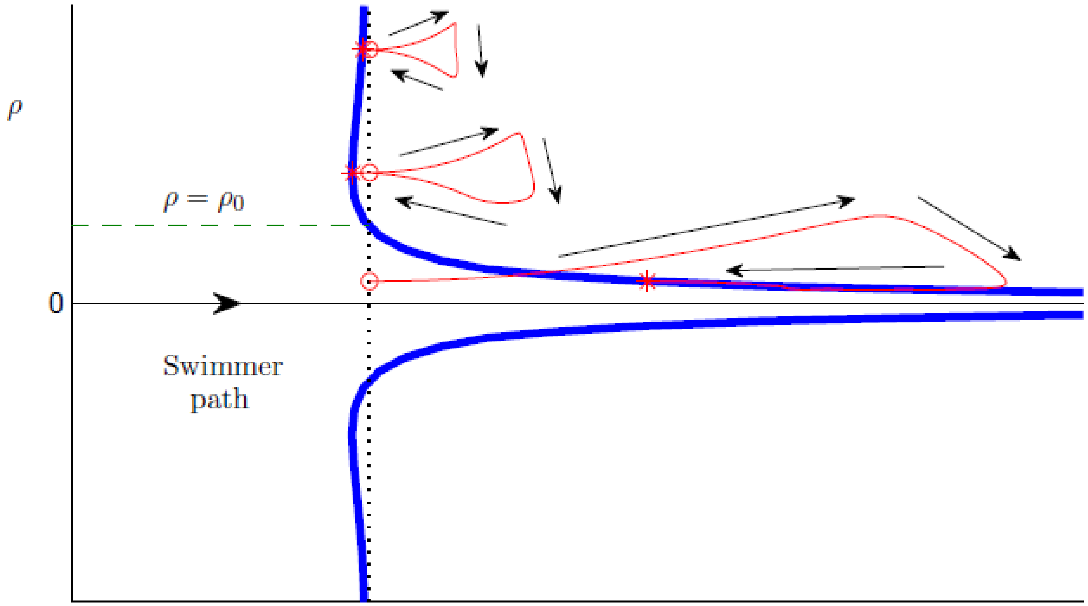
Entrainment



Far field entrainment:

$$\Delta = -C_1 \frac{\kappa^2}{V^2} \frac{1}{\rho^3} + C_2 \frac{\kappa Q_\perp}{V^2} \frac{1}{\rho^4} + O(\rho^{-5})$$

Darwin drift



Total fluid volume moved by swimmer

Darwin
Benjamin
Eames
Belcher
Hunt
Gobby
Dalziel
Leshansky
Pismen

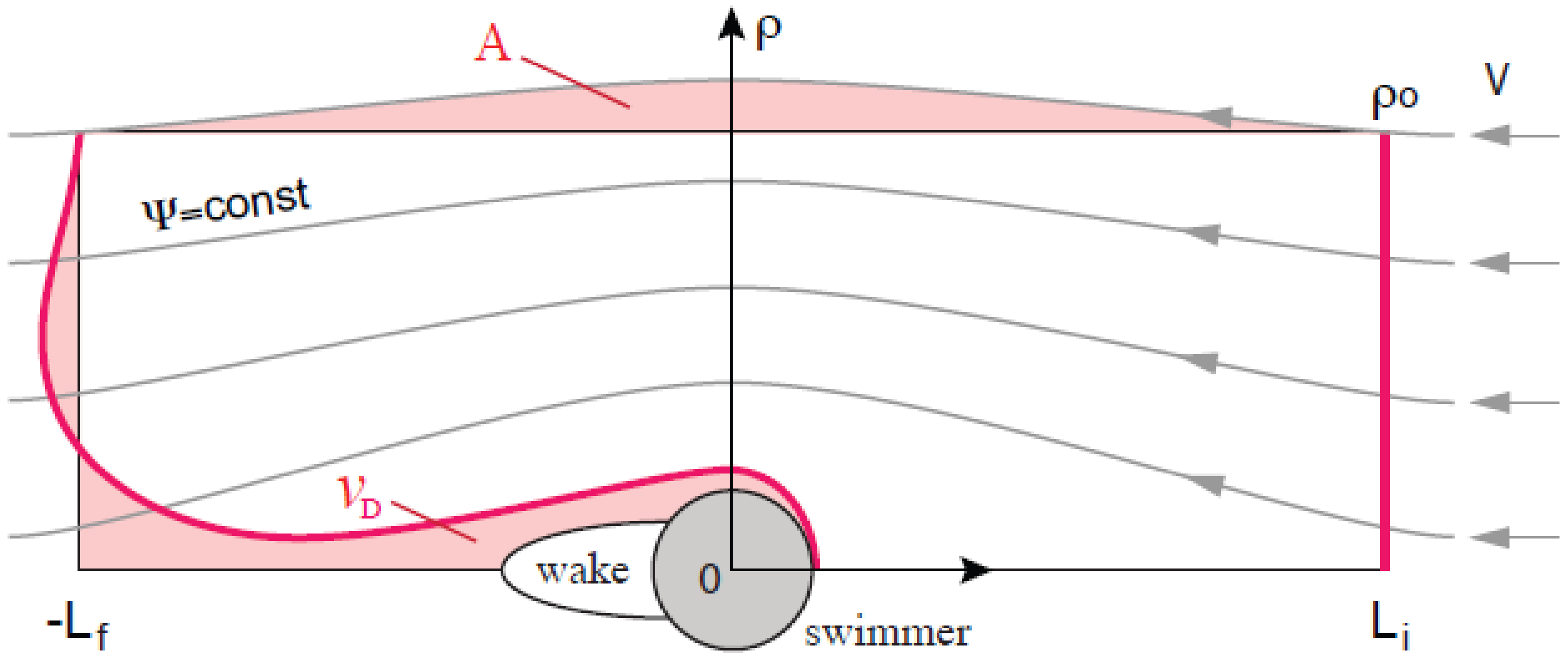
Darwin drift:

