Do fish stir the ocean?

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Biomixing

A controversial proposition:

Biomixing

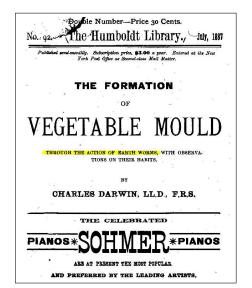
- There are many regions of the ocean that are relatively quiescent, especially in the depths (1 hairdryer/km³);
- Yet mixing occurs: nutrients eventually get dredged up to the surface somehow;
- What if organisms swimming through the ocean made a significant contribution to this?
- There could be a local impact, especially with respect to feeding and schooling;
- Also relevant in suspensions of microorganisms (Viscous Stokes regime).

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 $\kappa \approx 1.3$ cm² sec⁻¹. Thus temperature and salinity can be fitted by exponentiallike solutions to $\left[\kappa \cdot d^2/dz^2 - w \cdot d/dz\right]T$, S = 0, with $\kappa/w \approx 1$ km the appropriate "scale height." For Carbon 14 a decay term must be included, $\left[\right]^{12}C = \mu^{12}C$; a fitting of the solution to the observed ¹⁴C 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 $\sim 10^{-5}~\rm W~kg^{-1}$ 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.

Counterargument: Mixing efficiency

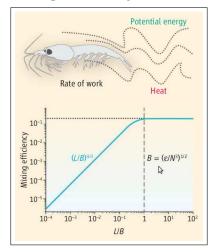
Visser (2007) counterargument:

The mixing efficiency is defined as

$$\Gamma = \frac{\text{change in potential energy}}{\text{work done}}$$

 Γ depends strongly on L/B, where L is the turbulence scale and B is the Ozmidov scale.*

For krill L = 1.5 cm, B = 3 to 10 m, so L/B = .005 to .0015. $\Gamma = 10^{-4}$ to 10^{-3} : little turbulent energy goes into mixing.

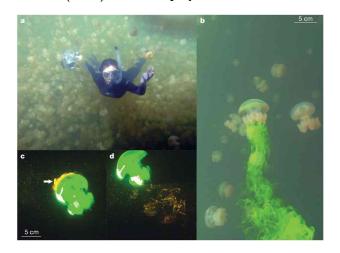


(from Visser (2007))

^{*} Vertical scale at which buoyancy force is comparable to inertial forces.)

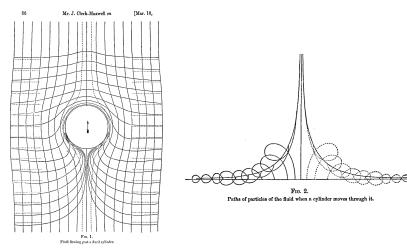
But it's not over...

Katija & Dabiri (2009) looked at jellyfish:



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

Displacement by a moving body



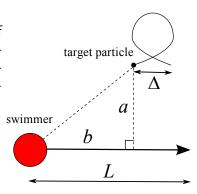
Maxwell (1869); Darwin (1953); Eames et al. (1994); Eames & Bush (1999)

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.



(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

$$d\mathbf{A}/V = 2 \operatorname{d} a \operatorname{d} b/V$$
 (2D) or $2\pi a \operatorname{d} a \operatorname{d} b/V$ (3D)

Replace average by integral:

$$\left\langle |\mathbf{x}|^2 \right\rangle = \frac{N}{V} \int \Delta_L^2(a,b) \, \mathrm{d}\mathbf{A}$$

Writing n = 1/V for the number density (there is only one swimmer) and N = Ut/L (L/U is the time between steps):

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

Effective diffusivity

Putting this together,

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

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

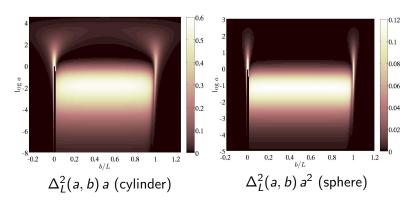
which defines the effective diffusivity κ .

