

# Simple models of stirring by swimming organisms

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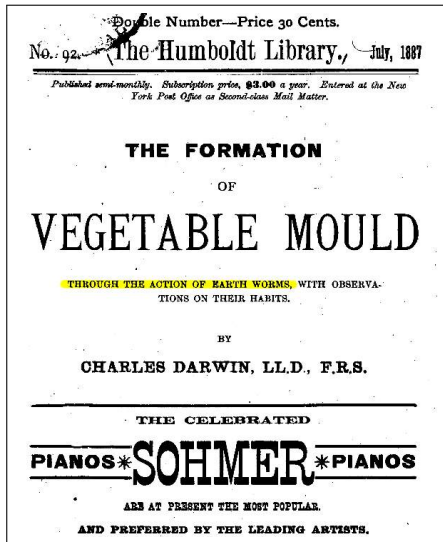
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## Bioturbation

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-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):

### 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  $^{14}\text{C}$  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."

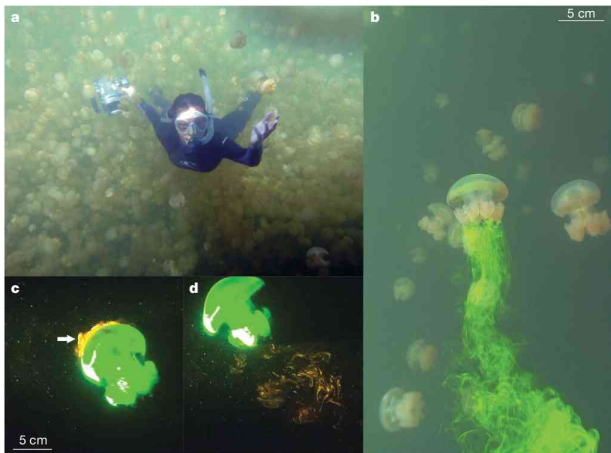
# Resurgence

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.

## *In situ* experiments

Katija & Dabiri (2009) looked at jellyfish:



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

# Displacement by a moving body

86

Mr. J. Clerk-Maxwell on

[Mar. 10,

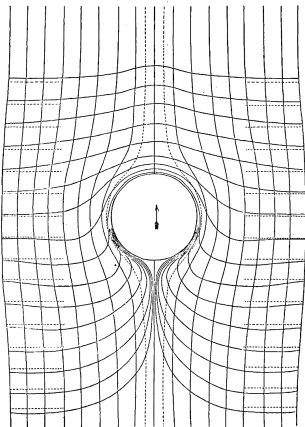


FIG. 1.

Fluid flowing past a fixed cylinder.

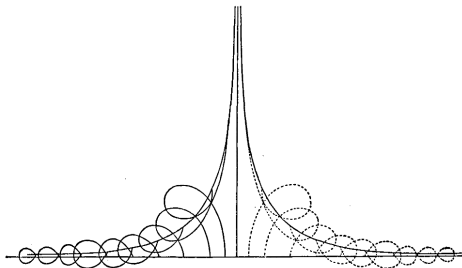


FIG. 2.

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

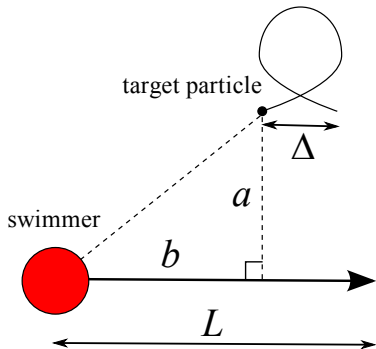
Maxwell (1869); Darwin (1953); Eames *et al.* (1994)

## 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.)

## Effective diffusivity

Putting this together,

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

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

which defines the **effective diffusivity**  $\kappa$ .

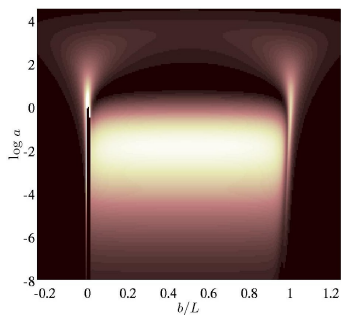
If the number density is low ( $nL^d \ll 1$ ), then encounters are rare and we can use this formula for a collection of particles.



