

Do fish stir the ocean?

Jean-Luc Thiffeault^{1,2} Steve Childress³ Zhi George Lin²

¹Department of Mathematics
University of Wisconsin – Madison

²Institute for Mathematics and its Applications
University of Minnesota – Twin Cities

³Courant Institute of Mathematical Sciences
New York University

Applied Math Colloquium, Columbia University, 9 March 2010

Biomixing

A controversial proposition:

- There are many regions of the ocean that are relatively quiescent, especially in the depths (**1 hairdryer/ km³**);
- 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).

Munk's Idea

Though it had been mentioned earlier, the first to seriously consider the role of 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 $w \approx 1.2 \text{ cm day}^{-1}$ and eddy diffusivity $\kappa \approx 1.3 \text{ cm}^2 \text{ sec}^{-1}$. 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 $\kappa/w \approx 1 \text{ km}$ the appropriate "scale height." For Carbon 14 a decay term must be included, $[\quad]^{14}\text{C} = \mu^{14}\text{C}$; a fitting of the solution to the observed ^{14}C distribution yields $\kappa/w^2 \approx 200 \text{ years}$ 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."

Basic claims

The idea lay dormant for almost 40 years; then

- Huntley & Zhou (2004) analyzed the swimming of 100 (!) species, ranging from bacteria to blue whales. Turbulent energy production is $\sim 10^{-5} \text{ W kg}^{-1}$ for 11 representative species.
- Total is comparable to energy dissipation by major storms.
- Another estimate comes from the solar energy captured: **63 TeraW**, something like 1% of which ends up as mechanical energy (Dewar *et al.*, 2006).
- Kunze *et al.* (2006) find that turbulence levels during the day in an inlet were **2 to 3 orders of magnitude** greater than at night, due to swimming krill.

Rain on the parade

Visser (2007) debunks these claims:

Let the turbulence be generated at a scale L , with a rate of turbulent energy dissipation ε .

The **buoyancy frequency** N is defined as

$$N^2 = -\frac{g}{\rho} \frac{d\rho}{dz}$$

where g is the gravitational acceleration and $\rho(z)$ is the density.

The **buoyancy length scale** (**Ozmidov scale**) is

$$B = (\varepsilon/N^3)^{1/2}$$

Mixing efficiency

The **mixing efficiency** is defined as

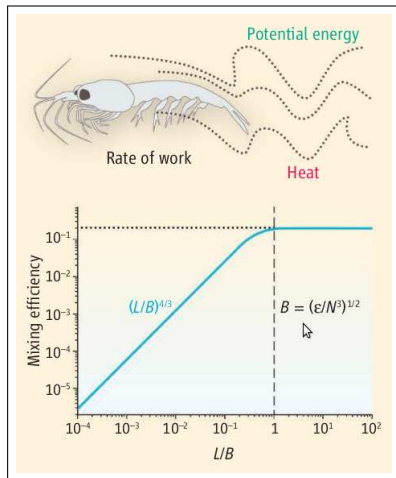
$$\Gamma = \frac{\text{change in potential energy}}{\text{work done}}$$

so $0 \leq \Gamma \leq 1$.

Visser's point is that Γ depends strongly on L/B .

For krill $L = 1.5$ cm, $B = 3$ to 10 m, so $L/B = .005$ to $.0015$.

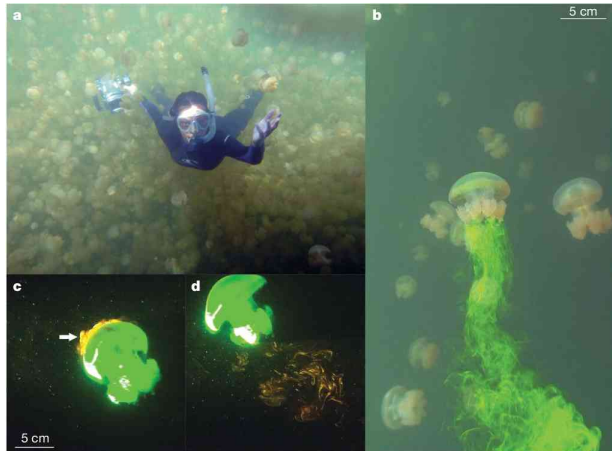
Conclude: $\Gamma = 10^{-4}$ to 10^{-3} : almost none of the turbulent energy goes into mixing.