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

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

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



We can make the simplification (for large L)

$$\Delta_L(a,b) = egin{cases} \Delta(a), & 0 \leq b \leq L; \\ 0, & ext{otherwise}, \end{cases}$$

that is, the displacement vanishes if the swimmer is moving away from the particle, or if the particle doesn't reach the swimmer. In that case we can do the *b* integral:

$$\kappa = \frac{Un}{2} \int_0^\infty \Delta^2(a) \, \mathrm{d}a,$$
 2D

$$\kappa = \frac{\pi U n}{3} \int_0^\infty \Delta^2(a) a \, \mathrm{d}a, \qquad 3D$$

There is no path length dependence.

Displacement for cylinders

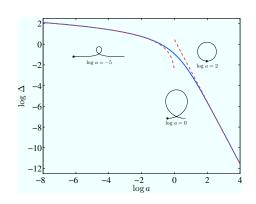
Small a: $\Delta \sim -\log a$

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

(Darwin, 1953)

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

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

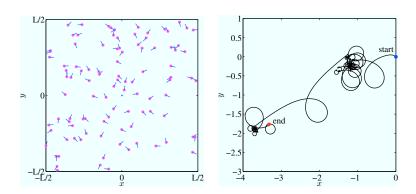


⇒ 97% dominated by "head-on" collisions (similar for spheres)

Numerical simulation

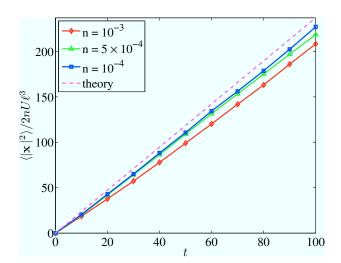
- Validate theory using simple simple simulations;
- Large periodic box;
- N swimmers (cylinders of radius 1), initially at random positions, swimming in random direction with constant speed U = 1;
- Target particle initially at origin advected by the swimmers;
- Since dilute, superimpose velocities;
- 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



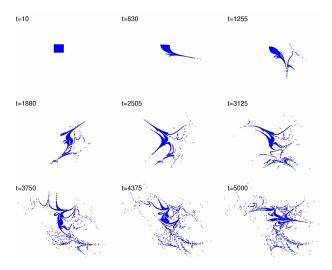
[movie 2] N = 100 cylinders, box size = 1000

How well does the dilute theory work?



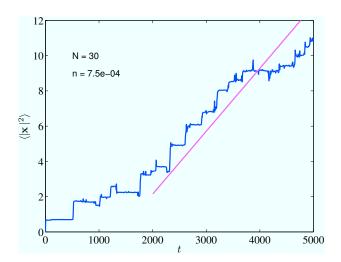
Biomixing Dilute theory Simulations Squirmers No-slip boundary Conclusions References

Cloud of particles



[movie 3] (30 cylinders)

Cloud dispersion proceeds by steps



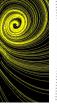
Squirmers

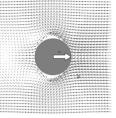
Considerable literature on transport due to microorganisms: Wu & Libchaber (2000); Hernandez-Ortiz et al. (2006); Saintillian & Shelley (2007); Ishikawa & Pedley (2007); Underhill et al. (2008); Ishikawa (2009); Leptos et al. (2009)

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

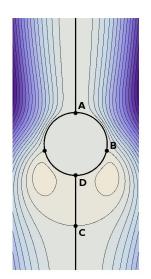
3D axisymmetric streamfunction for a typical squirmer, in cylindrical coordinates (ρ, z) :

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

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

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

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



Particle motion for squirmer

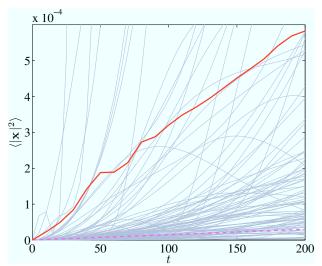
A particle near the squirmer's swimming axis initially (blue) moves towards the squirmer.

