Biomixing

when organisms stir their environment

Jean-Luc Thiffeault

Department of Mathematics
University of Wisconsin – Madison

Mathematics Colloquium
University of Utah, Salt Lake City, 28 March 2013

Supported by NSF grant DMS-1109315

Biomixing

A controversial proposition:

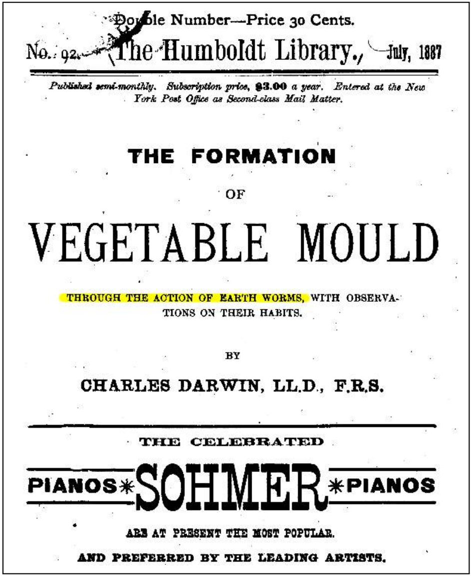
- There are many regions of the ocean that are relatively quiescent, especially in the depths (1 hairdryer/ km^3);
- Yet mixing occurs: nutrients eventually get dredged up to the surface somehow;
- What if organisms swimming through the ocean made a significant contribution to this?
- There could be a local impact, especially with respect to feeding and schooling;
- Also relevant in suspensions of microorganisms (viscous Stokes regime).
- In any case it's a nice applied math problem!

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.”



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.

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 $w \approx 1{\cdot}2$ cm day^{-1} and eddy diffusivity $\kappa \approx 1{\cdot}3$ 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 observed ^{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."

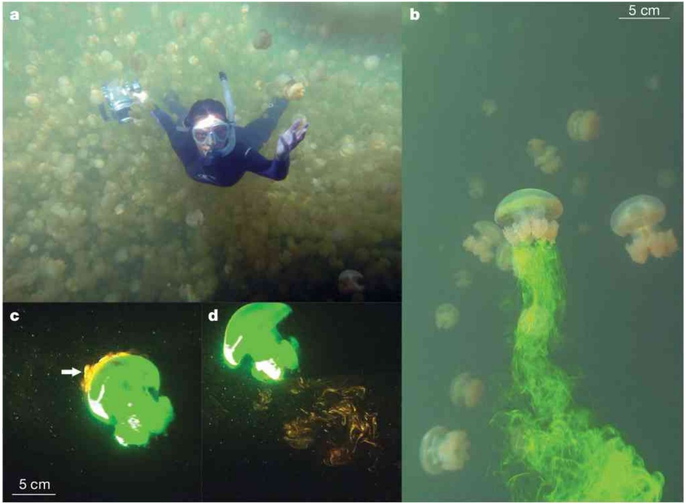
Ocean biomixing: Basic observations

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 $\sim 10^{-5}\ \mathrm{W\ kg^{-1}}$. 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.
- However, Kunze has failed to find this effect again on subsequent cruises. Visser (2007) has questioned whether small-scale turbulence can lead to overturning.

In situ experiments

Katija & Dabiri (2009) looked at jellyfish:



play movie (Palau's Jellyfish Lake.) Correct length scale is path length?

Displacement by a moving body

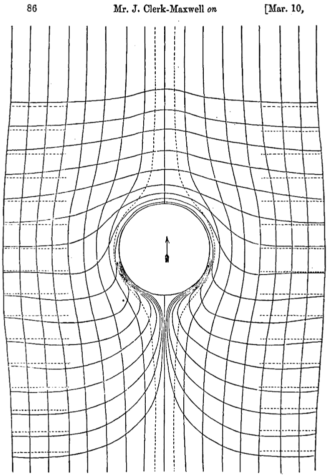


Fig. 1.
Fluid flowing past a fixed cylinder.

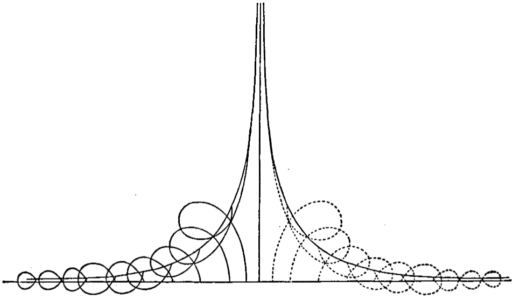


Fig. 2.
Paths of particles of the fluid when a cylinder moves through it.

