

Velocity fluctuations in suspensions of swimming microorganisms

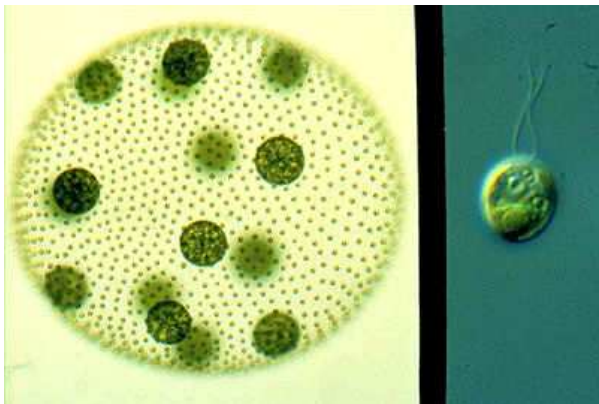
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Microswimmers

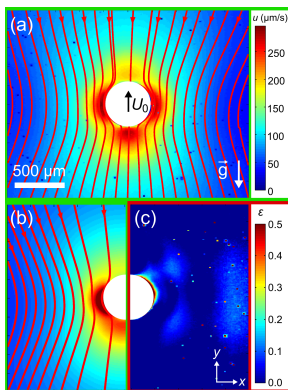


Volvox carteri and *Chlamydomonas reinhardtii*

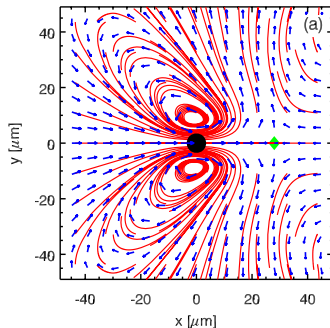
Chlammy is single-celled ($\sim 5 \mu\text{m}$); *Volvox* consists of several thousand chlammy-like cells ($\sim 200 \mu\text{m}$).

Velocity field

Volvox

Drescher *et al.* (2010)

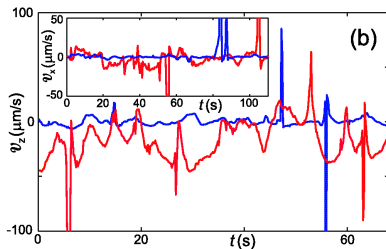
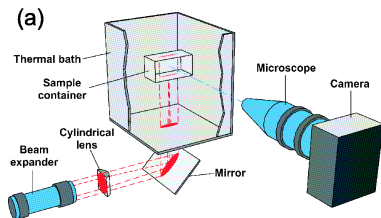
Chlamy

Guasto *et al.* (2010)

$$\mathbf{v}_{\text{fit}}(\mathbf{r}) = \frac{A_{\text{St}}}{r} (\mathbf{I} + \hat{\mathbf{r}}\hat{\mathbf{r}}) \cdot \hat{\mathbf{z}} + \frac{A_{\text{str}}}{r^2} (1 - 3(z/r)^2) \hat{\mathbf{r}} + \frac{A_{\text{sd}}}{3r^3} (\mathbf{I} - 3\hat{\mathbf{r}}\hat{\mathbf{r}}) \cdot \hat{\mathbf{z}}$$

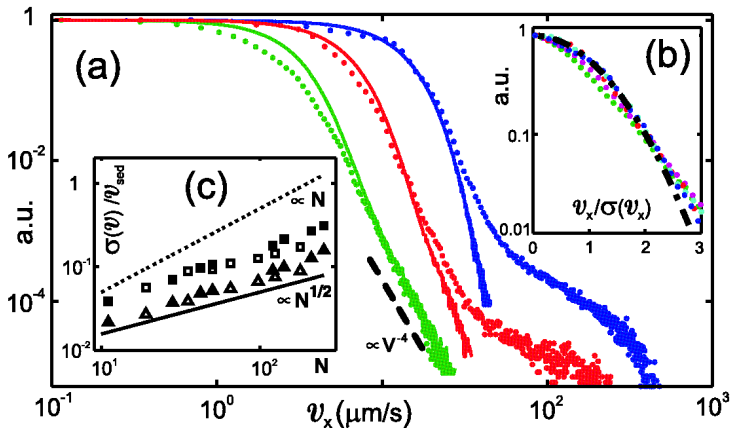
Measuring velocity fluctuations

Experiments of Rushkin *et al.* (2010) using *Volvox*:



Velocity measured at a fixed point.