$$v_D = \frac{4\pi Q_\perp}{V} - v_*,$$

$$v_* = v_s + v_{wake}$$

$$Q_\perp = -\frac{1}{2}\int_S f_z \rho^2 dS$$

Darwin drift



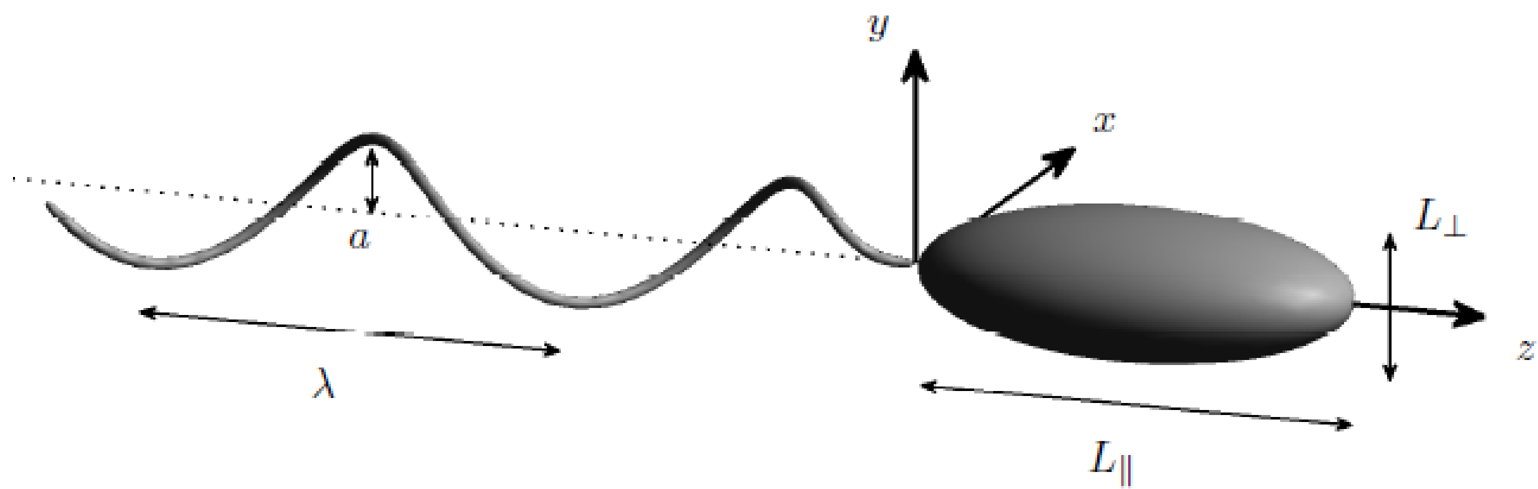
$$\psi(\rho_0, L_i)\Delta t + v_D + v_* - A = \psi_0(\rho_0, L_i)\Delta t$$

$$v_D = A(\rho_0) - v_*$$

Darwin drift:

$$v_D = \frac{4\pi Q_\perp}{V} - v_*,$$

$$v_* = v_s + v_{wake}$$

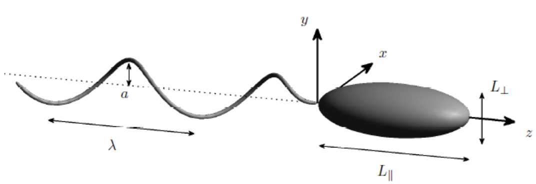


Base parameters: $L_{||}/L_\perp = 2$, $\lambda = 2$, $L = 10$, $a = \lambda/2\pi$.

Comparison of analytic and numerical results for the Darwin drift

TABLE 1. Base parameters: $L_{\|}/L_{\perp} = 2$, $\lambda = 2$, $L = 10$, $a = \lambda/2\pi$.

Shape	$Q_{\perp}/V$	v_D (from equation)	v_D (from simulations)
Base	-0.15	-6.10	-6.11
$L_{\|}/L_{\perp} = 0.5$	-0.68	-12.74	-12.78
$L_{\|}/L_{\perp} = 3.5$	-0.08	-5.24	-5.33
$L = 5$	-0.17	-6.36	-6.30
$L = 15$	-0.14	-5.98	-6.03
$\lambda = 0.5$	-0.20	-6.76	-6.78
$\lambda = 3.5$	-0.04	-4.71	-4.68
$\lambda = 8, L = 20$	0.58	3.04	3.07



