Biomixing for physicists
when organisms stir their environment

Jean-Luc Thiffeault[1]   Steve Childress[2]   Zhi George Lin[3]

[1]Department of Mathematics
University of Wisconsin – Madison

[2]Courant Institute of Mathematical Sciences
New York University

[3]Institute for Mathematics and its Applications
University of Minnesota – Twin Cities

Physics Colloquium
Auburn University, 7 September 2012
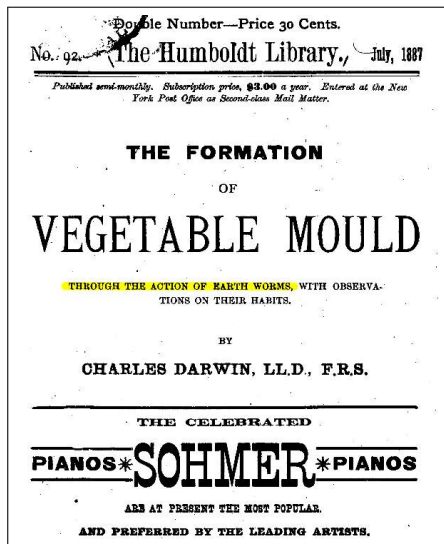
Biomixing

A controversial proposition:

- There are many regions of the ocean that are relatively quiescent, especially in the depths (1 hairdryer/ km^3);

- Yet mixing occurs: nutrients eventually get dredged up to the surface somehow;

- What if organisms swimming through the ocean made a significant contribution to this?

- There could be a local impact, especially with respect to feeding and schooling;

- Also relevant in suspensions of microorganisms (viscous Stokes regime).

Bioturbation

The earliest case studied of animals 'stirring' their environment is the subject of Darwin's last book.

This was suggested by his uncle and future father-in-law Josiah Wedgwood II, son of the famous potter.

"I was thus led to conclude that all the vegetable mould over the whole country has passed many times through, and will again pass many times through, the intestinal canals of worms."

Munk's Idea

Though it had been mentioned earlier, the first to seriously consider the role of ocean biomixing was Walter Munk (1966):

## Abyssal recipes

WALTER H. MUNK*

(*Received* 31 *January* 1966)

Abstract—Vertical distributions in the interior Pacific (excluding the top and bottom kilometer) are not inconsistent with a simple model involving a constant upward vertical velocity $w \approx 1 \cdot 2$ cm day^{-1} and eddy diffusivity $\kappa \approx 1 \cdot 3$ cm^2 sec^{-1}. Thus temperature and salinity can be fitted by exponential-like solutions to $[\kappa \cdot d^2/dz^2 - w \cdot d/dz]\, T, S = 0$, with $\kappa/w \approx 1$ km the appropriate " scale height." For Carbon 14 a decay term must be included, $[\quad]\,^{14}C = \mu\,^{14}C$; a fitting of the solution to the observed ^{14}C distribution yields $\kappa/w^2 \approx 200$ years for the appropriate " scale time," and permits w and

". . . I have attempted, without much success, to interpret [the eddy diffusivity] from a variety of viewpoints: from mixing along the ocean boundaries, from thermodynamic and biological processes, and from internal tides."

In situ experiments

Katija & Dabiri (2009) looked at jellyfish:
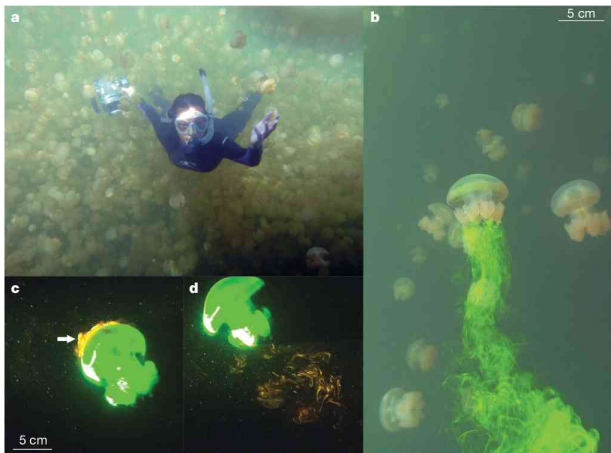
[movie 1] (Palau's Jellyfish Lake.)
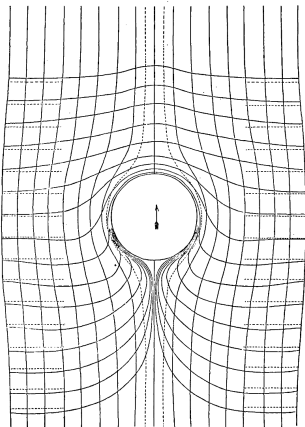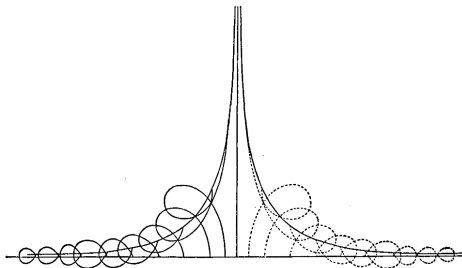
Displacement by a moving body

