Do fish stir the ocean?
and other tales of biomixing

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Fluid dynamics: From theory to experiment (Stevefest)
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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."
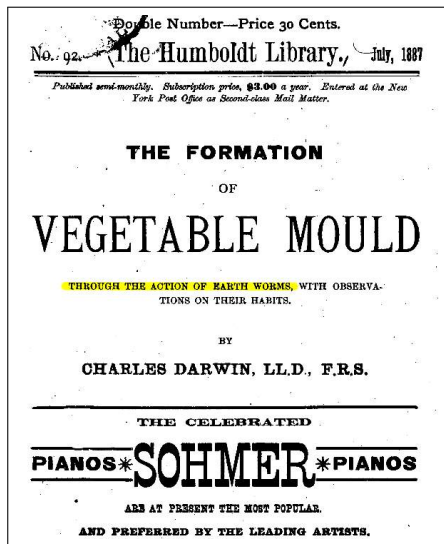
Munk's Idea

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 $w \approx 1.2$ cm day^{-1} and eddy diffusivity $\kappa \approx 1.3$ cm^2 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 $\kappa/w \approx 1$ km the appropriate " scale height." For Carbon 14 a decay term must be included, $[\quad]^{14}C = \mu^{14}C$; a fitting of the solution to the ob-served ^{14}C distribution yields $\kappa/w^2 \approx 200$ 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."

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 $\sim 10^{-5} \ \mathrm{W \ kg^{-1}}$ for 11 representative species.

- Total is comparable to energy dissipation by major storms.

- Another estimate comes from the solar energy captured: $63 \ \mathrm{TeraW}$, 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:
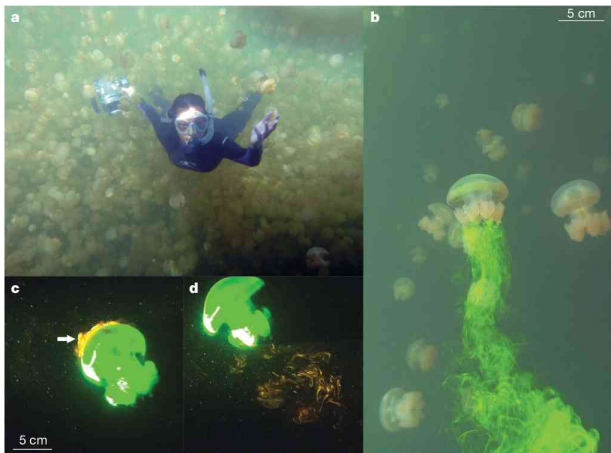
[movie 1] (Palau's Jellyfish Lake.)
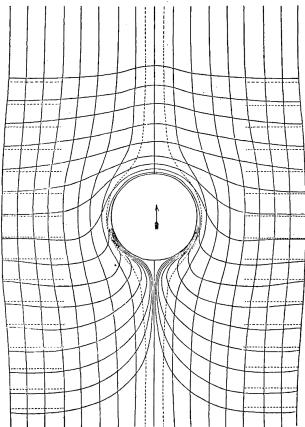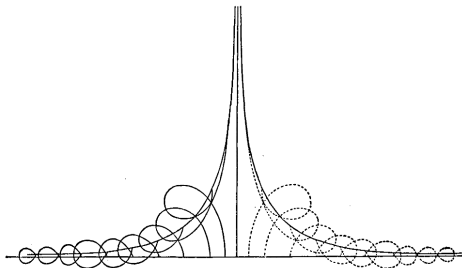
Displacement by a moving body

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

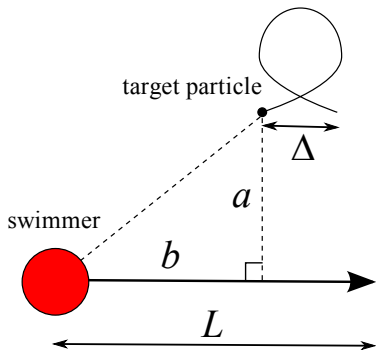Maxwell (1869); Darwin (1953); Eames *et al.* (1994)

A sequence of kicks

Inspired by Einstein's theory of diffusion (Einstein, 1905): 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.

target particle

Δ

a

swimmer

b

L

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

Effective diffusivity

Putting this together,

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

$$\langle |\mathbf{x}|^2 \rangle = \frac{2\pi Unt}{L} \int \Delta_L^2(a, b) a \, \mathrm{d}a \, \mathrm{d}b = 6\kappa t, \qquad \text{3D}$$
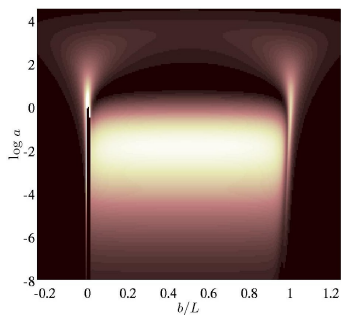
which defines the effective diffusivity κ.