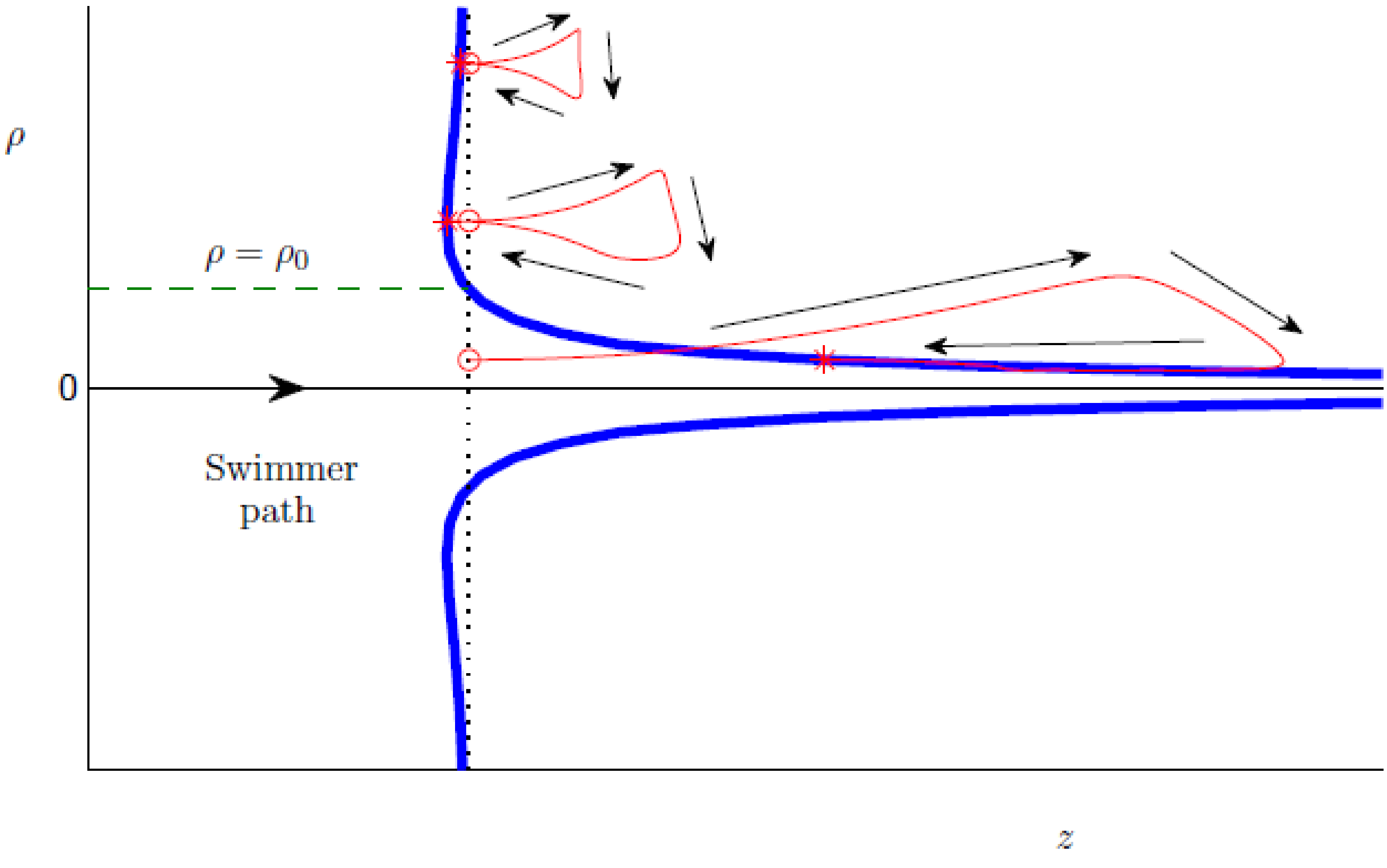
$$Q_{\perp} = -\frac{1}{2}\int_S f_z \rho^2 dS$$

Darwin drift:

$$v_D = \frac{4\pi Q_{\perp}}{V} - v_*,$$

$$v_* = v_s + v_{wake}$$

Entrainment



Comparison of analytic and numerical results for the Darwin drift

TABLE 1. Base parameters: $L_{\|}/L_{\perp} = 2$, $\lambda = 2$, $L = 10$, $a = \lambda/2\pi$.

Shape	$Q_{\perp}/V$	v_D (from equation)	v_D (from simulations)
Base	-0.15	-6.10	-6.11
$L_{\|}/L_{\perp} = 0.5$	-0.68	-12.74	-12.78
$L_{\|}/L_{\perp} = 3.5$	-0.08	-5.24	-5.33
$L = 5$	-0.17	-6.36	-6.30
$L = 15$	-0.14	-5.98	-6.03
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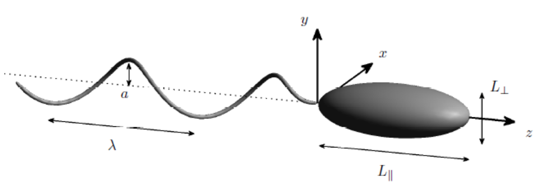

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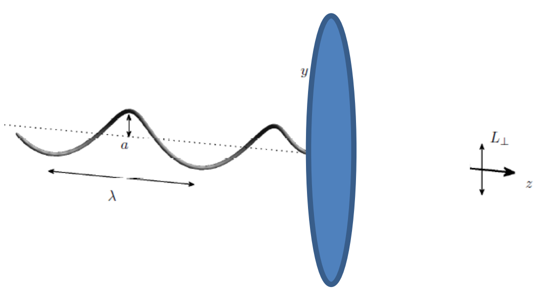