Fig. 2.
Paths of particles of the fluid when a cylinder moves through it.

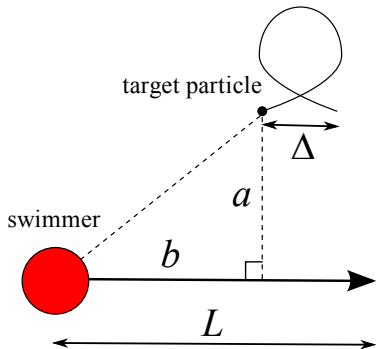Maxwell (1869); Darwin (1953); Eames *et al.* (1994)

A sequence of kicks

Inspired by Einstein's theory of diffusion (Einstein, 1956): a test particle initially at $\mathbf{x}(0) = 0$ undergoes N encounters with an axially-symmetric swimming body:

$$\mathbf{x}(t) = \sum_{k=1}^{N} \Delta_L(a_k, b_k)\,\hat{\mathbf{r}}_k$$

$\Delta_L(a, b)$ is the displacement, a_k, b_k are impact parameters, and $\hat{\mathbf{r}}_k$ is a direction vector.

target particle

Δ

a

swimmer

b

L

($a > 0$, but b can have either sign.)

After squaring and averaging, assuming isotropy:

$$\langle |\mathbf{x}|^2 \rangle = N \langle \Delta_L^2(a, b) \rangle$$

where a and b are treated as random variables with densities

$$\mathrm{d}\mathbf{A}/V = 2\,\mathrm{d}a\,\mathrm{d}b/V \quad (2D) \quad \text{or} \quad 2\pi a\,\mathrm{d}a\,\mathrm{d}b/V \quad (3D)$$

Replace average by integral:

$$\langle |\mathbf{x}|^2 \rangle = \frac{N}{V} \int \Delta_L^2(a, b)\,\mathrm{d}\mathbf{A}$$

Writing $n = 1/V$ for the number density (there is only one swimmer) and $N = Ut/L$ (L/U is the time between steps):

$$\langle |\mathbf{x}|^2 \rangle = \frac{Unt}{L} \int \Delta_L^2(a, b)\,\mathrm{d}\mathbf{A}$$

Effective diffusivity

Putting this together,

$$\langle |\mathbf{x}|^2 \rangle = \frac{2Unt}{L} \int \Delta_L^2(a, b) \, \mathrm{d}a \, \mathrm{d}b = 4\kappa t, \qquad \text{2D}$$

$$\langle |\mathbf{x}|^2 \rangle = \frac{2\pi Unt}{L} \int \Delta_L^2(a, b) a \, \mathrm{d}a \, \mathrm{d}b = 6\kappa t, \qquad \text{3D}$$
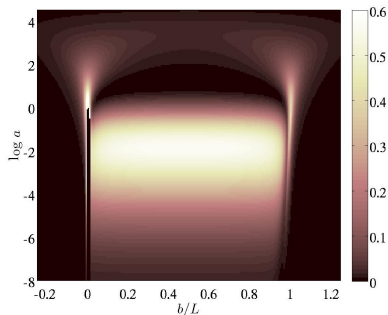
which defines the effective diffusivity κ.

