

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!**

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."

Double Number—Price 30 Cents.
No. 92. **The Humboldt Library,** July, 1887

Published semi-monthly. Subscription price, \$3.00 a year. Entered at the New York Post Office as Second-class Mail Matter.

THE FORMATION
OF
VEGETABLE MOULD

THROUGH THE ACTION OF EARTH WORMS, WITH OBSERVATIONS ON THEIR HABITS.

BY
CHARLES DARWIN, LL.D., F.R.S.

THE CELEBRATED
PIANOS * SOHMER * PIANOS

ARE AT PRESENT THE MOST POPULAR.
AND PREFERRED BY THE LEADING ARTISTS.

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 $w \approx 1.2 \text{ cm day}^{-1}$ 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, $[]^{14}\text{C} = \mu^{14}\text{C}$; 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

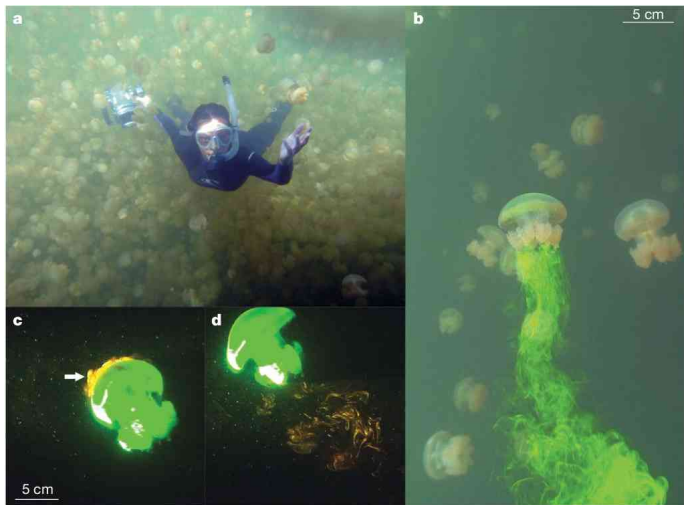
"... I have attempted, **without much success**, to interpret [the eddy diffusivity] from a variety of viewpoints: from mixing along the ocean boundaries, from thermodynamic and **biological processes**, and from internal tides."



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 $\sim 10^{-5} \text{ W kg}^{-1}$. 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.

Katija & Dabiri (2009) looked at jellyfish:



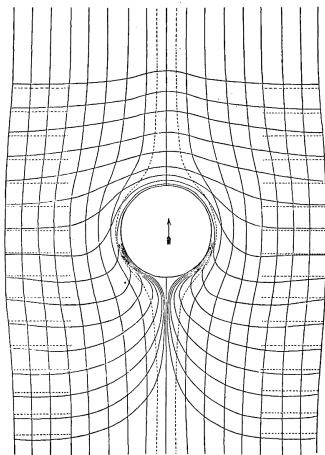


FIG. 1.
Fluid flowing past a fixed cylinder.

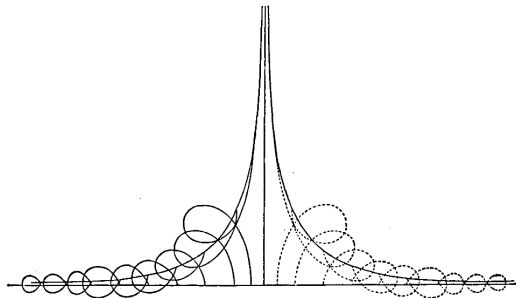


FIG. 2.
Paths of particles of the fluid when a cylinder moves through it.

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

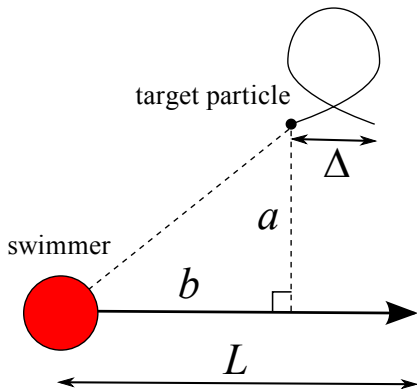
A sequence of kicks



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.)