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.
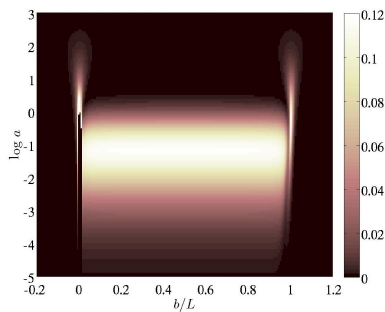
Simplifying assumption

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

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

$a \Delta_L^2(a, b)$ (cylinder) $a^2 \Delta_L^2(a, b)$ (sphere)
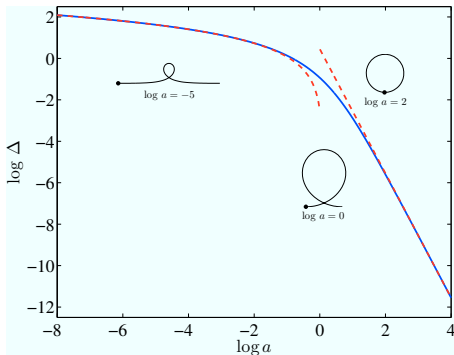
Displacement for cylinders

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

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

(Darwin, 1953)

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

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

$\implies$ 97% dominated by "head-on" collisions (similar for spheres)

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_{real} of realizations, and average.

A 'gas' of swimmers
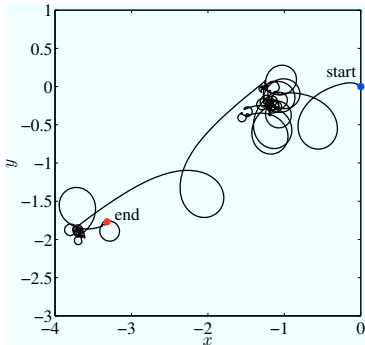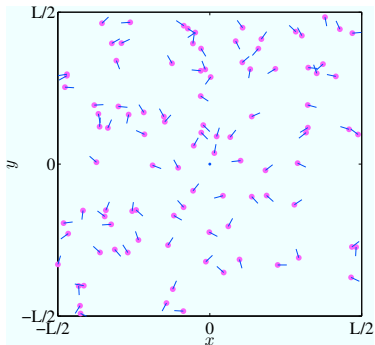
[movie 2] 100 cylinders, box size = 1000