PDF of velocity fluctuations



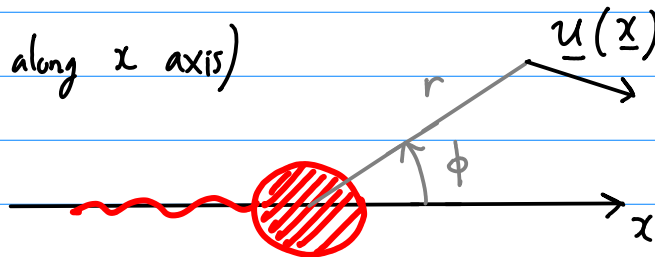
Number of Vol/vox : green (11), red (42), blue (210)

Circles are experiments: note cut-off at large v_x .

- DRESCHER, K. D., GOLDSTEIN, R. E., MICHEL, N., POLIN, M. & TUVAL, I. 2010 Direct measurement of the flow field around swimming microorganisms. *Phys. Rev. Lett.* **105**, 168101.
- GUASTO, J. S., JOHNSON, K. A. & GOLLUB, J. P. 2010 Oscillatory flows induced by microorganisms swimming in two-dimensions. *Phys. Rev. Lett.* **105**, 168102.
- 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.
- LIN, Z., THIFFEAULT, J.-L. & CHILDRESS, S. 2010 Stirring by squirmers. *J. Fluid Mech.* In press.
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- THIFFEAULT, J.-L. & CHILDRESS, S. 2010 Stirring by swimming bodies. *Phys. Lett. A* **374**, 3487–3490.
- 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.
- WEISS, J. B., PROVENZALE, A. & MCWILLIAMS, J. C. 1998 Lagrangian dynamics in high-dimensional point-vortex systems. *Phys. Fluids* **10** (8), 1929–1941.

Velocity field due to one swimmer:

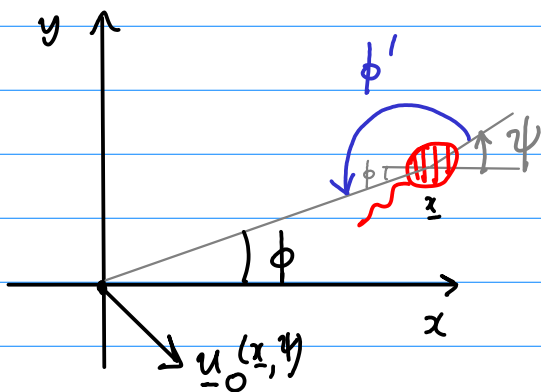
(oriented along x axis)



$$\underline{x} = r(\cos \phi, \sin \phi)$$

$$\underline{u} = u(r, \phi)\hat{x} + v(r, \phi)\hat{y}$$

Now assume this swimmer is at position \underline{x} , angle ψ : what is the velocity field induced by the swimmer at O , the origin?



$$\phi' = \phi - \psi - \pi$$

Rotate ϕ by $-(\psi + \pi)$.

After also rotating direction, get

$$\underline{u}_0(\underline{x}, \psi) = R_{\psi} \underline{u}(R_{\psi+\pi}^{-1} \underline{x})$$

where $R_{\psi} = \begin{pmatrix} \cos \psi & -\sin \psi \\ \sin \psi & \cos \psi \end{pmatrix}$ is a rotation matrix.