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

(The squirmer moves from bottom to top.)

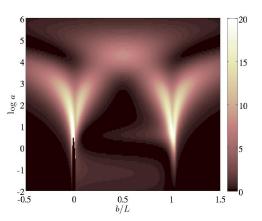


Squirmers: Transport



Measured slope is 20 times larger than theory predicts! Oops!

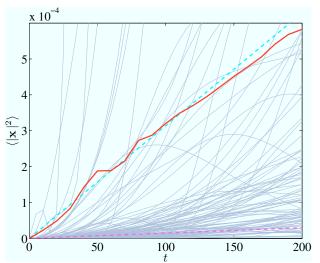
Revisit simplifying assumption



Cannot at all be approximated by a 'hat' in b!

Dominated by trajectories that 'stop short,' due to pulling-in effect of this more realistic swimmer. Do the full double integral.

Squirmers: Transport revisited



The cyan line is the double integral. Still independent of path length (assumed large).

Sphere in viscous fluid

A natural question is what happens in the presence of viscosity, which greatly increases the "sticking" to the swimmer's surface?



(from Camassa et al., Sphere Passing Through Corn Syrup)

This is a mechanism that has been suggested for enhanced transport by jellyfish (Katija & Dabiri, 2009)

No-slip correction

We expect the diffusivity to depend on the path length for a no-slip boundary: fluid gets dragged along.

Divergence of displacement for a no-slip surface (Eames et al. (2003)):

$$\Delta(a) \sim {C\ell^2 \over a}$$
 compare to $\log a$ for slip walls; $C = {\rm const.} = \sqrt{2/3} \, \pi$ for sphere; $\ell = {\rm characteristic}$ body size.

This more severe singularity prevents our integral from converging: cut-off at maximum displacement.

$$\kappa \sim rac{\pi}{3} \ \textit{Un} \int_{\Delta^{-1}(L)}^{\infty} \Delta^2(a) a \, \mathrm{d} a \sim rac{\pi}{3} \ \textit{Un} \ell^4 \ \textit{C}^2 \log(L/\ell)$$

Logarithmic in the path length L.

So, do the fish stir the ocean?

- Consider spheres of radius 1 cm (the size of typical krill) moving at 5 cm/sec, with $n=5\times 10^{-3}$ cm⁻³, we get an effective diffusivity of 7×10^{-3} cm²/sec.
- This is 5 times the thermal molecular value $1.5 \times 10^{-3}~{\rm cm^2/sec}$, and about 500 times the molecular value $1.6 \times 10^{-5}~{\rm cm^2/sec}$ 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;
- Viscous flow dominated by sticking and have a log dependence on path length (though more work needed);

Future work:

- Wake models and turbulence:
- PDF of scalar concentration;
- Buoyancy effects;
- Schooling: longer length scale?

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- 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.
- EAMES, I., GOBBY, D. & DALZIEL, S. B. 2003 Fluid displacement by Stokes flow past a spherical droplet. J. Fluid Mech. 485, 67–85.
- EINSTEIN, A. 1905 Investigations on the Theory of the Brownian Movement. (Dover, New York, 1956).
- 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. & PEDLEY, T. J. 2007 The rheology of a semi-dilute suspension of swimming model micro-organisms. J. Fluid Mech. 588, 399–435.
- 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.
- $\mathrm{Munk},\ \mathrm{W.\ H.}$ 1966 Abyssal recipes. Deep-Sea Res. 13, 707–730.
- Pedley, T. J. & Kessler, J. O. 1992 Hydrodynamic phenomena in suspensions of swimming microorganisms. *Annu. Rev. Fluid Mech.* 24, 313–358.
- 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. 2010 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.
- VISSER, A. W. 2007 Biomixing of the oceans? Science 316 (5826), 838-839.
- WU, X.-L. & LIBCHABER, A. 2000 Particle diffusion in a quasi-two-dimensional bacterial bath. Phys. Rev. Lett. 84, 3017–3020.