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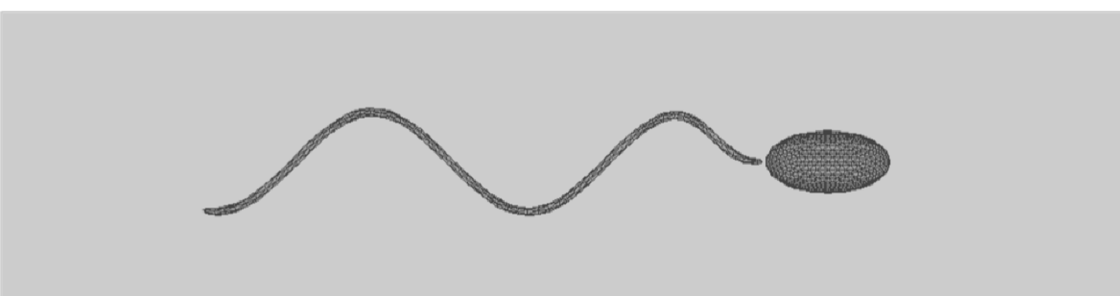
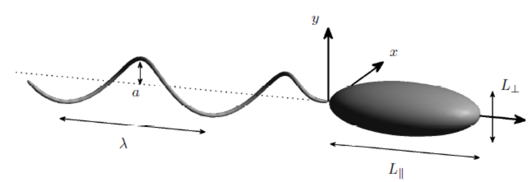
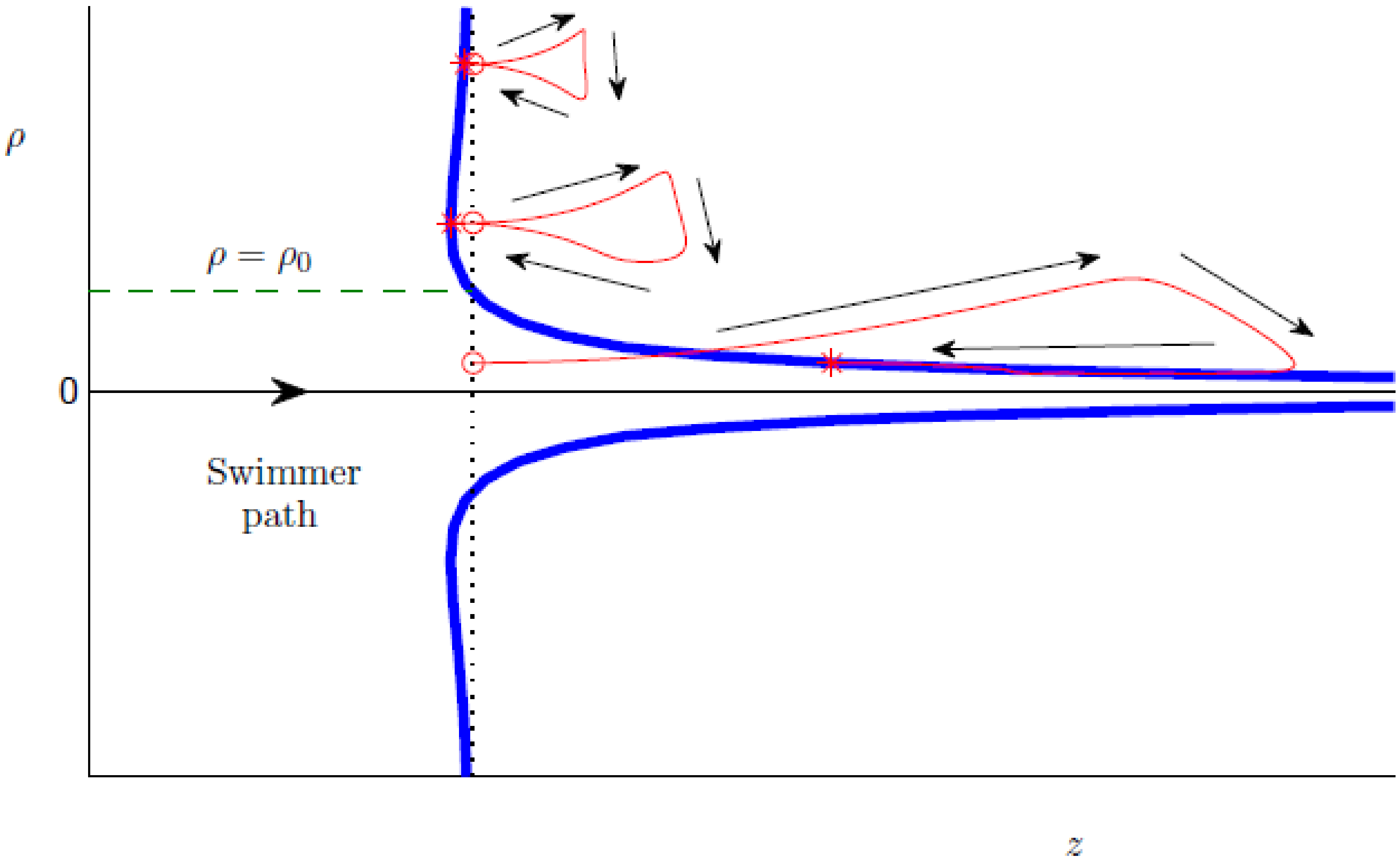




