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when organisms stir their environment

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Mechanical Engineering Seminar University of California, Santa Barbara, 26 November 2012 Supported by NSF grants DMS-0806821 and DMS-1109315





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).

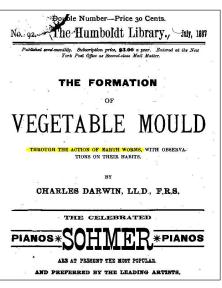
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Bioturbation

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-inlaw 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."



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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)

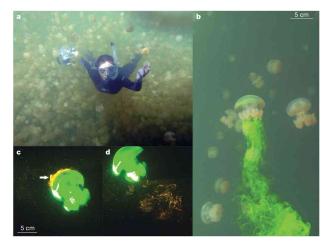
Abstract—Vertical distributions in the interior Pacific (excluding the top and bottom kilometer) are not inconsistent with a simple model involving a constant upward vertical velocity $w \approx 1/2$ cm day⁻¹ and eddy diffusivity $x \approx 1/3$ cm²sec⁻¹. Thus temperature and salinity can be fitted by exponential like solutions to $[x \cdot d^2/dz^2 - w \cdot d/dz] T$, S = 0, with $x/w \approx 1$ km the appropriate "scale height." For Carbon 14 a decay term must be included, $[]^{14}C = \mu^{14}C$; a fitting of the solution to the observed ¹⁴C distribution yields $x/w^2 \approx 200$ 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."

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In situ experiments

Katija & Dabiri (2009) looked at jellyfish:



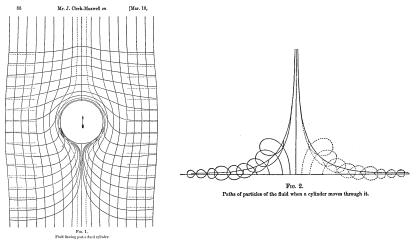
[movie 1] (Palau's Jellyfish Lake.)

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Displacement by a moving body



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



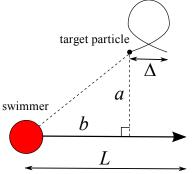
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A sequence of kicks

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.



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

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After squaring and averaging, assuming isotropy:

$$\left< |{f x}|^2 \right> = N \left< \Delta_L^2(a,b) \right>$$

where a and b are treated as random variables with densities

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

Replace average by integral:

$$\left< |\mathbf{x}|^2 \right> = \frac{N}{V} \int \Delta_L^2(a, b) \, \mathrm{d}\mathbf{A}$$

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

$$\left< |\mathbf{x}|^2 \right> = rac{Unt}{L} \int \Delta_L^2(a, b) \, \mathrm{d}\mathbf{A}$$

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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.

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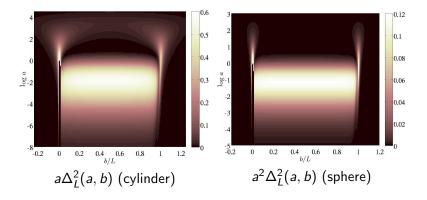
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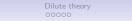
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Inviscid cylinders and spheres (treadmill swimmer)

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





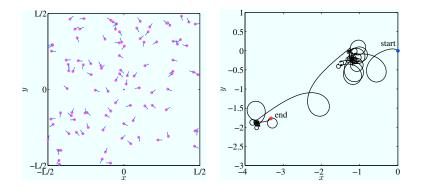
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Numerical simulation

- 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 $N_{\rm real}$ of realizations, and average.

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A 'gas' of swimmers



[movie 2] 100 cylinders, box size = 1000

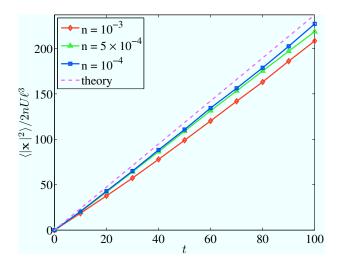
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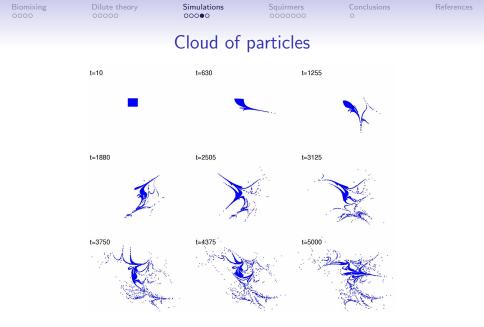
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How well does the dilute theory work?

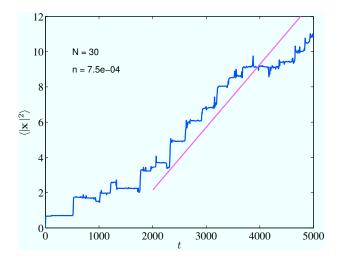




[movie 3] (30 cylinders)

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Cloud dispersion proceeds by steps



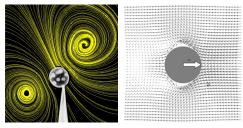
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Squirmers

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)

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Typical squirmer

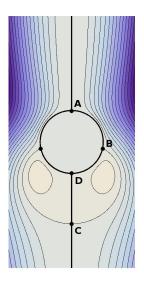
3D axisymmetric streamfunction for a typical squirmer, in cylindrical coordinates (ρ , z):

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

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

 β is the amplitude of the stresslet (distinguises pushers/pullers).

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



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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.)

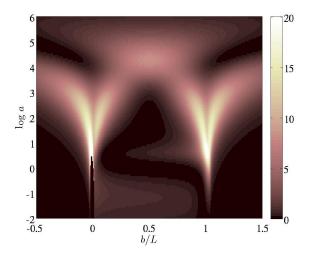


[movie 4]

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Squirmer displacements $a^2 \Delta_L^2(a, b)$



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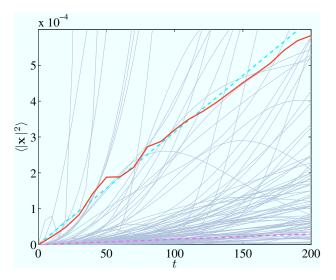
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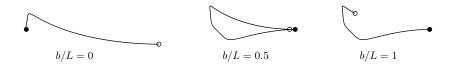
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Squirmers: Transport





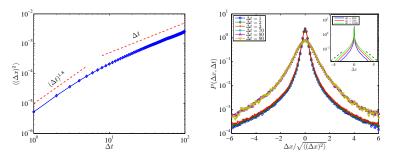
The two peaks in the displacement plot come from 'incomplete' trajectories:



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).



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.



- 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?

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