(from Visser (2007))

But it's not over...

Katija & Dabiri (2009) looked at jellyfish:



[movie 1]

Displacement by a moving body

86

Mr. J. Clerk-Maxwell on

[Mar. 10,

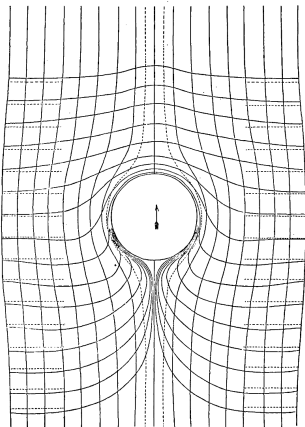


FIG. 1.

Fluid flowing past a fixed cylinder.

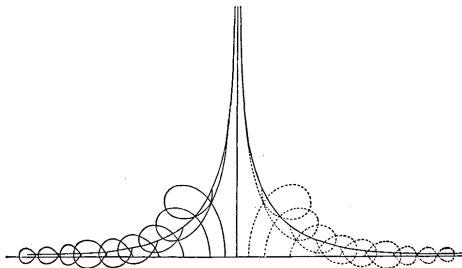


FIG. 2.

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

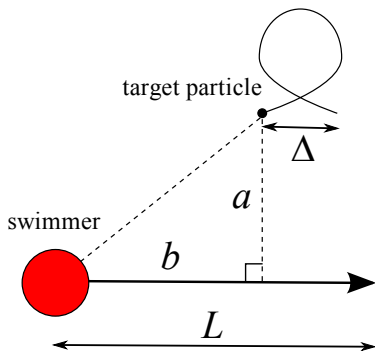
Maxwell (1869); Darwin (1953); Eames *et al.* (1994); Eames & Bush (1999)

A sequence of kicks

Inspired by Einstein's theory of diffusion (Einstein, 1905): 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.



($a > 0$, 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

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

Replace average by integral:

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

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

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

Effective diffusivity

Putting this together,

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

$$\langle |\mathbf{x}|^2 \rangle = \frac{2\pi Unt}{L} \int \Delta_L^2(a, b) a da db = 6\kappa t, \quad \text{3D}$$

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.

The first simplification we can make (for large L) is

$$\Delta_L(a, b) = \begin{cases} \Delta(a), & 0 \leq b \leq L; \\ 0, & \text{otherwise,} \end{cases}$$

that is, the displacement vanishes if the swimmer is moving away from the particle, or if the particle doesn't reach the swimmer. In that case we can do the b integral:

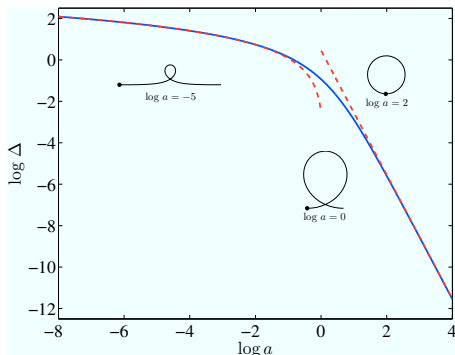
$$\kappa = \frac{Un}{2} \int_0^\infty \Delta^2(a) da, \quad \text{2D}$$

$$\kappa = \frac{\pi Un}{3} \int_0^\infty \Delta^2(a) a da, \quad \text{3D}$$

There is no path length dependence.

Contribution to displacement

Small a : $\Delta \sim -\log a$, large a : $\Delta \sim a^{-3}$ (Darwin, 1953)



$$\int_0^1 \Delta^2(a) da \simeq 2.31, \text{ whilst } \int_1^\infty \Delta^2(a) da \simeq .06.$$

\implies 97% dominated by “head-on” collisions

Origin of the singularity

At the leading and trailing 'edges' of a body, there is a hyperbolic point. Locally,

$$\dot{x} = -\lambda x, \quad \dot{y} = \lambda y$$

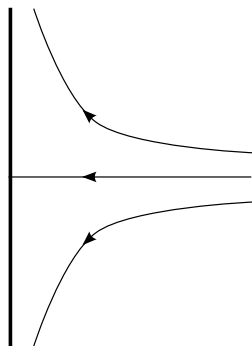
so that $y(t) = y_0 \exp(\lambda t)$. The time it takes to go from $y_0 = a$ to $y > a$ is

$$t = \lambda^{-1} \log(y/a) \sim -\lambda^{-1} \log a$$

which is the source of the logarithmic divergence of the displacement:

$$\Delta \sim -2U\lambda^{-1} \log a, \quad a \ll 1$$

The factor of 2 is for leading+trailing edges.