Now, the velocity at the origin is due to a superposition of N swimmers.

$$\underline{u}_N = \sum_{k=1}^N \underline{u}_0(\underline{x}_k, \psi_k)$$

Consider only horizontal component

What is the probability that $u_N = u$ for N swimmers?

$$P_N(u) = \int \delta(u_0(x_1, \psi_1) + \dots + u_0(x_N, \psi_N) - u) \times \frac{d\psi_1}{2\pi} \dots \frac{d\psi_N}{2\pi} \frac{dV_1}{V} \dots \frac{dV_N}{V}$$

The characteristic function is the Fourier transform

$$e^{-S_N(k)} = \int P_N(u) e^{-iku} du$$

Make use of δ -function:

$$\begin{aligned} e^{-S_N(k)} &= \int e^{-ik(u_0(x_1, \psi_1) + \dots + u_0(x_N, \psi_N))} \frac{d\psi_1}{2\pi} \dots \frac{d\psi_N}{2\pi} \frac{dV_1}{V} \dots \frac{dV_N}{V} \\ &= \left(\frac{1}{2\pi V} \int e^{-ik u_0(x, \psi)} d\psi dV \right)^N = e^{-Ns(k)} \end{aligned}$$

$$u_0(x, \psi) = \cos \psi u(r, \phi - \psi - \pi) - \sin \psi v(r, \phi - \psi - \pi)$$

$$dV = r dr d\phi$$

Let $\phi' = \phi - \psi - \pi$.

$$e^{-s(k)} = \frac{1}{2\pi V} \int_0^{2\pi} d\psi \int_0^{2\pi} d\phi' \int r dr e^{-ik(\cos \psi u(r, \phi') - \sin \psi v(r, \phi'))}$$

Now let $u(r, \phi) = U(r, \phi) \cos \alpha(r, \phi)$

$v(r, \phi) = U(r, \phi) \sin \alpha(r, \phi)$

$$e^{-s(k)} = \frac{1}{2\pi V} \int_0^{2\pi} d\phi' \int r dr \int_0^{2\pi} d\psi e^{-ik U(r, \phi') \cos(\psi + \alpha(r, \phi'))}$$

Now let $\psi' = \psi + \alpha(r, \phi')$.

$$e^{-s(k)} = \frac{1}{2\pi V} \int_0^{2\pi} d\phi' \int r dr \int_0^{2\pi} d\psi' e^{-ik U(r, \phi') \cos \psi'}$$

$$= \frac{1}{V} \int_0^{2\pi} d\phi' \int r dr J_0(k U(r, \phi'))$$

← Bessel func.

$$e^{-s(k)} = \frac{1}{V} \int dV J_0(k U(\underline{x}))$$

Only magnitude matters, since directions uniformly distributed.

Actually more convenient to rewrite as:

$$e^{-s(k)} = 1 - \frac{1}{V} \int dV (1 - J_0(k U(\underline{x})))$$

Now consider a circular domain, and assume

$$U(\underline{x}) = \frac{A}{r^n}$$

$n=1$: point vortices or sources

$n=2$: point dipole

$$e^{-s(k)} = 1 - \frac{2\pi}{V} \int_0^R (1 - J_0(kA/r^n)) r dr$$

For small r , $J_0(\infty) \rightarrow 0$, so integral converges

$$\text{For large } r, \quad 1 - J_0(kA/r^n) = \frac{k^2 A^2}{4} \frac{1}{r^{2n}} + O\left(\left(\frac{kA}{r^n}\right)^4\right),$$

so integrand $\sim r^{1-2n}$.

The limit $R \rightarrow \infty$ thus diverges for $1-2n \geq -1 \Leftrightarrow n \leq 1$.

