# Lecture 2: Stirring by swimming organisms

#### [Jean-Luc Thiffeault](http://www.math.wisc.edu/~jeanluc)

[Department of Mathematics](http://www.math.wisc.edu) [University of Wisconsin – Madison](http://www.wisc.edu)

Summer Program in Geophysical Fluid Dynamics, Woods Hole 23 June 2010



## **Biomixing**

A controversial proposition:

- There are many regions of the ocean that are relatively quiescent, especially in the depths  $(1\text{ hairdryer}/\text{ km}^3);$
- 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;
- <span id="page-1-0"></span>• Also relevant in suspensions of microorganisms (Viscous Stokes regime).

#### **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."



## 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<sup>-1</sup> and eddy diffusivity  $\kappa \approx 1.3 \text{ cm}^2 \text{ sec}^{-1}$ . Thus temperature and salinity can be fitted by exponentiallike solutions to  $\left[x \cdot d^2/dz^2 - w \cdot d/dz\right]T$ ,  $S = 0$ , with  $\kappa/w \approx 1$  km the appropriate " scale height." For Carbon 14 a decay term must be included,  $[14C = \mu^{14}C]$  a fitting of the solution to the observed <sup>14</sup>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."

## Basic claims

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 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:



[\[movie 1\]](http://www.math.wisc.edu/~jeanluc/movies/nature08207-s4.mpg) (Palau's [Jellyfish Lake.](http://en.wikipedia.org/wiki/Jellyfish_Lake))

[Biomixing](#page-1-0) **[Dilute theory](#page-6-0) [Simulations](#page-9-0) [Squirmers](#page-14-0) [References](#page-24-0)** References

<span id="page-6-0"></span>

## Displacement by a moving body



Maxwell (1869); Darwin (1953); Eames et al. (1994); Eames & Bush (1999)

[Biomixing](#page-1-0) **[Dilute theory](#page-6-0) [Simulations](#page-9-0) [Squirmers](#page-14-0) [References](#page-24-0)** References

#### Cylinders and spheres: Displacements





[Biomixing](#page-1-0) **[Dilute theory](#page-6-0) [Simulations](#page-9-0) [Squirmers](#page-14-0) [References](#page-24-0)** References

#### Displacement for cylinders



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

<span id="page-9-0"></span>

## Numerical simulation

- Validate theory using simple simple simulations;
- Large periodic box;
- N 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  $|x(t)|^2$ , repeat for a large number  $N_{\text{real}}$  of realizations, and average.

## A 'gas' of swimmers



[\[movie 2\]](http://www.math.wisc.edu/~jeanluc/movies/cylinder_gas.avi)  $N = 100$  cylinders, box size = 1000

### How well does the dilute theory work?





## Cloud of particles



[\[movie 3\]](http://www.math.wisc.edu/~jeanluc/movies/swimmers_mov.avi) (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); 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)



<span id="page-14-0"></span>

## 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  $= 1$ .

Note that  $\beta = 0$  is the sphere in potential flow.

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.)



[\[movie 4\]](http://www.math.wisc.edu/~jeanluc/movies/squirmer_flyby.avi)

## Squirmer displacements



## Squirmers: Transport



## Squirmers: Trajectories



# Far field: Displacements



## Far field: transport



## Finite Reynolds number: Displacements



## Finite Reynolds number: Transport





Blake, J. R. 1971 A spherical envelope approach to ciliary propulsion. J. Fluid Mech. 46, 199–208.

Darwin, C. G. 1953 Note on hydrodynamics. Proc. Camb. Phil. Soc. 49 (2), 342–354.

- Dewar, W. K., Bingham, R. J., Iverson, R. L., Nowacek, D. P., St. Laurent, L. C. & Wiebe, P. H. 2006 Does the marine biosphere mix the ocean? J. Mar. Res. 64, 541–561.
- DRESCHER, K., LEPTOS, K., TUVAL, I., ISHIKAWA, T., PEDLEY, T. J. & GOLDSTEIN, R. E. 2009 Dancing volvox: hydrodynamic bound states of swimming algae. Phys. Rev. Lett. 102, 168101.
- Eames, I., Belcher, S. E. & Hunt, J. C. R. 1994 Drift, partial drift, and Darwin's proposition. J. Fluid Mech. 275, 201–223.
- Eames, I. & Bush, J. W. M. 1999 Longitudinal dispersion by bodies fixed in a potential flow. Proc. R. Soc. Lond. A 455, 3665–3686.

HERNANDEZ-ORTIZ, J. P., DTOLZ, C. G. & GRAHAM, M. D. 2006 Transport and collective dynamics in suspensions of confined swimming particles. Phys. Rev. Lett. 95, 204501.

HUNTLEY, M. E. & ZHOU, M. 2004 Influence of animals on turbulence in the sea. Mar. Ecol. Prog. Ser. 273. 65–79.

Ishikawa, T. 2009 Suspension biomechanics of swimming microbes. J. Roy. Soc. Interface 6, 815–834.

ISHIKAWA, T., SIMMONDS, M. P. & PEDLEY, T. J. 2006 Hydrodynamic interaction of two swimming model micro-organisms. J. Fluid Mech. 568, 119-160.

KATIJA, K. & DABIRI, J. O. 2009 A viscosity-enhanced mechanism for biogenic ocean mixing. Nature 460, 624–627.

KUNZE, E., DOWER, J. F., BEVERIDGE, I., DEWEY, R. & BARTLETT, K. P. 2006 Observations of biologically generated turbulence in a coastal inlet. Science 313, 1768–1770.

LEPTOS, K. C., GUASTO, J. S., GOLLUB, J. P., PESCI, A. I. & GOLDSTEIN, R. E. 2009 Dynamics of enhanced tracer diffusion in suspensions of swimming eukaryotic microorganisms. Phys. Rev. Lett. 103, 198103.

LIGHTHILL, M. J. 1952 On the squirming motion of nearly spherical deformable bodies through liquids at very small Reynolds numbers. Comm. Pure Appl. Math. 5, 109–118.

MAXWELL, J. C. 1869 On the displacement in a case of fluid motion. Proc. London Math. Soc. s1-3 (1), 82-87.

SAINTILLIAN, D. & SHELLEY, M. J. 2007 Orientational order and instabilities in suspensions of self-locomoting rods. Phys. Rev. Lett. 99, 058102.

Thiffeault, J.-L. & Childress, S. 2009 Stirring by swimming bodies, <http://arxiv.org/abs/0911.5511>.

Underhill, P. T., Hernandez-Ortiz, J. P. & Graham, M. D. 2008 Diffusion and spatial correlations in suspensions of swimming particles. Phys. Rev. Lett. 100, 248101.

<span id="page-24-0"></span>WU, X.-L. & LIBCHABER, A. 2000 Particle diffusion in a quasi-two-dimensional bacterial bath. Phys. Rev. Lett. 84, 3017–3020.