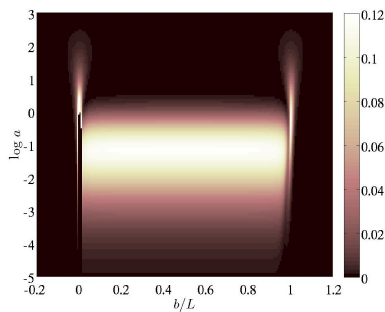
## Simplifying assumption

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

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



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



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

## Displacement for cylinders

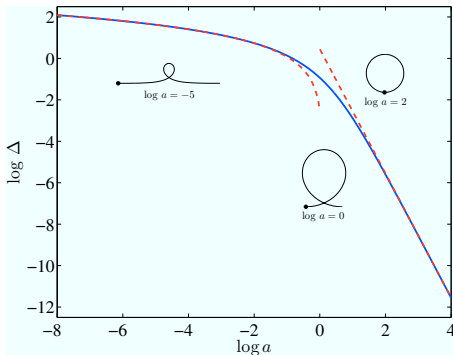
Small  $a$ :  $\Delta \sim -\log a$

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

(Darwin, 1953)

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

$$\int_1^\infty \Delta^2(a) da \simeq .06$$

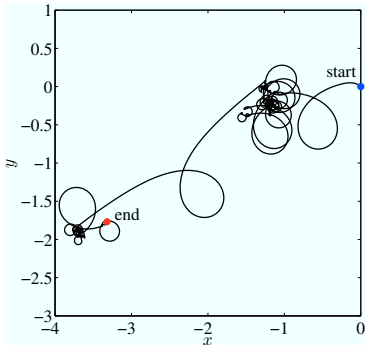
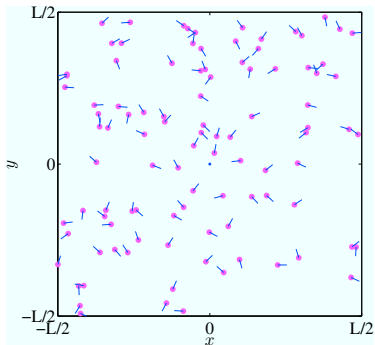


⇒ 97% dominated by “head-on” collisions (similar for spheres)

## Numerical simulation

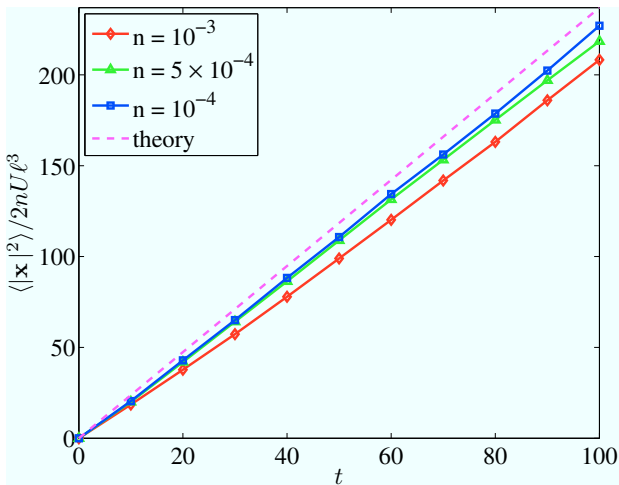
- Validate theory using simple simple simulations;
- Large periodic box;
- $N_{\text{swim}}$  swimmers (cylinders of radius 1), initially at random positions, swimming in random direction with constant speed  $U = 1$ ;
- Target particle initially at origin advected by the swimmers;
- Since dilute, superimpose 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?



# Cloud of particles

t=10



t=630



t=1255



t=1880



t=2505



t=3125



t=3750



t=4375

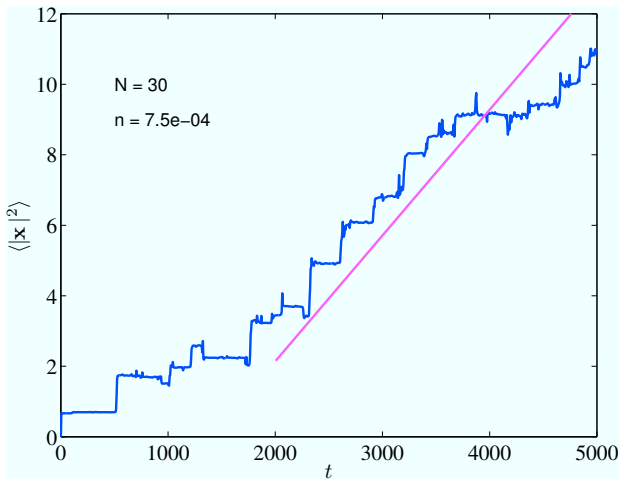


t=5000



[movie 3] (30 cylinders)