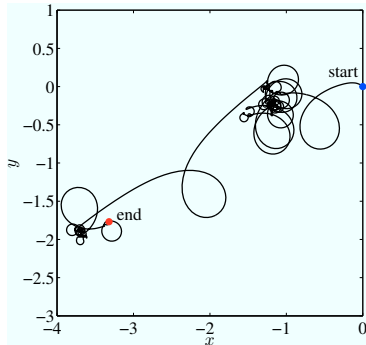
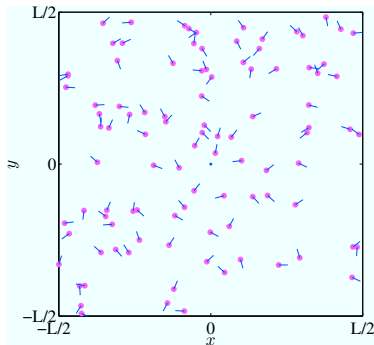


($\Delta(a) \sim 1/a$
for no-slip surface.)

Numerical simulation

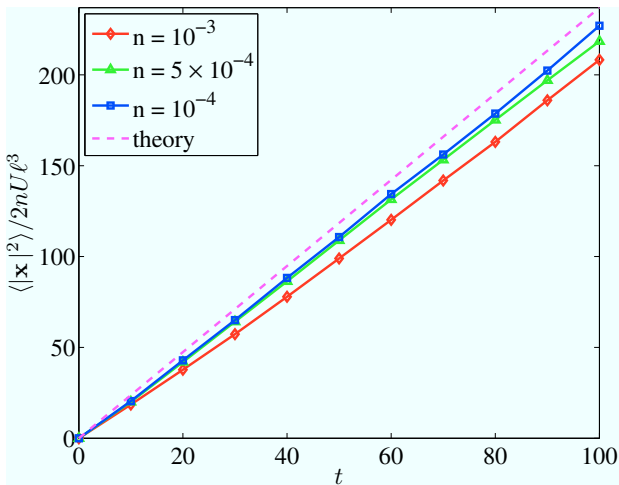
- Validate theory using simple simple simulations;
- Periodic box of size;
- N swimmers (spheres of radius 1), initially at random positions, swimming in random direction with constant speed $U = 1$;
- Target particle initially at origin advected by the swimmers;
- Since dilute, superimpose velocities;
- Integrate for some time, compute $|\mathbf{x}(t)|^2$, repeat for a large number N_{real} of realizations, and average.

A 'gas' of swimmers

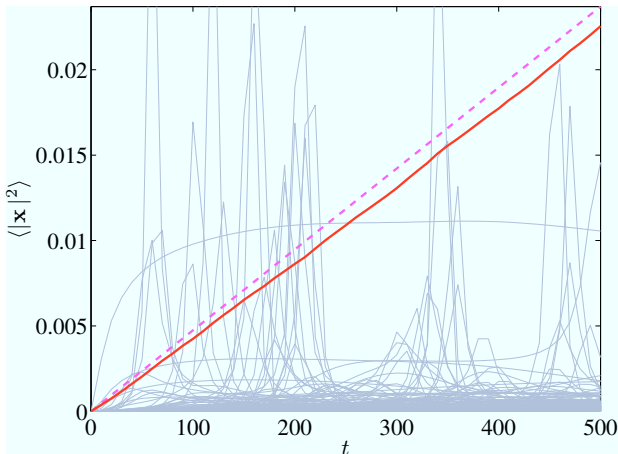


[movie 2] $N = 100$ swimmers, box size = 1000

How well does the dilute theory work?