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**):

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



Putting this together,

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

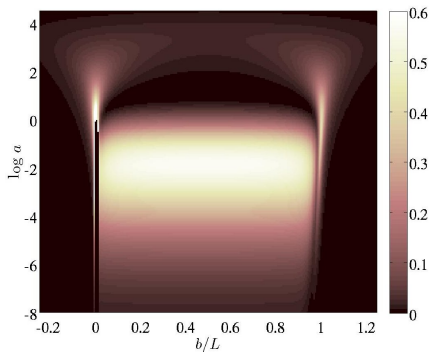
$$\langle |\mathbf{x}|^2 \rangle = \frac{2\pi Unt}{L} \int \Delta_L^2(a, b) a da db = 6\kappa t, \quad \text{3D}$$

which defines the **effective diffusivity** κ .

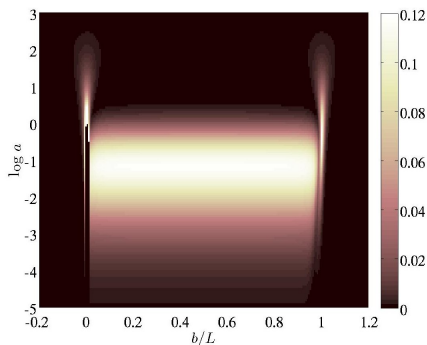
If the number density is low ($nL^d \ll 1$), then encounters are rare and we can use this formula for a collection of particles.

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

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



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

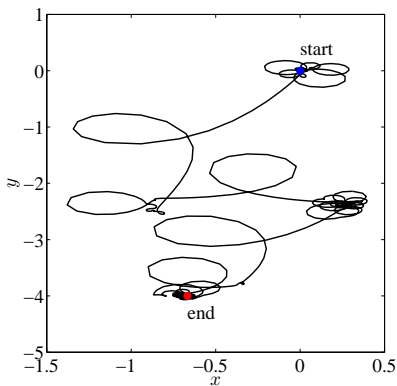
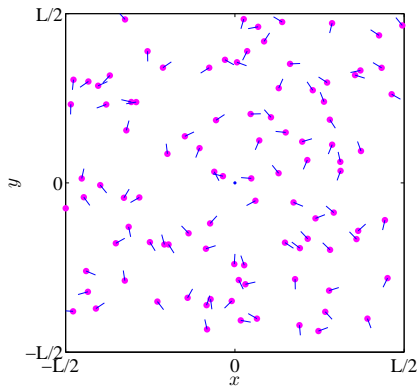


$a^2\Delta_L^2(a, b)$ (sphere)



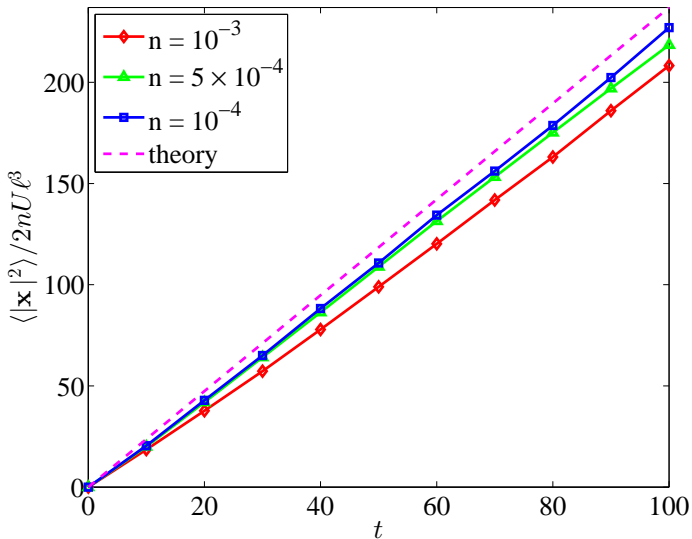
- Validate theory using simple simple simulations;
- Large periodic box;
- N_{swim} swimmers (cylinders of radius 1), initially at random positions, swimming in random direction with constant speed $U = 1$;
- Target particle initially at origin advected by the swimmers;
- Since dilute, superimpose velocities;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

A 'gas' of swimmers



play movie 100 cylinders, box size = 1000

How well does the dilute theory work?