If the number density is low ($nL^d \ll 1$), then encounters are rare and we can use this formula for a collection of particles.
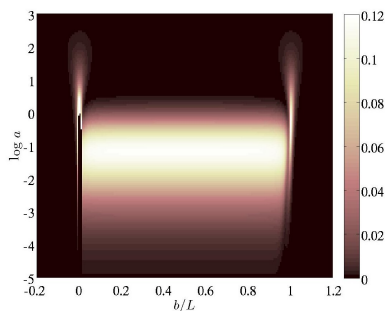
Inviscid cylinders and spheres (treadmill swimmer)

$$\kappa = \tfrac{\pi}{3} U n \int a^2 \Delta_L^2(a, b) \, \mathrm{d}(\log a) \, \mathrm{d}(b/L) \qquad \text{3D}$$

Notice $\Delta_L(a, b)$ is nonzero for $0 < b < L$; otherwise independent of b and L $\implies$ have to cross point of closest approach.


$a\Delta_L^2(a, b)$ (cylinder) $\qquad\qquad$ $a^2\Delta_L^2(a, b)$ (sphere)

Numerical simulation

- Validate theory using simple simple simulations;

- Large periodic box;

- N_{swim} swimmers (cylinders of radius 1), initially at random positions, swimming in random direction with constant speed $U = 1$;

- Target particle initially at origin advected by the swimmers;

- Since dilute, superimpose velocities;

- Integrate for some time, compute $|\mathbf{x}(t)|^2$, repeat for a large number N_{real} of realizations, and average.

A 'gas' of swimmers
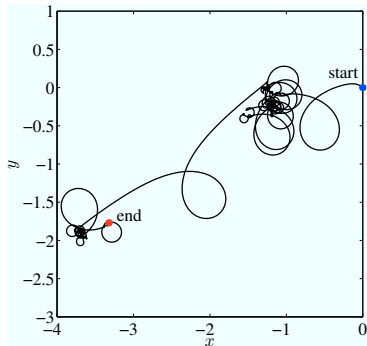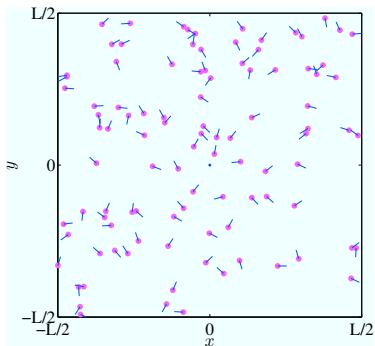
[movie 2] 100 cylinders, box size $= 1000$

How well does the dilute theory work?
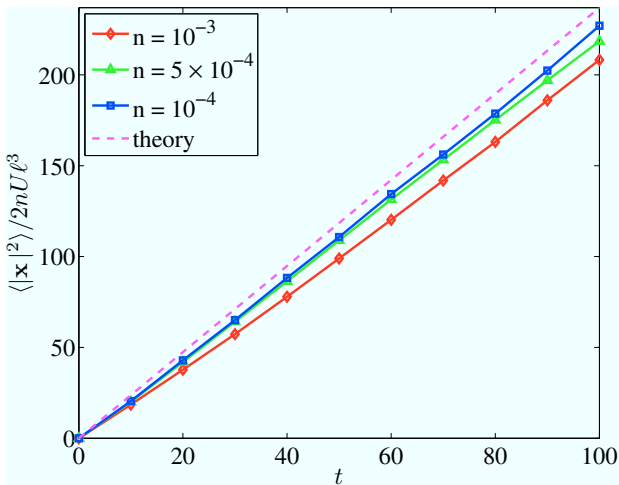
Cloud of particles
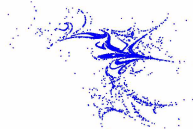
[movie 3]   **(30 cylinders)**
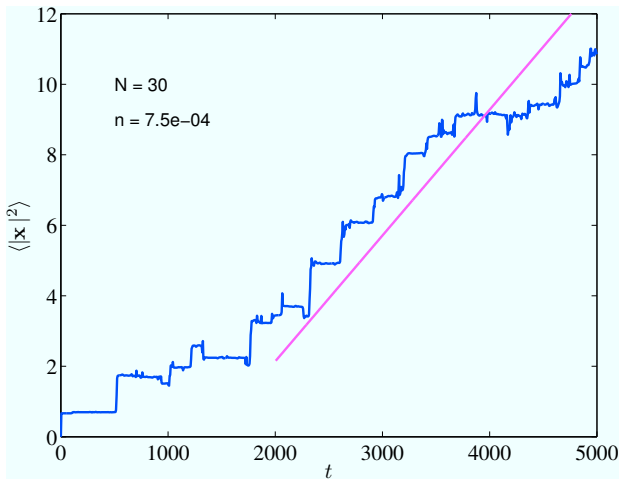
Cloud dispersion proceeds by steps