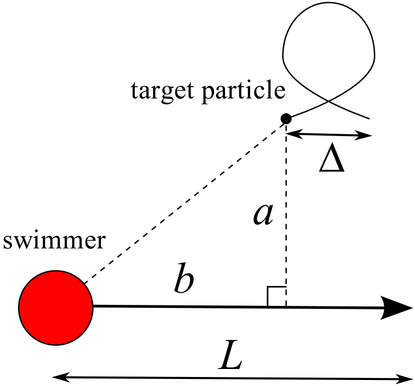
Maxwell (1869); Darwin (1953); Eames *et al.* (1994)

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:

$$\left\langle |\mathbf{x}|^2 \right\rangle = N \left\langle \Delta_L^2(a,b) \right\rangle$$

where a and b are treated as random variables with densities

$$\mathrm{d}\mathbf{A}/V = 2\,\mathrm{d}a\,\mathrm{d}b/V \quad (\text{2D}) \quad \text{or} \qquad 2\pi a\,\mathrm{d}a\,\mathrm{d}b/V \quad (\text{3D})$$

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):

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

Effective diffusivity

Putting this together,

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

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

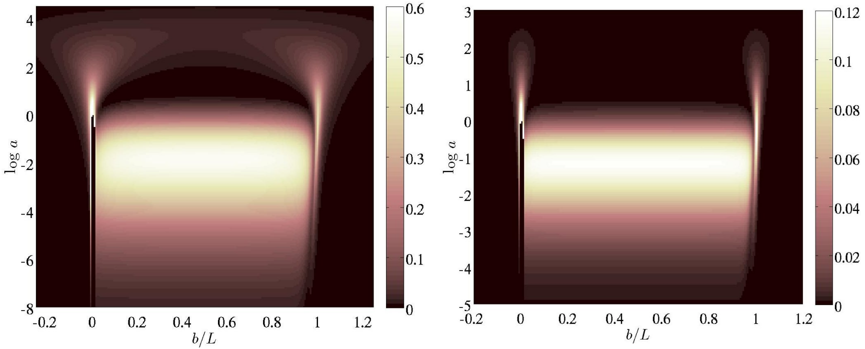
which defines the effective diffusivity κ.

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.

Inviscid cylinders and spheres

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

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

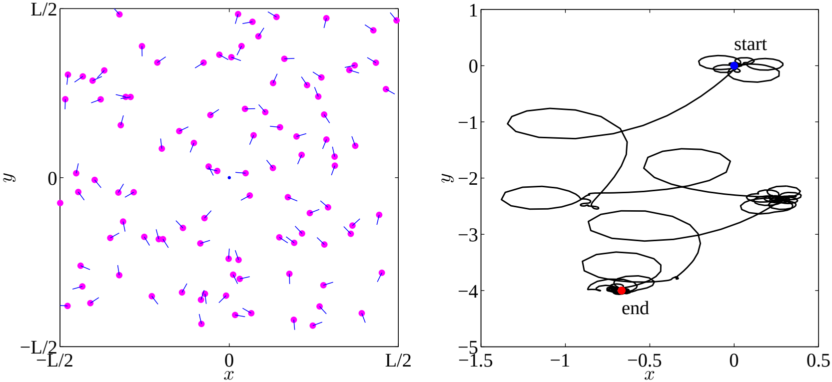


$a\Delta_L^2(a,b)$ (cylinder) $a^2\Delta_L^2(a,b)$ (sphere)

Numerical simulation

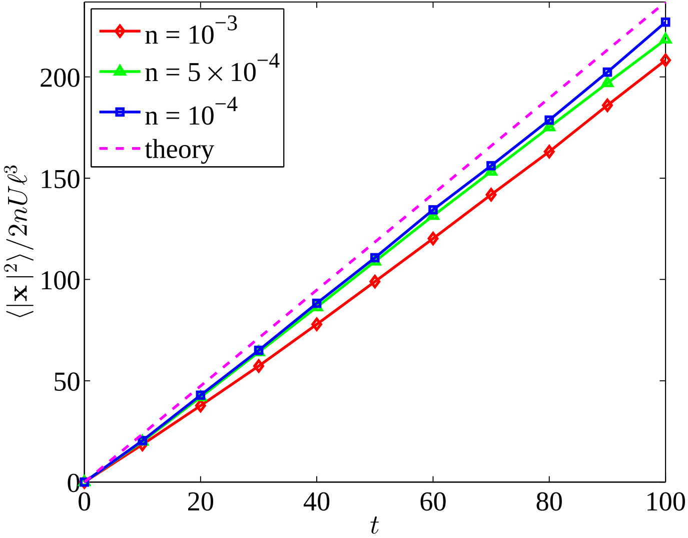
- Validate theory using simple simple simulations;
- Large periodic box;
- N_{swim} swimmers (cylinders of radius 1), initially at random positions, swimming in random direction with constant speed $U = 1$;
- Target particle initially at origin advected by the swimmers;
- Since dilute, superimpose velocities;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