Diffusion is dominated by rare events



2×10^6 realizations of $N = 10$ cylinders, with box size = 1000

Cloud of particles

t=10



t=630



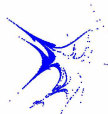
t=1255



t=1880



t=2505



t=3125



t=3750



t=4375

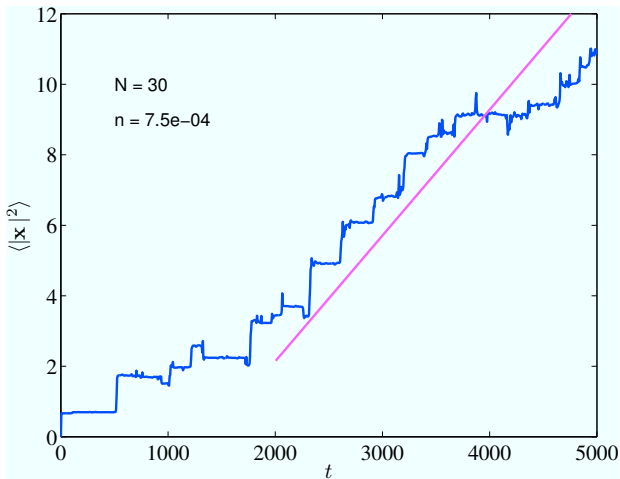


t=5000



[movie 3] (30 cylinders)

Cloud dispersion proceeds by steps

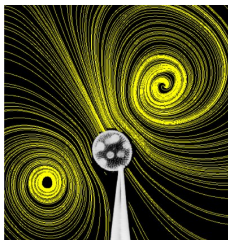


Squirmers

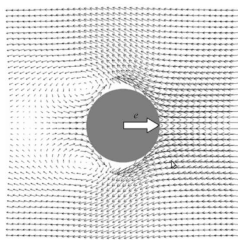
Considerable literature on transport due to microorganisms: Wu & Libchaber (2000); Hernandez-Ortiz *et al.* (2006); Saintillian & Shelley (2007); Ishikawa & Pedley (2007); Underhill *et al.* (2008); Ishikawa (2009); Leptos *et al.* (2009)

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

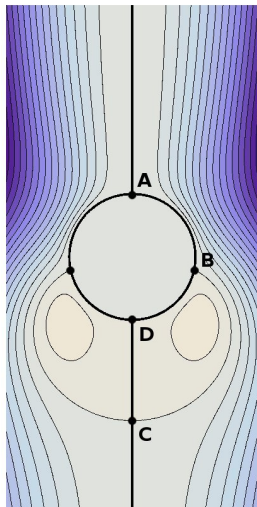
3D axisymmetric streamfunction for a typical squirmer, in cylindrical coordinates (ρ, z) :

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

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

Note that $\beta = 0$ is the sphere in potential flow.

We will use $\beta = 5$ for most of the remainder.

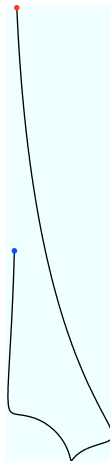


Particle motion for squirmer

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

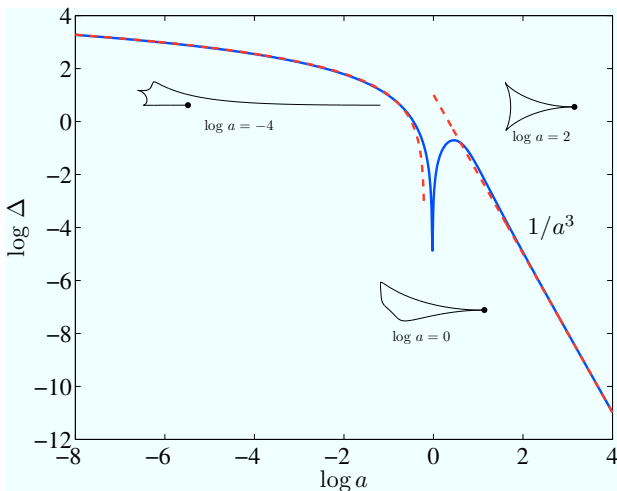
After the squirmer has passed the particle follows in the squirmer's wake.

(The squirmer moves from bottom to top.)

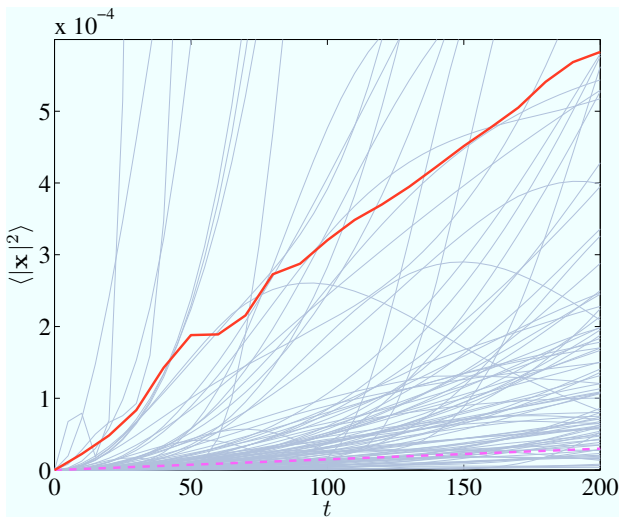


[movie 4]