## How well does the dilute theory work?
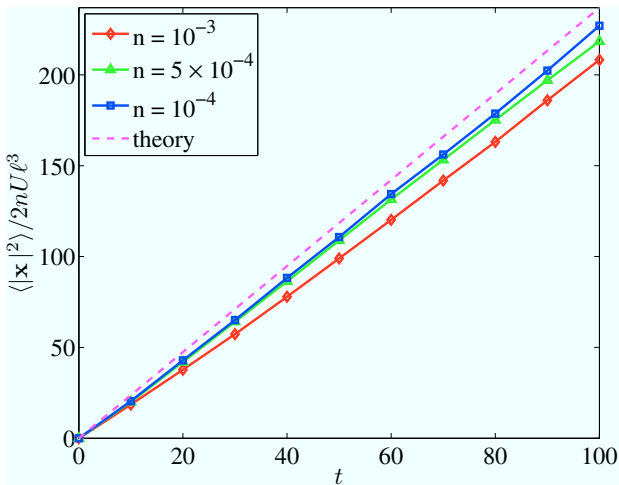
Squirmers

Considerable literature on transport due to microorganisms: Wu & Libchaber (2000); Hernandez-Ortiz *et al.* (2006); Saintillian & Shelley (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).
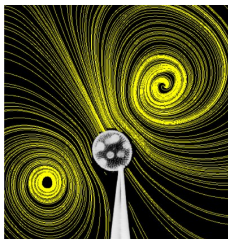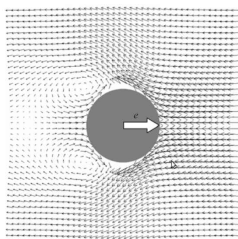
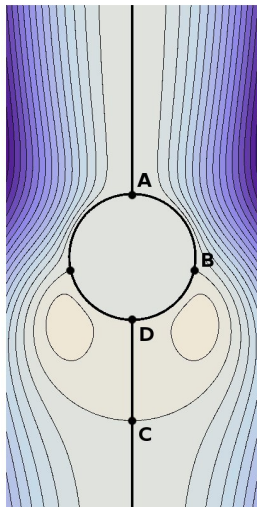(Drescher *et al.*, 2009)   (Ishikawa *et al.*, 2006)

Typical squirmer

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

$$\psi = -\tfrac{1}{2}\rho^2 + \frac{1}{2r^3}\,\rho^2 + \frac{3\beta}{4r^3}\,\rho^2 z\left(\frac{1}{r^2} - 1\right)$$
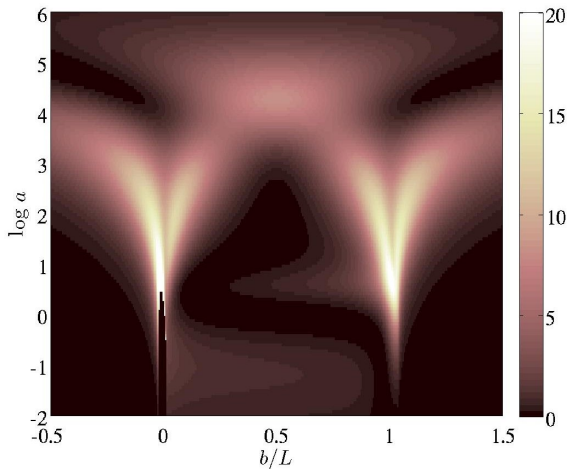
where $r = \sqrt{\rho^2 + z^2}$, $U = 1$, radius of squirmer $= 1$.

β is the amplitude of the stresslet (distinguises pushers/pullers).
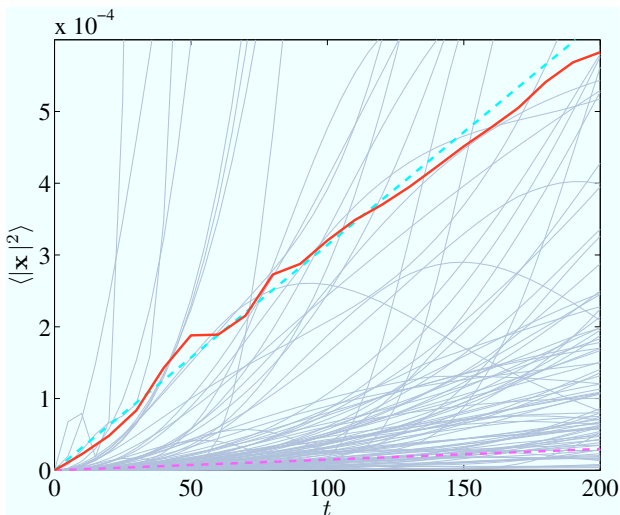
We will use $\beta = 5$ for most of the remainder.

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

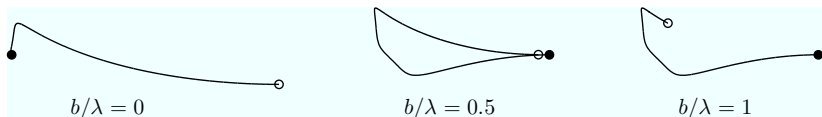# Squirmers: Transport

Squirmers: Trajectories

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

$b/\lambda = 0$ $b/\lambda = 0.5$ $b/\lambda = 1$

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 $a^2\Delta_L^2(a, b)$
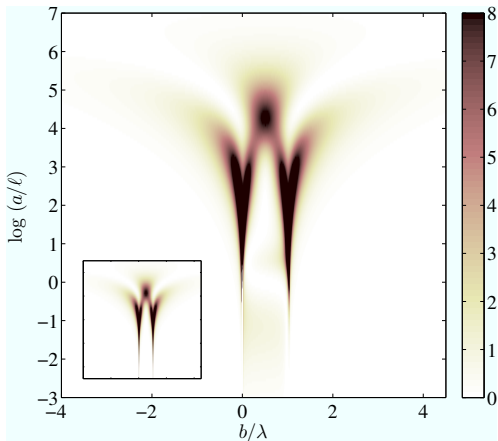
inset: only stresslet term (far field) ($\lambda \equiv L$)

Unlike potential sphere, mid-range field dominates.