A ‘gas’ of swimmers

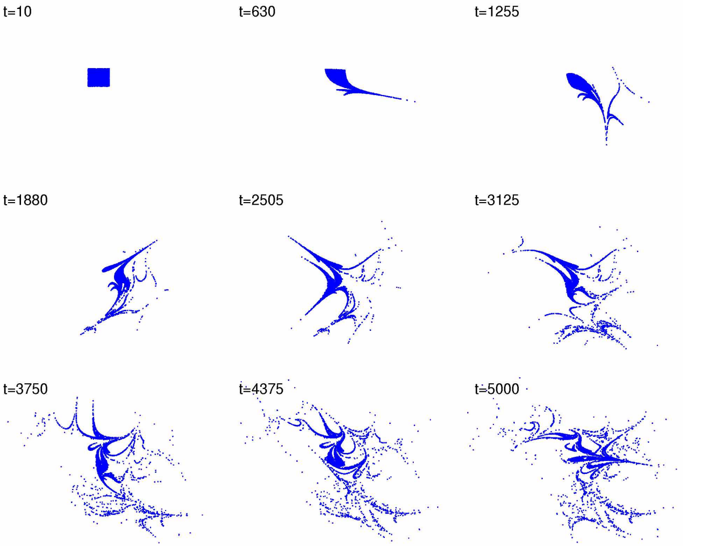


play movie 100 cylinders, box size = 1000

How well does the dilute theory work?

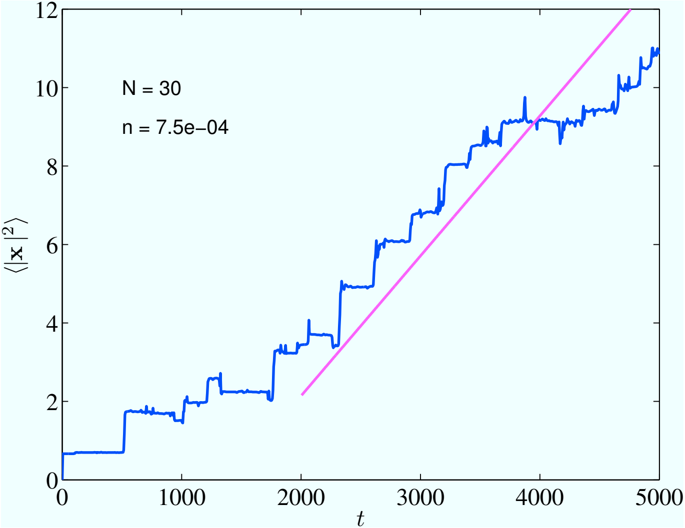


Cloud of particles



play movie (30 cylinders)

Cloud dispersion proceeds by steps

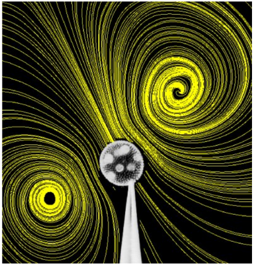


Squirmers

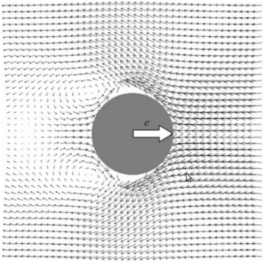
Considerable literature on transport due to microorganisms: Wu & Libchaber (2000); Hernandez-Ortiz *et al.* (2005); Saintillian & Shelley (2007); Ishikawa & Pedley (2007); Underhill *et al.* (2008); Ishikawa (2009); Leptos *et al.* (2009)

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

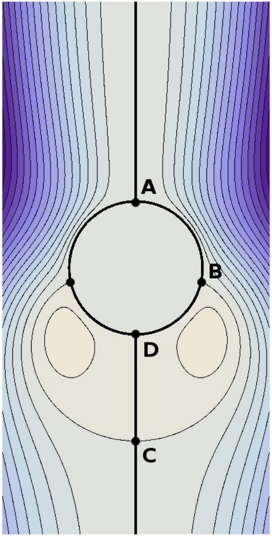
3D axisymmetric streamfunction for a typical squirmer, in cylindrical coordinates (ρ, z):

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

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.