Displacement for squirmer



Squirmers: Transport

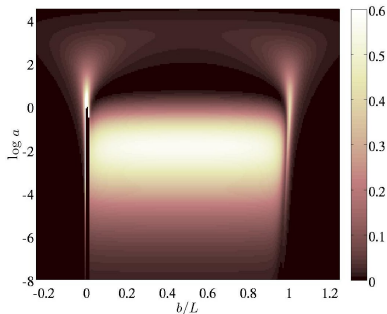


Measured slope is **20** times larger than **theory predicts!** Oops!

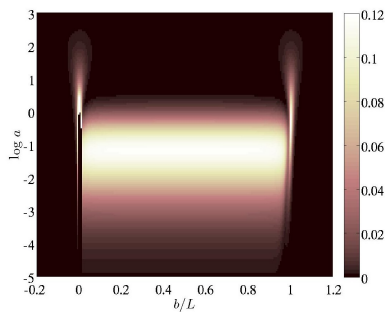
Revisit assumptions

$$\kappa = \frac{\pi}{3} Un \int \Delta_L^2(a, b) a^2 d(\log a) d(b/L) \quad \text{3D}$$

We had assumed $\Delta_L(a, b)$ was only nonzero on $0 < b < L$, and was otherwise independent of L .

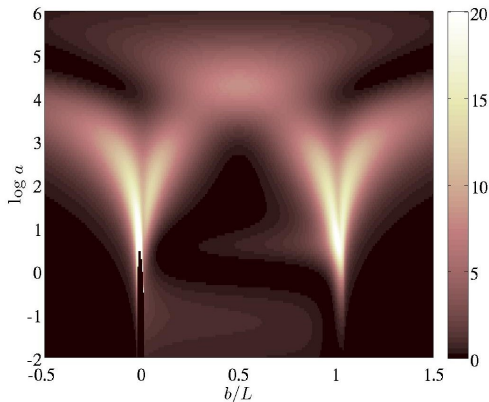


$\Delta_L^2(a, b) a$ (cylinder)



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

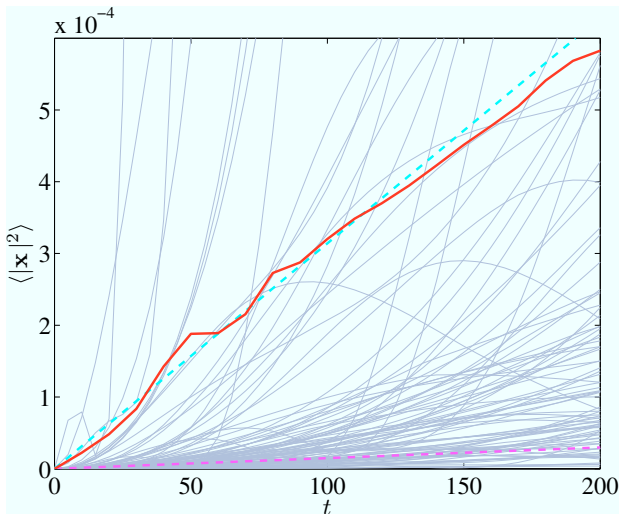
Not so for the squirmers!



Cannot at all be approximated by a 'hat' in b !

Dominated by trajectories that 'stop short': the **sucking-in** effect of this more realistic swimmer.

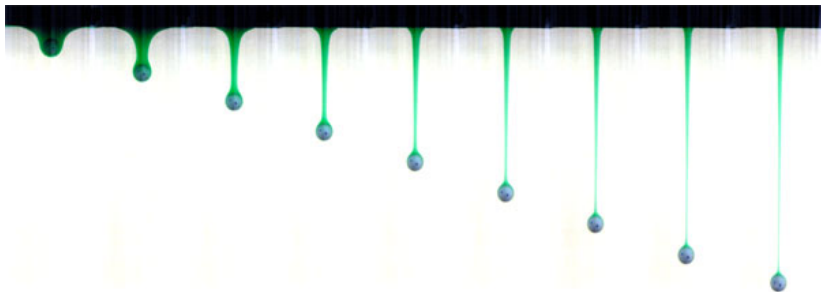
Squirmers: Transport revisited



The cyan line is the double integral. Still independent of path length (assumed large).