Squirmers

Considerable literature on transport due to microorganisms: Wu & Libchaber (2000); Hernandez-Ortiz *et al.* (2006); Saintillian & Shelley (2007); Ishikawa & Pedley (2007); Underhill *et al.* (2008); Ishikawa (2009); Leptos *et al.* (2009)

Lighthill (1952), Blake (1971), and more recently Ishikawa *et al.* (2006) have considered squirmers:

- Sphere in Stokes flow;
- Steady velocity specified at surface, to mimic cilia;
- Steady swimming condition imposed (no net force on fluid).
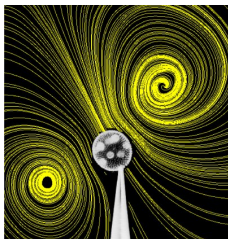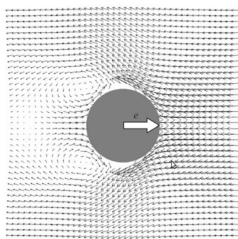
(Drescher *et al.*, 2009)   (Ishikawa *et al.*, 2006)

Typical squirmer

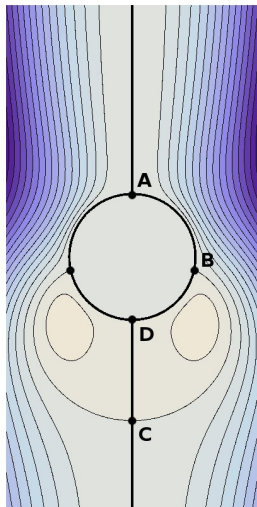3D axisymmetric streamfunction for a typical squirmer, in cylindrical coordinates (ρ, z):

$$\psi = -\tfrac{1}{2}\rho^2 + \frac{1}{2r^3}\,\rho^2 + \frac{3\beta}{4r^3}\,\rho^2 z\left(\frac{1}{r^2} - 1\right)$$

where $r = \sqrt{\rho^2 + z^2}$, $U = 1$, radius of squirmer $= 1$.

β is the amplitude of the stresslet (distinguises pushers/pullers).
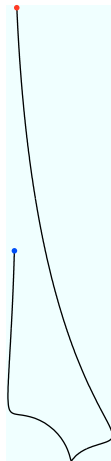
We will use $\beta = 5$ for most of the remainder.

Particle motion for squirmer

A particle near the squirmer's swimming axis initially (blue) moves towards the squirmer.

After the squirmer has passed the particle follows in the squirmer's wake.

(The squirmer moves from bottom to top.)

[movie 4]

