Simple models of stirring by swimming organisms

Jean-Luc Thiffeault\textsuperscript{1}  Steve Childress\textsuperscript{2}  Zhi George Lin\textsuperscript{3}

\textsuperscript{1}Department of Mathematics\newline University of Wisconsin – Madison

\textsuperscript{2}Courant Institute of Mathematical Sciences\newline New York University

\textsuperscript{3}Institute for Mathematics and its Applications\newline University of Minnesota – Twin Cities

Applied Math Colloquium, Northwestern University\newline 28 March 2011
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):

"...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."
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 $\sim 10^{-5}$ 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.
**In situ experiments**

Katija & Dabiri (2009) looked at jellyfish:

[movie 1] (Palau’s Jellyfish Lake.)
Displacement by a moving body

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 \( x(0) = 0 \) undergoes \( N \) encounters with an axially-symmetric swimming body:

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

\( \Delta_L(a, b) \) is the displacement, \( a_k, b_k \) are impact parameters, and \( \hat{r}_k \) is a direction vector. (\( a > 0 \), but \( b \) can have either sign.)
Putting this together,

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

2D

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

3D

which defines the effective diffusivity $\kappa$.

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.
Simplifying assumption

\[ \kappa = \frac{\pi}{3} Un \int a^2 \Delta^2_L(a, b) \, d(\log a) \, d(b/L) \quad 3D \]

Notice \( \Delta_L(a, b) \) is nonzero for \( 0 < b < L \); otherwise independent of \( b \) and \( L \).

\( a \Delta^2_L(a, b) \) (cylinder) \hspace{2cm} \( a^2 \Delta^2_L(a, b) \) (sphere)
Displacement for cylinders

Small $a$: $\Delta \sim -\log a$

Large $a$: $\Delta \sim a^{-3}$

(Darwin, 1953)

\[
\int_0^1 \Delta^2(a) da \simeq 2.31
\]

\[
\int_1^\infty \Delta^2(a) da \simeq 0.06
\]

$\Rightarrow$ 97% dominated by “head-on” collisions (similar for spheres)
Numerical simulation

- Validate theory using simple simple simulations;
- Large periodic box;
- $N_{\text{swim}}$ 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 $N_{\text{real}}$ of realizations, and average.
A ‘gas’ of swimmers

[Movie 2] 100 cylinders, box size = 1000
How well does the dilute theory work?

\[
\frac{\langle |x|^2 \rangle}{2nU^3} = \begin{cases} 
10^{-3} \\
5 \times 10^{-4} \\
10^{-4}
\end{cases}
\]
Cloud of particles

(movie 3) (30 cylinders)
Cloud dispersion proceeds by steps

\[ \langle |x|^2 \rangle \]

\[ N = 30 \]
\[ n = 7.5 \times 10^{-4} \]
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 \((\rho, z)\):

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

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

\( \beta \) is the amplitude of the stresslet (distinguishes 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:

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).
Far field: Displacements $a^2 \Delta_L^2(a, b)$

inset: only stresslet term (far field) ($\lambda \equiv L$)

Unlike potential sphere, mid-range field dominates.
Transport as a function of $\beta$

When stresslet dominates, effective diffusivity $\sim \beta^2$:

At these low densities, no difference between pushers and pullers.
Finite Reynolds number: Displacements

\[ \log \left( \frac{a}{\ell} \right) \]

\[ b/\lambda \]

\[ -0.5 \quad 0 \quad 0.5 \quad 1 \quad 1.5 \]

\[ -2 \quad -1 \quad 0 \quad 1 \quad 2 \quad 3 \quad 4 \]

\[ 0 \quad 1 \quad 2 \quad 3 \quad 4 \quad 5 \quad 6 \quad 7 \quad 8 \quad 9 \quad 10 \]
Finite Reynolds number: Transport

\[ \frac{\kappa}{U_n l^4} = 5.9 Re^{-0.61} \]
• Variance exhibits similar short-time anomalous scaling as in Wu & Libchaber (2000);
• PDF 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

- 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, for long path length;
- Get semi-analytic formula for pusher/pullers at low densities;
- 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?
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.