CANNOT ASSUME INFINITE VOLUME FOR VORTICES! ($n=1$)

But in a way this makes thing easier: for large R , the value of the integral is dominated by large R :

$$e^{-s(k)} \approx 1 - \frac{2\pi}{V} \frac{k^2 A^2}{4} \int_l^R r^{1-2n} dr, \quad n \leq 1$$

← cut-off: come back later. (needed for $n=1$)

$$= 1 - \frac{\pi k^2 A^2}{2V} \log(R/l)$$

Recall $e^{-S_N(k)} = e^{-Ns(k)}$, so

$$e^{-S_N(k)} = \left(1 - \frac{\pi k^2 A^2}{2V} \log(R/l)\right)^N$$

number density of vortices
↓
 $N = cV$

$$= \left(1 - \frac{\pi k^2 A^2 c}{2N} \log(R/l)\right)^N \approx \exp\left(-\frac{\pi k^2 A^2 c}{2} \log\left(\frac{R}{l}\right)\right)$$

Gaussian!
for large N .

Now go back to u : $P_N(u) = \frac{1}{2\pi} \int e^{-S_N(k)} e^{iku} dk$

Get a Gaussian PDF with mean zero and variance

$$\sigma^2 = \pi A^2 c \log(R/\ell)$$

$\sim N \log N$, as in Weiss, Provenzale, McWilliams 198.

For $n > 1$, can take limit $R \rightarrow \infty$: (implies $N \rightarrow \infty$, constant c)

$$e^{-s(k)} = 1 - \frac{2\pi}{V} \int_0^\infty (1 - J_0(kA/r^n)) r dr, \quad n > 1$$

$$= 1 + \frac{2\pi}{V} \frac{1}{2} \left(\frac{|k|A}{2}\right)^{2/n} \frac{\Gamma(-1/n)}{\Gamma(1/n)}$$

$$e^{-S_N(k)} = e^{-Ns(k)} \approx \exp\left(-\pi c \left(\frac{|k|A}{2}\right)^{2/n} \frac{\Gamma(-1/n)}{\Gamma(1/n)}\right)$$

for large N .

$$= \exp(-C_n |k|^{2/n}), \quad n > 1$$

$n = 2$ is particularly simple: $e^{-S_N(k)} = e^{-\pi c A |k|}$
(inviscid cylinders)

Inverse transform:

$$P(u) = \frac{Ac}{(\pi Ac)^2 + u^2}$$

Lorentzian

Note that for $n > 1$ the second moment diverges, as observed by Rushkin (in 3D). Cure this with a finite-size cut-off:

$$\sigma^2 = \langle u^2 \rangle = \int_0^{u_{\max}} P(u) u^2 du$$

with $u_{\max} = \frac{A}{l^n}$, where l is the organism size.

For $n=2$, get $\sigma^2 = \left(\frac{A}{l}\right)^2 c - \pi A^2 c^2 \operatorname{arccot}(\pi c l^2)$

Since $cl^2 \ll 1$ (low density), $\sigma^2 \approx \left(\frac{A}{l}\right)^2 c$.

Note that we can call $u_{\max} = \frac{A}{l^2} = U$, the swimming velocity.
Then:

$$\sigma^2 \approx U^2 l^2 c$$

Strong dependence on cylinder radius

$$\phi = \pi l^2 c = \text{volume fraction}$$

Can we use σ^2 to estimate effective diffusivity?

vortices: yes but no (see Weiss et al.)

dipoles: definitely no

Stokeslet: maybe...

$$D = \lim_{T \rightarrow \infty} \int_0^T \langle u(0)u(t) \rangle dt$$

Green-Kubo

$$\approx \langle u^2(0) \rangle T \text{ if } \delta\text{-correlated}$$

3D: boundary between divergence and convergence at large r
is $n = 3/2$ (fractional)

$n = 1$: Stokeslet (Gaussian) ← strong volume dependence

$n = 2$: stresslet

$n = 3$: source doublet

Other interesting extensions:

- "mixed" singularities (Völvog)
- noise
- images
- Oseen corrections
- time-dependence
- match to data and simulations