Sphere in viscous fluid

A natural question is what happens in the presence of viscosity, which greatly increases the “**sticking**” to the swimmer’s surface?



(from Camassa et al., *Sphere Passing Through Corn Syrup*)

This is a mechanism that has been suggested for enhanced transport by jellyfish (Katija & Dabiri, 2009)

No-slip correction

We expect the diffusivity to depend on the path length for a no-slip boundary: fluid gets dragged along.

Divergence of displacement for a no-slip surface (Eames *et al.* (2003)):

$$\Delta(a) \sim \frac{Cl^2}{a} \quad (\text{rather than log for slip walls})$$

This more severe singularity prevents our integral from converging: cut-off at maximum displacement.

$$\kappa \sim \frac{\pi}{3} Un \int_{\Delta^{-1}(L)}^{\infty} \Delta^2(a) a da \sim \frac{\pi}{3} Unl^4 C^2 \log L$$

Logarithmic in the path length L : not great news for biomixing.

So, do the fish stir the ocean?

- Consider spheres of radius 1 cm (the size of typical **krill**) moving at 5 cm/sec, with $n = 5 \times 10^{-3} \text{ cm}^{-3}$, we get an effective diffusivity of $7 \times 10^{-3} \text{ cm}^2/\text{sec}$.
- This is **5 times** the **thermal molecular value** $1.5 \times 10^{-3} \text{ cm}^2/\text{sec}$, and about 500 times the molecular value $1.6 \times 10^{-5} \text{ cm}^2/\text{sec}$ for **salt**.
- With **viscosity**: assume correlation length of $L \simeq 1 \text{ m}$; for rigid spheres: $\kappa \simeq 0.8 \text{ cm}^2/\text{sec}$, about **500 times the thermal molecular value**.
- But buoyancy is the enemy. . . need mechanism to keep fluid from sinking back.

(Numerical values from Visser (2007).)

Conclusions

- Biomixing: **no verdict yet**;
- Simple **dilute model** works well for a range of swimmers;
- Slip surfaces have an effective diffusivity that is **independent of path length**;
- Viscous flow dominated by **sticking** and have a **log dependence** on path length (though more work needed);

Future work:

- Wake models and turbulence;
- PDF of scalar concentration;
- **Buoyancy effects**;
- Schooling: longer length scale?

This work was supported by the Division of Mathematical Sciences of the US National Science Foundation, under grants DMS-0806821 (J-LT) and DMS-0507615 (SC). ZGL is supported by NSF through the Institute for Mathematics and Applications.

- BLAKE, J. R. 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.
- 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.
- EAMES, I., BELCHER, S. E. & HUNT, J. C. R. 1994 Drift, partial drift, and Darwin's proposition. *J. Fluid Mech.* **275**, 201–223.
- EAMES, I. & BUSH, J. W. M. 1999 Longitudinal dispersion by bodies fixed in a potential flow. *Proc. R. Soc. Lond. A* **455**, 3665–3686.
- EAMES, I., GOBBY, D. & DALZIEL, S. B. 2003 Fluid displacement by Stokes flow past a spherical droplet. *J. Fluid Mech.* **485**, 67–85.
- EINSTEIN, A. 1905 *Investigations on the Theory of the Brownian Movement*. (Dover, New York, 1956).
- 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.
- KATLIJA, 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.
- MAXWELL, J. C. 1869 On the displacement in a case of fluid motion. *Proc. London Math. Soc.* **s1-3** (1), 82–87.
- MUNK, W. H. 1966 Abyssal recipes. *Deep-Sea Res.* **13**, 707–730.
- PEDLEY, T. J. & KESSLER, J. O. 1992 Hydrodynamic phenomena in suspensions of swimming microorganisms. *Annu. Rev. Fluid Mech.* **24**, 313–358.
- 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, <http://arxiv.org/abs/0911.5511>.
- 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.
- VISSER, A. W. 2007 Biomixing of the oceans? *Science* **316** (5826), 838–839.
- WU, X.-L. & LIBCHABER, A. 2000 Particle diffusion in a quasi-two-dimensional bacterial bath. *Phys. Rev. Lett.* **84**, 3017–3020.