Squirmer displacements $a^2\Delta_L^2(a, b)$
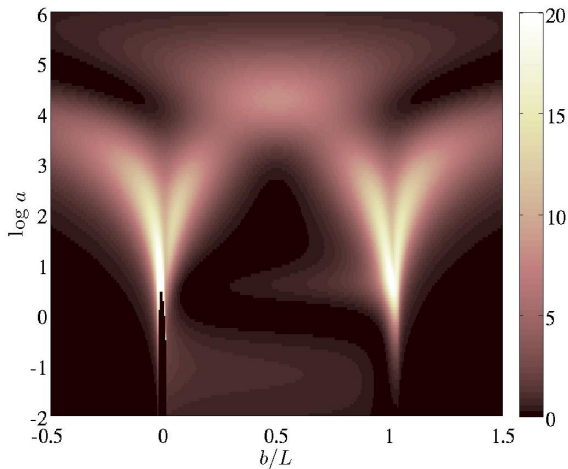
Squirmers: Transport
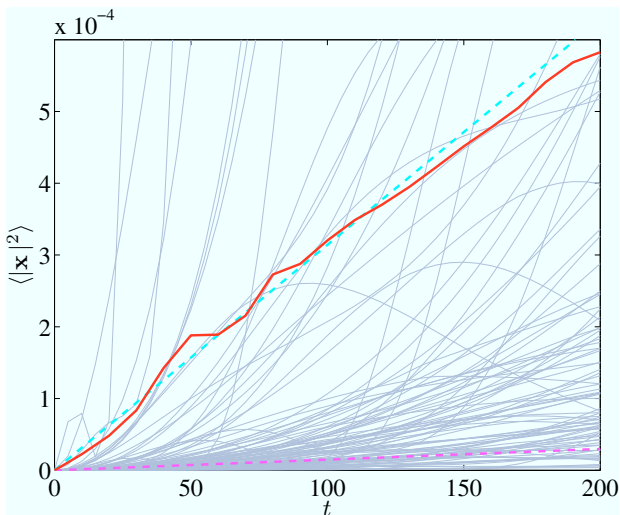
Squirmers: Trajectories

The two peaks in the displacement plot come from 'incomplete' trajectories:

$b/L = 0$ $b/L = 0.5$ $b/L = 1$
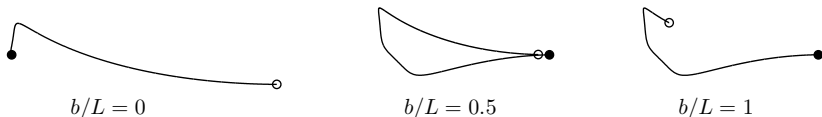
For long path length, the effective diffusivity is independent of the swimming path length, and yet the dominant contribution arises from the finiteness of the path (uncorrelated turning directions).

Non-Gaussian PDFs of displacement
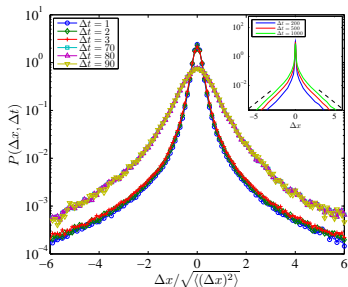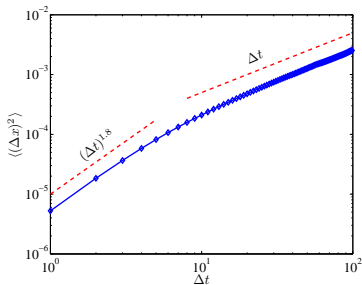
- Variance exhibits similar short-time anomalous scaling as in Wu & Libchaber (2000);
- PDF qualitatively matches experiments of Leptos *et al.* (2009). In our case, exponential tails are due to sticking at the stagnation points on the squirmer's body.

Conclusions

- Simple dilute model works well for a range of swimmers;
- Slip surfaces have an effective diffusivity that is independent of path length, for long path length;
- No-slip flows dominated by sticking and have a log dependence on path length;

Future work:

- Wake models and turbulence;
- PDF of scalar concentration;
- Buoyancy effects for the ocean case;
- Higher densities;
- Schooling: longer length scale?

BLAKE, J. 1971 A spherical envelope approach to ciliary propulsion. *J. Fluid Mech.* **46**, 199–208.

DARWIN, C. G. 1953 Note on hydrodynamics. *Proc. Camb. Phil. Soc.* **49** (2), 342–354.

DEWAR, W. K., BINGHAM, R. J., IVERSON, R. L., NOWACEK, D. P., ST. LAURENT, L. C. & WIEBE, P. H. 2006 Does the marine biosphere mix the ocean? *J. Mar. Res.* **64**, 541–561.

DOMBROWSKI, C., CISNEROS, L., CHATKAEW, S., GOLDSTEIN, R. E. & KESSLER, J. O. 2004 Self-concentration and large-scale coherence in bacterial dynamics. *Phys. Rev. Lett.* **93** (9), 098103.

DRESCHER, K., LEPTOS, K., TUVAL, I., ISHIKAWA, T., PEDLEY, T. J. & GOLDSTEIN, R. E. 2009 Dancing *volvox*: hydrodynamic bound states of swimming algae. *Phys. Rev. Lett.* **102**, 168101.