Entrainment



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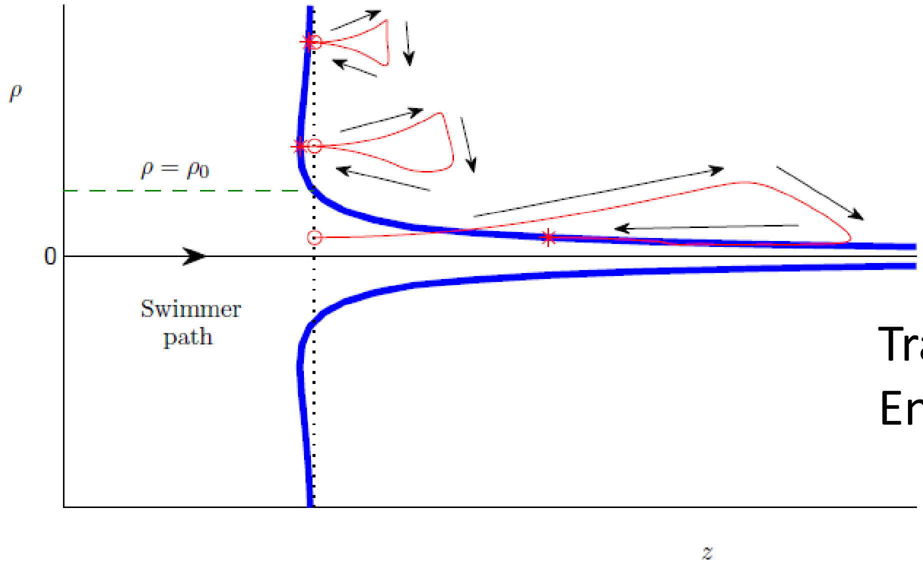


Tracer moves in loops far from swimmer

Entrainment close to the swimmer

Volume of fluid moved by the swimmer:

Darwin drift:

$$v_D = \frac{4\pi Q_\perp}{V} - v_*,$$

$$v_* = v_s + v_{wake}$$

$$D_{entr} \approx \frac{1}{6} n\, V\, a\, \frac{4\pi}{3} a^3$$

Low Reynolds number swimming

The Scallop theorem

Dipolar flow fields

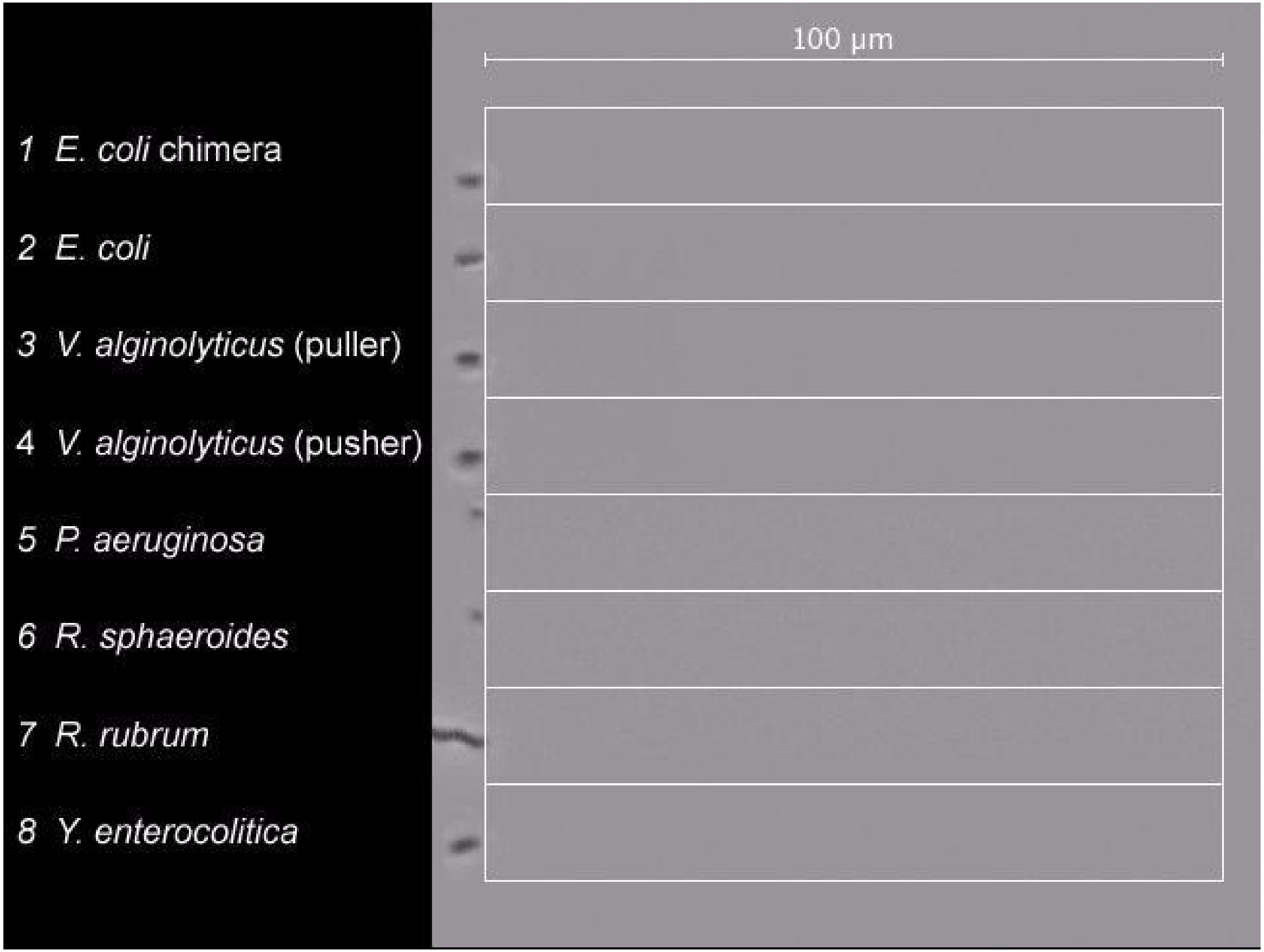
Stirring by microswimmers

Loops

Entrainment

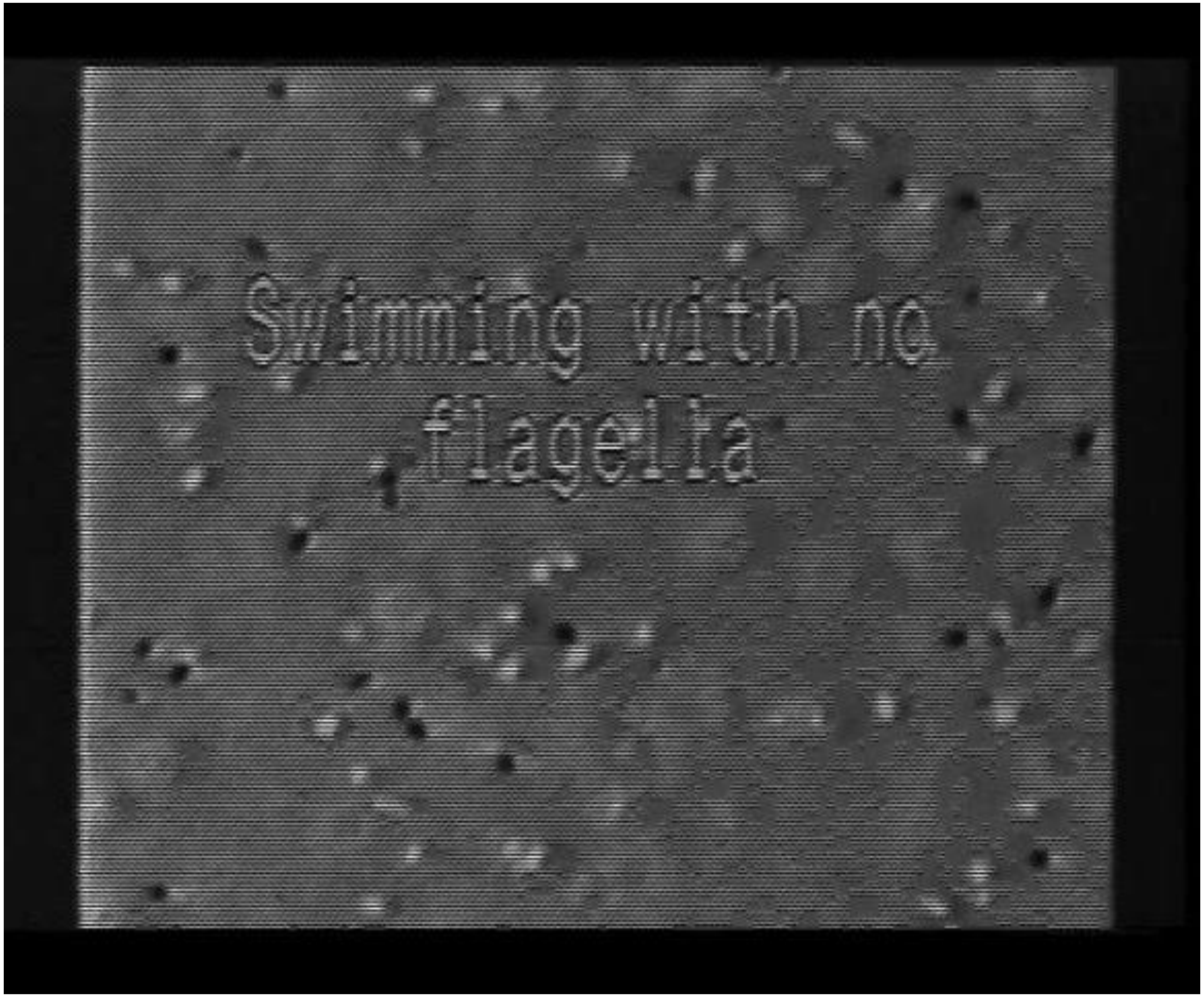
Random re-orientations

!!!!!   Bacterial Olympics: 100 micrometres   !!!!