## Cloud dispersion proceeds by steps

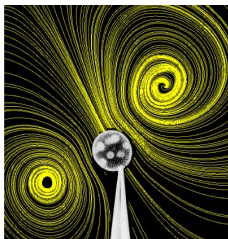


## Squirmers

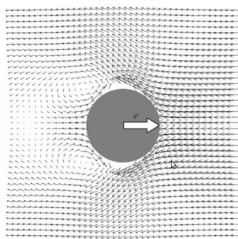
Considerable literature on transport due to microorganisms: Wu & Libchaber (2000); Hernandez-Ortiz *et al.* (2006); Saintillian & Shelley (2007); Ishikawa & Pedley (2007); Underhill *et al.* (2008); Ishikawa (2009); Leptos *et al.* (2009)

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

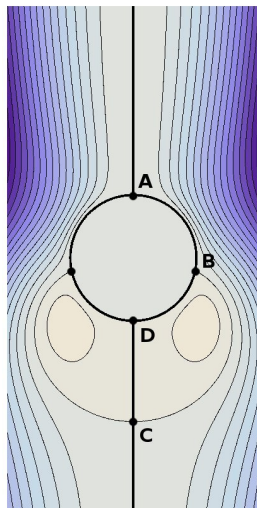
3D axisymmetric streamfunction for a typical squirmer, in cylindrical coordinates  $(\rho, z)$ :

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

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.

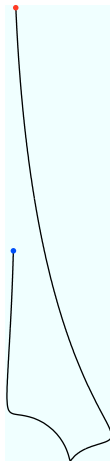


## Particle motion for squirmer

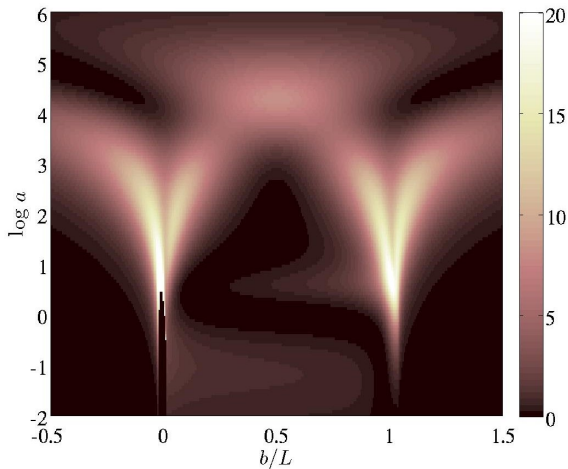
A particle near the squirmer's swimming axis initially (blue) moves towards the squirmer.

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

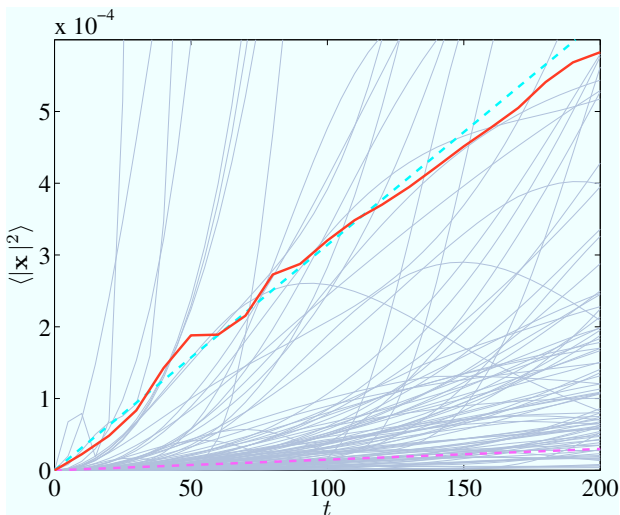
(The squirmer moves from bottom to top.)