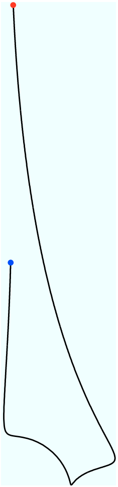


Particle motion for squirmer

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

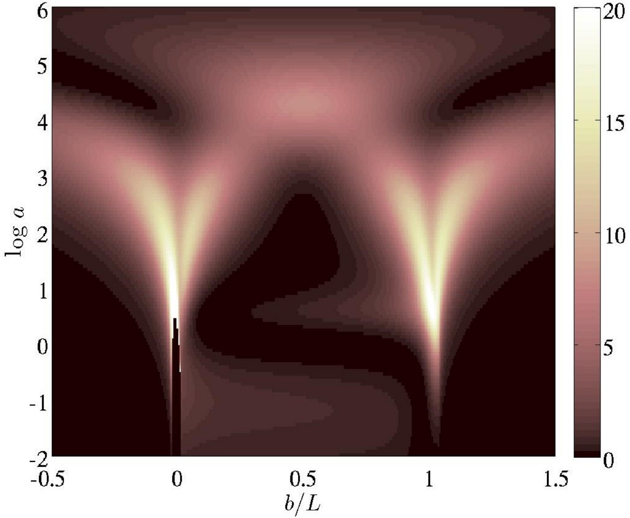
After the squirmer has passed the particle follows in the squirmer's wake.

(The squirmer moves from bottom to top.)



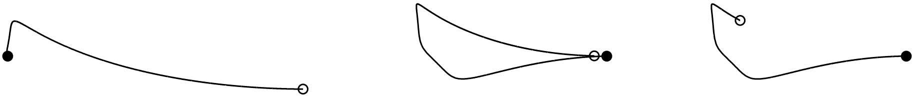
play movie

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



Squirmers: Trajectories

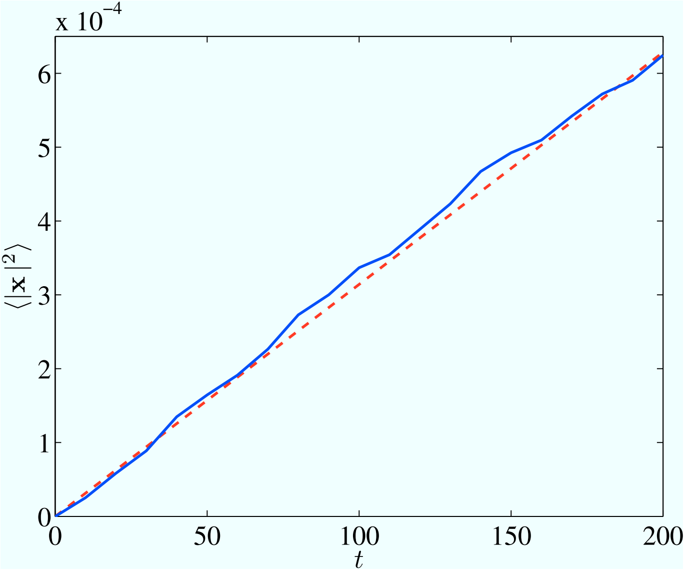
The two peaks in the displacement plot come from ‘incomplete’ trajectories:



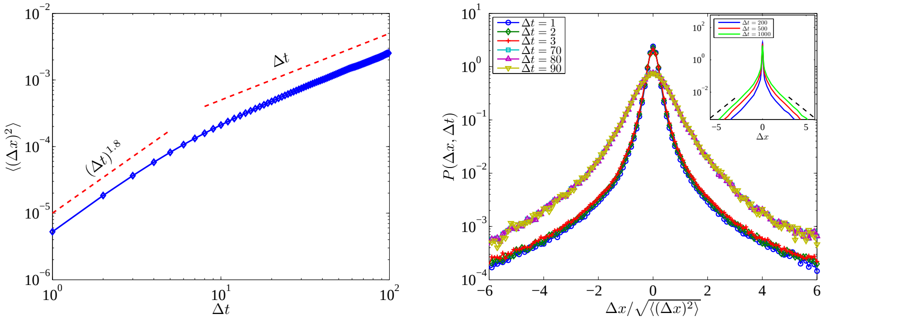
$b/L = 0$ $\quad$ $b/L = 0.5$ $\quad$ $b/L = 1$

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).