Cloud of particles



t=10



t=630



t=1255



t=1880



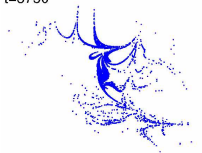
t=2505



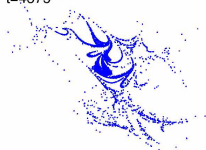
t=3125



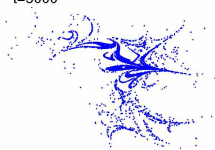
t=3750



t=4375



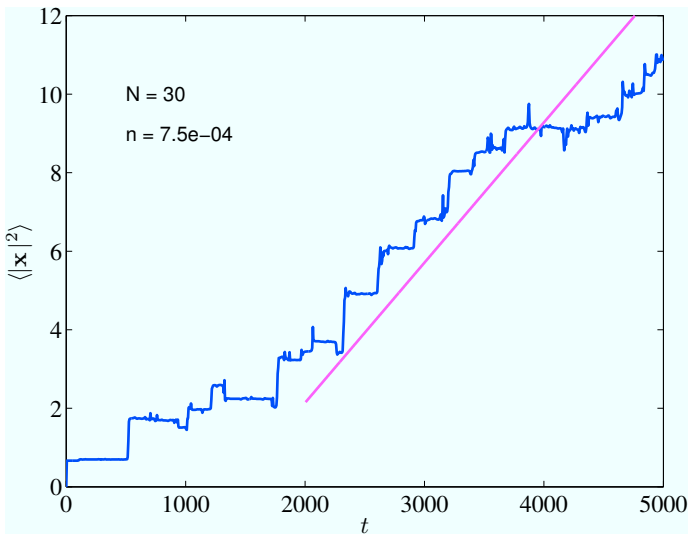
t=5000



play movie

(30 cylinders)

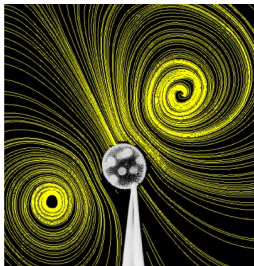
Cloud dispersion proceeds by steps



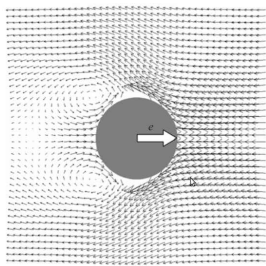
Considerable literature on transport due to microorganisms: Wu & Libchaber (2000); Hernandez-Ortiz *et al.* (2005); Saintillan & Shelley (2007); Ishikawa & Pedley (2007); Underhill *et al.* (2008); Ishikawa (2009); Leptos *et al.* (2009)

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)

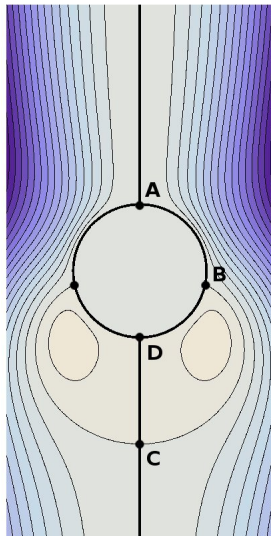
3D axisymmetric streamfunction for a typical squirmer, in cylindrical coordinates (ρ, z) :

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

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

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

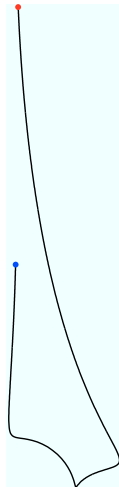
We will use $\beta = 5$ for most of the remainder.



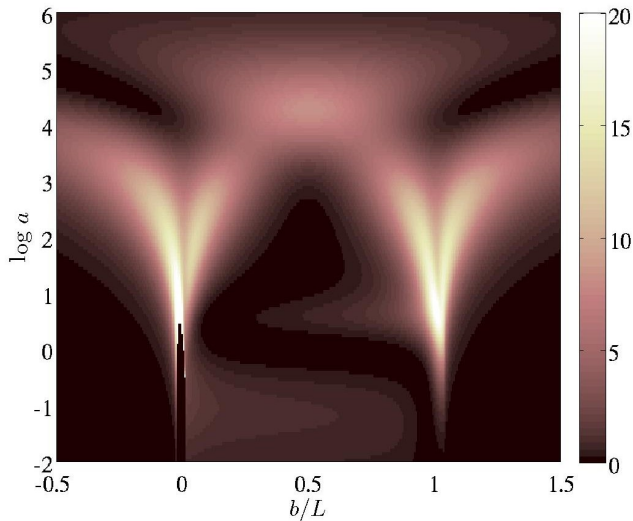
A particle near the squirmer's swimming axis initially (blue) moves towards the squirmer.

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

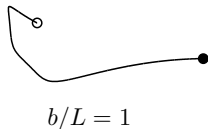
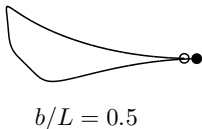
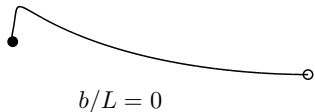
(The squirmer moves from bottom to top.)