Transport as a function of β

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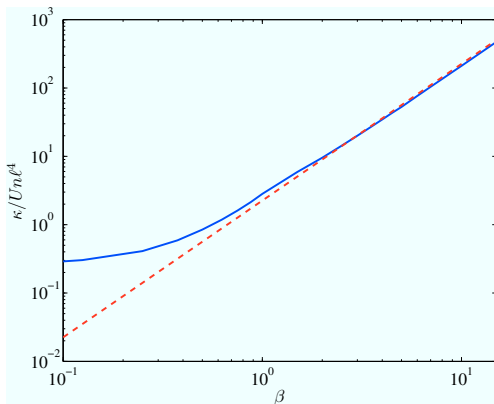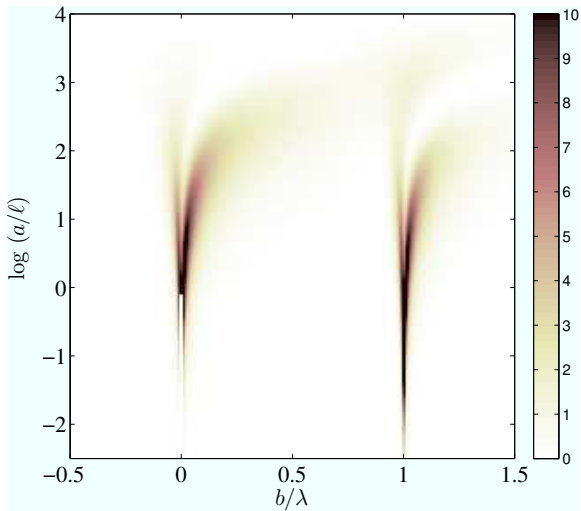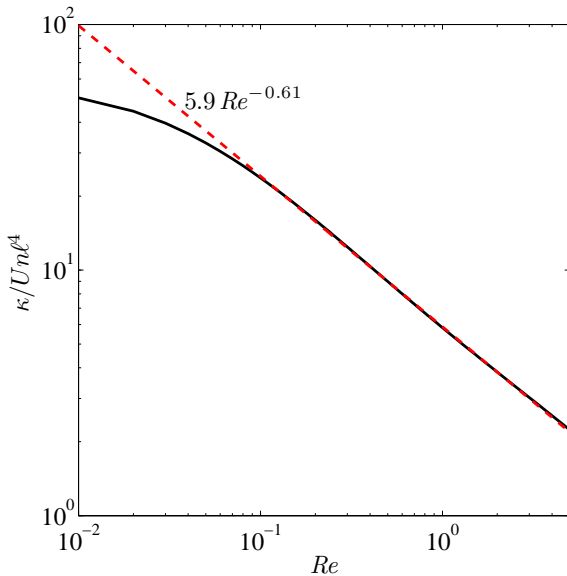

At these low densities, no difference between pushers and pullers.

Finite Reynolds number: Displacements

Finite Reynolds number: Transport

So, do the fish stir the ocean?

- Consider spheres of radius $1\ \mathrm{cm}$ (the size of typical krill) moving at $5\ \mathrm{cm/sec}$, with $n = 5 \times 10^{-3}\ \mathrm{cm}^{-3}$, we get an effective diffusivity of $7 \times 10^{-3}\ \mathrm{cm}^2/\mathrm{sec}$.

- This is 5 times the thermal molecular value $1.5 \times 10^{-3}\ \mathrm{cm}^2/\mathrm{sec}$, and about 500 times the molecular value $1.6 \times 10^{-5}\ \mathrm{cm}^2/\mathrm{sec}$ for salt.

- With viscosity: assume correlation length of $L \simeq 1\ \mathrm{m}$; for rigid spheres: $\kappa \simeq 0.8\ \mathrm{cm}^2/\mathrm{sec}$, about 500 times the thermal molecular value. (Compare to Munk's $1.3\ \mathrm{cm}^2/\mathrm{sec}$)

- But buoyancy is the enemy... need mechanism to keep fluid from sinking back.

(Numerical values from Visser (2007).)

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;
- Schooling: longer length scale?

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