Squirmers: Transport

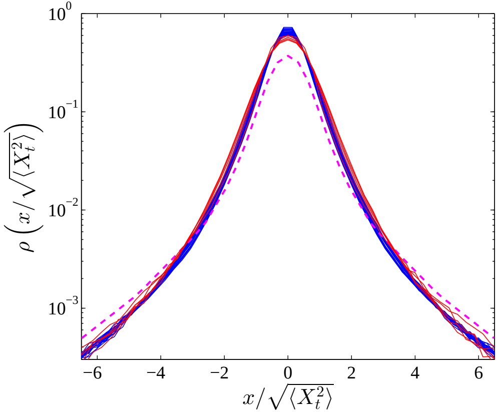


Non-Gaussian PDFs of displacement



- Variance exhibits similar short-time ballistic scaling as in Wu & Libchaber (2000) (due to smoothness);
- PDF qualitatively 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.

PDF: Theory vs experiment



The normalized PDF for experimental data (dashed) agrees well with simple swimmer models, with no adjustable paramameters. This is consistent with a dominant far-field.

Conclusions

- 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;
- 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?

References I

Blake, J. R. (1971). *J. Fluid Mech.* **46**, 199–208.

Darwin, C. G. (1953). *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). *J. Mar. Res.* **64**, 541–561.

Dombrowski, C., Cisneros, L., Chatkaew, S., Goldstein, R. E., & Kessler, J. O. (2004). *Phys. Rev. Lett.* **93** (9), 098103.

Drescher, K., Leptos, K., Tuval, I., Ishikawa, T., Pedley, T. J., & Goldstein, R. E. (2009). *Phys. Rev. Lett.* **102**, 168101.

Drescher, K. D., Goldstein, R. E., Michel, N., Polin, M., & Tuval, I. (2010). *Phys. Rev. Lett.* **105**, 168101.

Dunkel, J., Putz, V. B., Zaid, I. M., & Yeomans, J. M. (2010). *Soft Matter,* **6**, 4268–4276.

Eames, I., Belcher, S. E., & Hunt, J. C. R. (1994). *J. Fluid Mech.* **275**, 201–223.

Einstein, A. (1956). *Investigations on the Theory of the Brownian Movement*. New York: Dover.

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

Hernandez-Ortiz, J. P., Dtolz, C. G., & Graham, M. D. (2005). *Phys. Rev. Lett.* **95**, 204501.

Huntley, M. E. & Zhou, M. (2004). *Mar. Ecol. Prog. Ser.* **273**, 65–79.

Ishikawa, T. (2009). *J. Roy. Soc. Interface,* **6**, 815–834.

Ishikawa, T. & Pedley, T. J. (2007). *J. Fluid Mech.* **588**, 399–435.

References II

Ishikawa, T., Simmonds, M. P., & Pedley, T. J. (2006). *J. Fluid Mech.* **568**, 119–160.

Katija, K. & Dabiri, J. O. (2009). *Nature,* **460**, 624–627.

Kunze, E., Dower, J. F., Beveridge, I., Dewey, R., & Bartlett, K. P. (2006). *Science,* **313**, 1768–1770.

Leptos, K. C., Guasto, J. S., Gollub, J. P., Pesci, A. I., & Goldstein, R. E. (2009). *Phys. Rev. Lett.* **103**, 198103.

Lighthill, M. J. (1952). *Comm. Pure Appl. Math.* **5**, 109–118.

Lin, Z., Thiffeault, J.-L., & Childress, S. (2011). *J. Fluid Mech.* **669**, 167–177. http://arxiv.org/abs/1007.1740.

Maxwell, J. C. (1869). *Proc. London Math. Soc.* **s1-3** (1), 82–87.

Oseen, C. W. (1910). *Ark. Mat. Astr. Fys.* **6** (29), 1–20.

Saintillian, D. & Shelley, M. J. (2007). *Phys. Rev. Lett.* **99**, 058102.

Thiffeault, J.-L. & Childress, S. (2010). *Phys. Lett. A,* **374**, 3487–3490.

Underhill, P. T., Hernandez-Ortiz, J. P., & Graham, M. D. (2008). *Phys. Rev. Lett.* **100**, 248101.

Visser, A. W. (2007). *Science,* **316** (5826), 838–839.

Wu, X.-L. & Libchaber, A. (2000). *Phys. Rev. Lett.* **84**, 3017–3020.