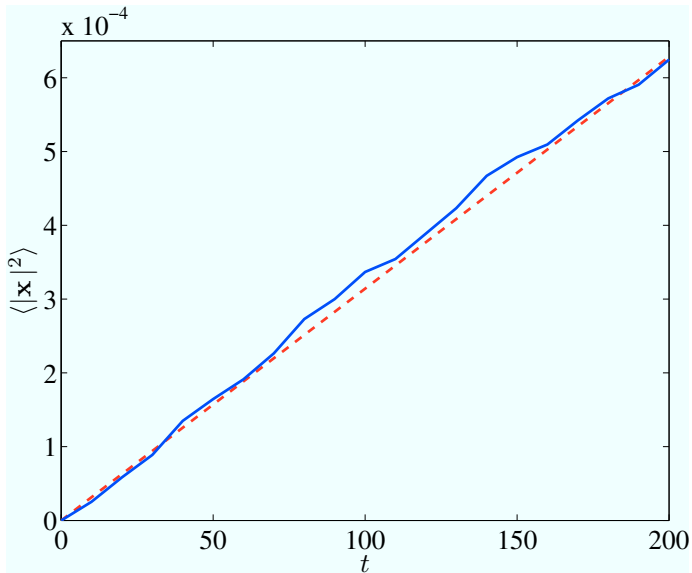
Squirmer displacements $a^2 \Delta_L^2(a, b)$

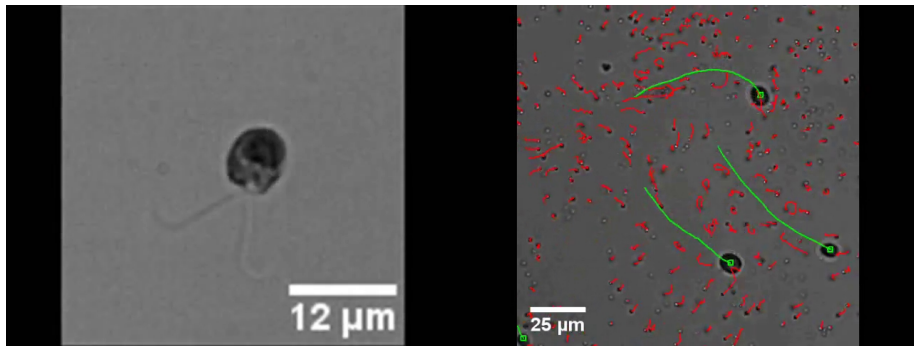


The two peaks in the displacement plot come from 'incomplete' trajectories:



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**).





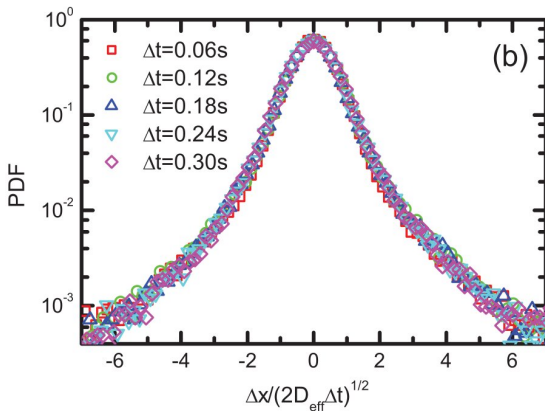
play movie

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

Probability density of displacements



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]

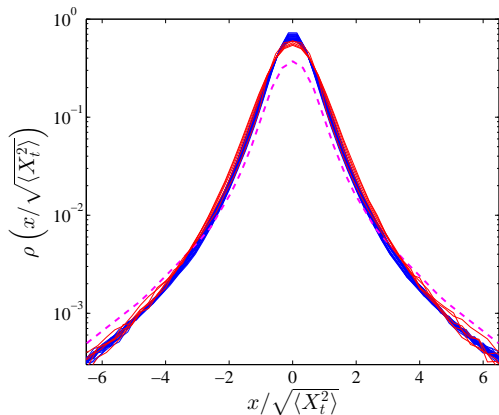
Leptos *et al.* (2009) claim a reasonable fit of their PDF with the form

$$P_{\Delta t}(\Delta x) = \frac{1-f}{\sqrt{2\pi} \delta_g} e^{-(\Delta x)^2/2\delta_g^2} + \frac{f}{2\delta_e} e^{-|\Delta x|/\delta_e}$$

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).



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.

- 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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