[movie 4]

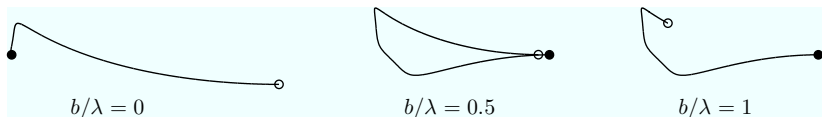
Squirmer displacements  $a^2 \Delta_L^2(a, b)$ 

# Squirmers: Transport



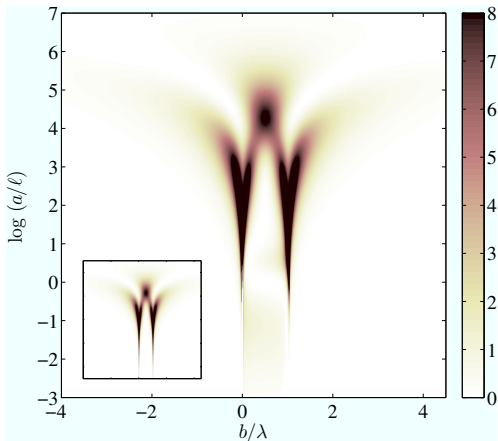
## Squirmers: Trajectories

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

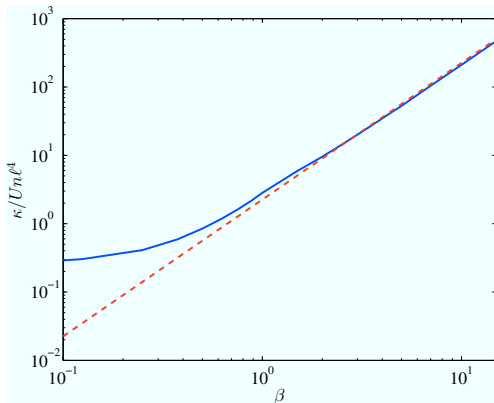


inset: only stresslet term (far field) ( $\lambda \equiv L$ )

Unlike potential sphere, mid-range field dominates.

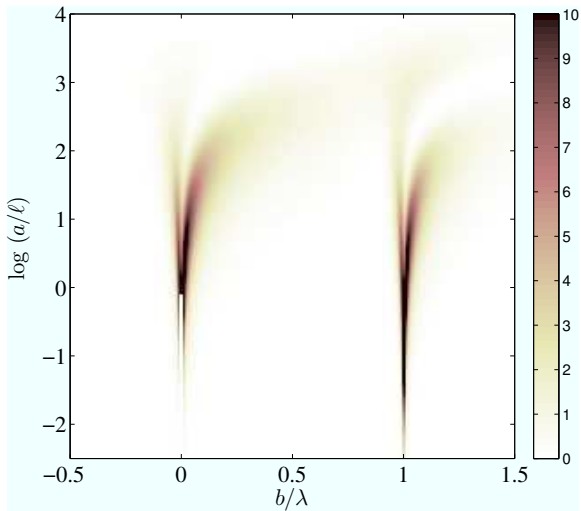
## Transport as a function of $\beta$

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



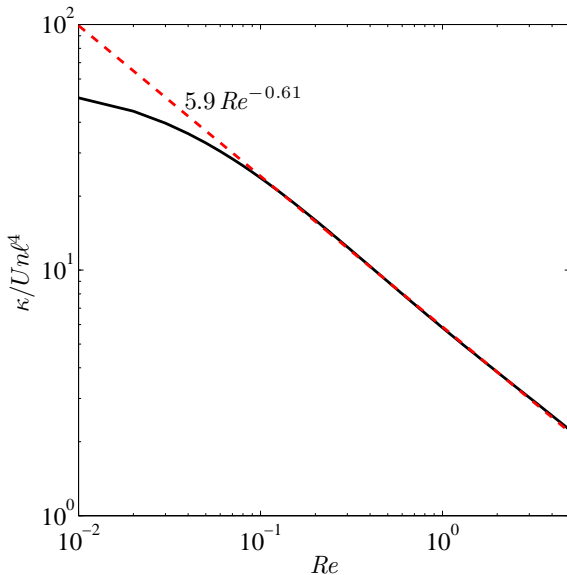
At these low densities, no difference between pushers and pullers.

## Finite Reynolds number: Displacements

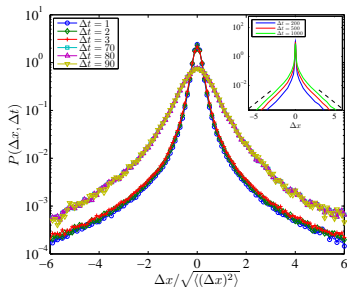
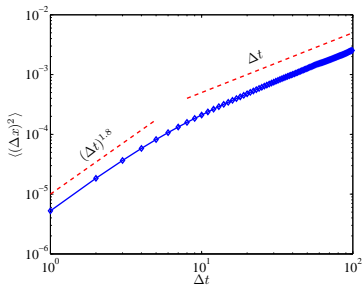




## Finite Reynolds number: Transport



## Non-Gaussian PDFs of displacement



- 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?

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