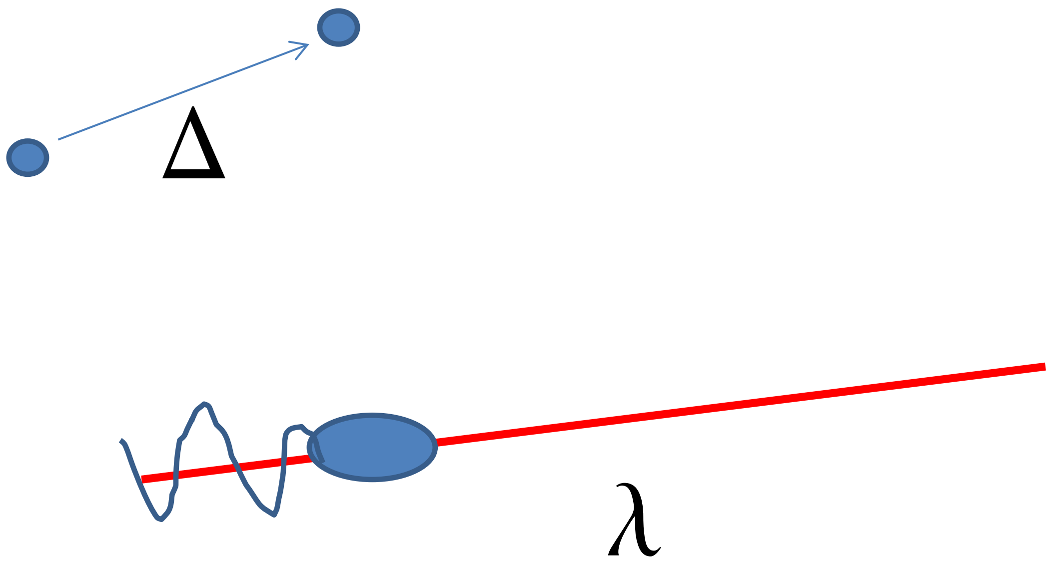
Judith Armitage,
Oxford biophysics

Random reorientations



http://mcb.harvard.
edu/Faculty/Berg.html

Random reorientations



$$\langle \Delta^2 \rangle = (Vol\, n_s)\, \frac{1}{Vol} \int d^d\mathbf{r_i}\, \Delta^2(\mathbf{r_i})$$

$$D = \langle \Delta^2 \rangle / \, (2\, d\, t) = \frac{1}{2d} \frac{n\, V}{\lambda} \int d^d\mathbf{r_i}\, \Delta^2(\mathbf{r_i})$$

Lin, Thiffeault, Childress JFM (2011)

$$\mathbf{u}\,(\mathbf{r},\mathbf{k}) = (\mathbf{k}\cdot\nabla)\,\mathbf{U}_0\,(\mathbf{r},\mathbf{k}) + O(r^{-4})$$

Lagrangian derivative at the position of the tracer $\mathbf{r}_T$:

$$\frac{d\mathbf{U}_0}{dt} = (\mathbf{V}\cdot\nabla)\,\mathbf{U}_0 - \left(\frac{d\mathbf{r}_T}{dt}\cdot\nabla\right)\mathbf{U}_0, \quad \mathbf{V} = V\mathbf{k}$$

Eulerian derivative:

$$\frac{d\mathbf{U}_0}{dt} \approx V\,(\mathbf{k}\cdot\nabla)\,\mathbf{U}_0$$

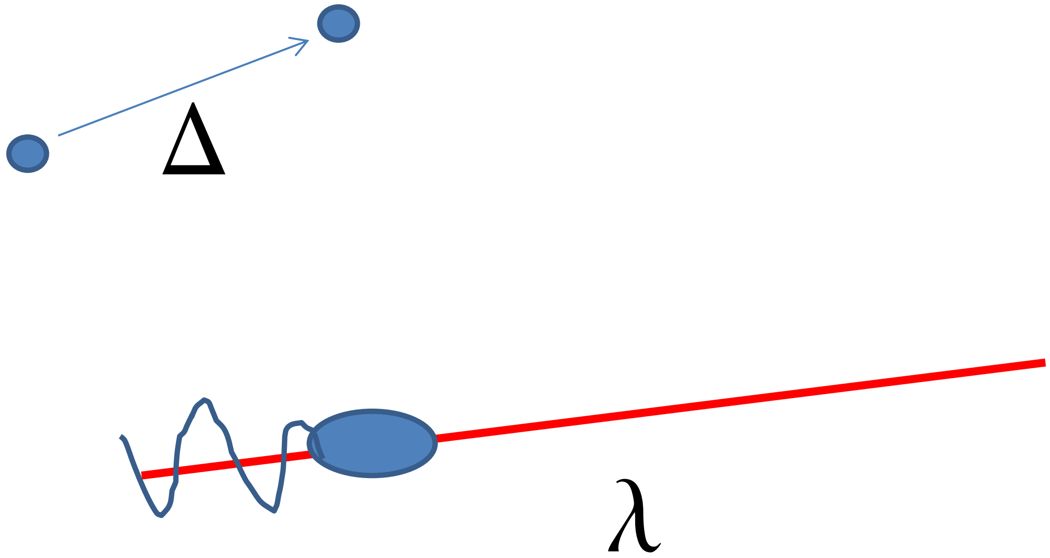
tracer velocity:

$$\frac{1}{V}\frac{d\mathbf{U}_0}{dt} \approx \frac{d\mathbf{r}_T}{dt}$$

total tracer displacement:

$$\Delta\mathbf{r}_T = \int_{-\infty}^{+\infty}\frac{d\mathbf{r}_T}{dt}dt = -\frac{\kappa}{V}\,(\mathbf{U}_0(+\infty) - \mathbf{U}_0(-\infty)) = \mathbf{0}$$

Random reorientations



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Lin, Thiffeault, Childress JFM (2011)

Random reorientations

$d > d_*(m) = 2(m-1)$

Regular (eg dipolar swimmer, m=2, d=3)

$$D_{rr} \sim \tilde{\kappa}_m^2 \, n \, V \, \lambda^{d-2m+1} \, a^{2m}$$

- Independent of swimmer run length for dipolar swimmers in 3D
  Lin, Thiffeault, Childress JFM (2011)
- Distribution of tracer run lengths converges to a Gaussian