DRESCHER, K. D., GOLDSTEIN, R. E., MICHEL, N., POLIN, M. & TUVAL, I. 2010 Direct measurement of the flow field around swimming microorganisms. *Phys. Rev. Lett.* **105**, 168101.

DUNKEL, J., PUTZ, V. B., ZAID, I. M. & YEOMANS, J. M. 2010 Swimmer-tracer scattering at low Reynolds number. *Soft Matter* **6**, 4268–4276.

EAMES, I., BELCHER, S. E. & HUNT, J. C. R. 1994 Drift, partial drift, and Darwin's proposition. *J. Fluid Mech.* **275**, 201–223.

EINSTEIN, A. 1956 *Investigations on the Theory of the Brownian Movement*. New York: Dover.

GUASTO, J. S., JOHNSON, K. A. & GOLLUB, J. P. 2010 Oscillatory flows induced by microorganisms swimming in two-dimensions. *Phys. Rev. Lett.* **105**, 168102.

HERNANDEZ-ORTIZ, J. P., DTOLZ, C. G. & GRAHAM, M. D. 2006 Transport and collective dynamics in suspensions of confined swimming particles. *Phys. Rev. Lett.* **95**, 204501.

HUNTLEY, M. E. & ZHOU, M. 2004 Influence of animals on turbulence in the sea. *Mar. Ecol. Prog. Ser.* **273**, 65–79.

ISHIKAWA, T. 2009 Suspension biomechanics of swimming microbes. *J. Roy. Soc. Interface* **6**, 815–834.

ISHIKAWA, T. & PEDLEY, T. J. 2007 The rheology of a semi-dilute suspension of swimming model micro-organisms. *J. Fluid Mech.* **588**, 399–435.

ISHIKAWA, T., SIMMONDS, M. P. & PEDLEY, T. J. 2006 Hydrodynamic interaction of two swimming model micro-organisms. *J. Fluid Mech.* **568**, 119–160.

KATIJA, K. & DABIRI, J. O. 2009 A viscosity-enhanced mechanism for biogenic ocean mixing. *Nature* **460**, 624–627.

KUNZE, E., DOWER, J. F., BEVERIDGE, I., DEWEY, R. & BARTLETT, K. P. 2006 Observations of biologically generated turbulence in a coastal inlet. *Science* **313**, 1768–1770.

LEPTOS, K. C., GUASTO, J. S., GOLLUB, J. P., PESCI, A. I. & GOLDSTEIN, R. E. 2009 Dynamics of enhanced tracer diffusion in suspensions of swimming eukaryotic microorganisms. *Phys. Rev. Lett.* **103**, 198103.

LIGHTHILL, M. J. 1952 On the squirming motion of nearly spherical deformable bodies through liquids at very small Reynolds numbers. *Comm. Pure Appl. Math.* **5**, 109–118.

LIN, Z., THIFFEAULT, J.-L. & CHILDRESS, S. 2011 Stirring by squirmers. *J. Fluid Mech.* **669**, 167–177.

MAXWELL, J. C. 1869 On the displacement in a case of fluid motion. *Proc. London Math. Soc.* **s1-3** (1), 82–87.

OSEEN, C. W. 1910 Über die Stokessche formel und über eine verwandte aufgabe in der hydrodynamik. *Ark. Mat. Astr. Fys.* **6** (29), 1–20.

SAINTILLIAN, D. & SHELLEY, M. J. 2007 Orientational order and instabilities in suspensions of self-locomoting rods. *Phys. Rev. Lett.* **99**, 058102.

THIFFEAULT, J.-L. & CHILDRESS, S. 2010 Stirring by swimming bodies. *Phys. Lett. A* **374**, 3487–3490.

UNDERHILL, P. T., HERNANDEZ-ORTIZ, J. P. & GRAHAM, M. D. 2008 Diffusion and spatial correlations in suspensions of swimming particles. *Phys. Rev. Lett.* **100**, 248101.

WU, X.-L. & LIBCHABER, A. 2000 Particle diffusion in a quasi-two-dimensional bacterial bath. *Phys. Rev. Lett.* **84**, 3017–3020.