Biomixing

when organisms stir their environment

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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) and aquaculture.
- In any case it's a nice applied math problem!

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 swimming of 100 (!) species, ranging from bacteria to blue whales. Typical turbulent energy production is $\sim 10^{-5}$ W kg⁻¹. 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.
- However, Kunze has failed to find this effect again on subsequent cruises. Visser (2007) has questioned whether small-scale turbulence can lead to overturning.

In situ experiments



Katija & Dabiri (2009) looked at jellyfish:



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(Palau's Jellyfish Lake.) Correct length scale is path length?

Displacement by a moving body



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





Inspired by Einstein's theory of diffusion (Einstein, 1956): a test particle initially at $\mathbf{x}(0) = 0$ undergoes Nencounters 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:

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

where a and b are treated as random variables with densities

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

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



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.



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





- 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.

A 'gas' of swimmers





play movie 100 cylinders, box size = 1000

How well does the dilute theory work?





Cloud of particles





(30 cylinders)

Cloud dispersion proceeds by steps





Considerable literature on transport due to microorganisms: Wu & Libchaber (2000); Hernandez-Ortiz *et al.* (2005); 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).







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

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.





- 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.)





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





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).



Squirmers: Transport









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[Guasto, J. S., Johnson, K. A., & Gollub, J. P. (2010). Phys. Rev. Lett. 105, 168102]

Probability density of displacements

W

Non-Gaussian PDF with 'exponential' tails:



[Leptos, K. C., Guasto, J. S., Gollub, J. P., Pesci, A. I., & Goldstein, R. E. (2009). *Phys. Rev. Lett.* **103**, 198103]

W

Leptos et al. (2009) claim a reasonable fit of their PDF with the form

$$\mathcal{P}_{\Delta t}(\Delta x) = rac{1-f}{\sqrt{2\pi}\,\delta_g}\,\mathrm{e}^{-(\Delta x)^2/2\delta_g^2} + rac{f}{2\delta_e}\,\mathrm{e}^{-|\Delta x|/\delta_e}$$

They observe the scalings $\delta_g \sim A_g(\Delta t)^{1/2}$ and $\delta_e \sim A_e(\Delta t)^{1/2}$, where A_g and A_e depend on ϕ .

They call this a diffusive scaling, since $\Delta x \sim \Delta t^{1/2}$. Their point is that this is strange, since the distribution is not Gaussian.

Commonly observed in diffusive processes that are a combination of trapped and hopping dynamics (Wang *et al.*, 2012).

PDF: Theory vs experiment





The normalized PDF for experimental data (dashed) agrees well with simple swimmer models, with no adjustable parameters. This is consistent with a dominant far-field.

Conclusions



- Simple dilute model works well for a range of swimmers;
- For the inviscid case, close impacts are most important.
- In the Stokes limit, particles are significantly displaced up to a few swimmer radii away.
- Turning is crucial, otherwise particle trajectories are almost closed.
- The dilute model also reproduces PDFs observed in experiments.

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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