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$d < d_*(m) = 2(m-1)$

Singular (eg quadrupolar swimmer, m=3, d=3)

$$D_{rr} \sim \tilde{\kappa}_m^2 \, n \, V \, \lambda^{-1} \, a^{d+2},$$

- Distribution of tracer run lengths is a truncated Levy distribution

Entrainment | Random reorientations

Regular (eg dipolar swimmer, m=2, d=3)

$$\frac{D_{rr}}{D_{entr}} \approx \frac{\tilde{\kappa}^2 \; n \; V \;\; a^4}{n \; V \;\; a^4} \sim \tilde{\kappa}^2$$

Singular (eg quadrupolar swimmer, m=3, d=3)

$$\frac{D_{rr}}{D_{entr}} \approx \frac{\tilde{\kappa}^2 \; n \; V \; \lambda^{-1} \; a^5}{n \; V \;\; a^4} \sim \tilde{\kappa}^2 \frac{a}{\lambda}$$

Random reorientations

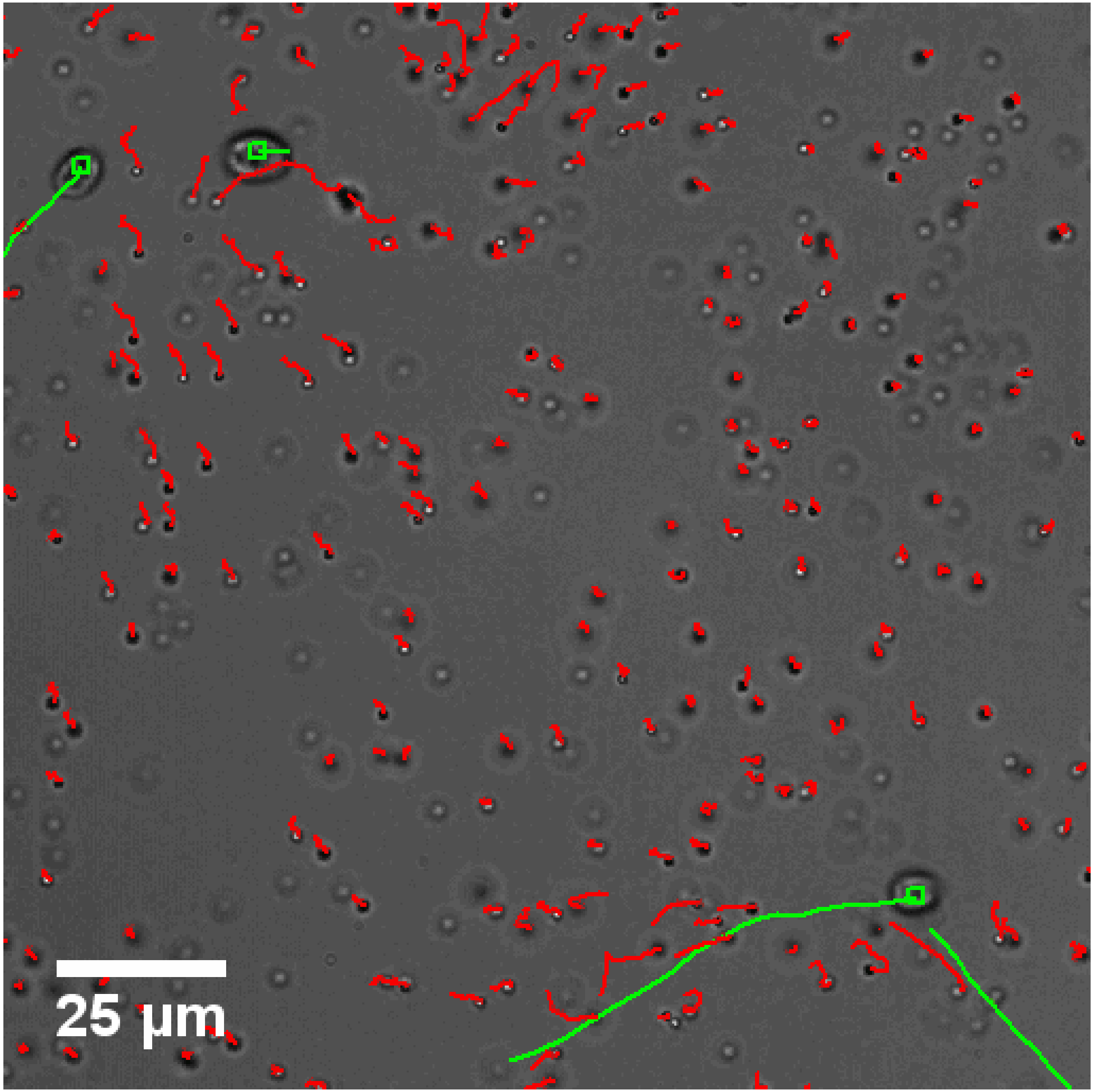
For 3D dipolar swimmers

$$D_{rr} = \frac{4\pi}{3} \kappa_m^2 \, n \, V \, a^4$$

independent of swimmer run length.

In the regular case (eg 3D dipolar swimmers)
diffusion due to random reorientations is dominant
distribution of lengths of tracer paths Gaussian

In the singular case (eg 3D quadrupolar swimmers)
diffusion due to entrainment is dominant:
tracer paths lengths form a truncated Levy distribution



Guasto website

Open questions

Correlated re-orientations

Denser swimmer suspensions

Surfaces and confinement

Links between stirring, swimmer structure and stroke and biological fitness