Turbulent transport and unmixing of motile phytoplankton

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W.M. Durham et al, *Nature Comm* **4**, 2148 (2013)
F. De Lillo et al, *Phys Rev Lett* **112**, 044502 (2014).

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Turbulent Transport and Mixing
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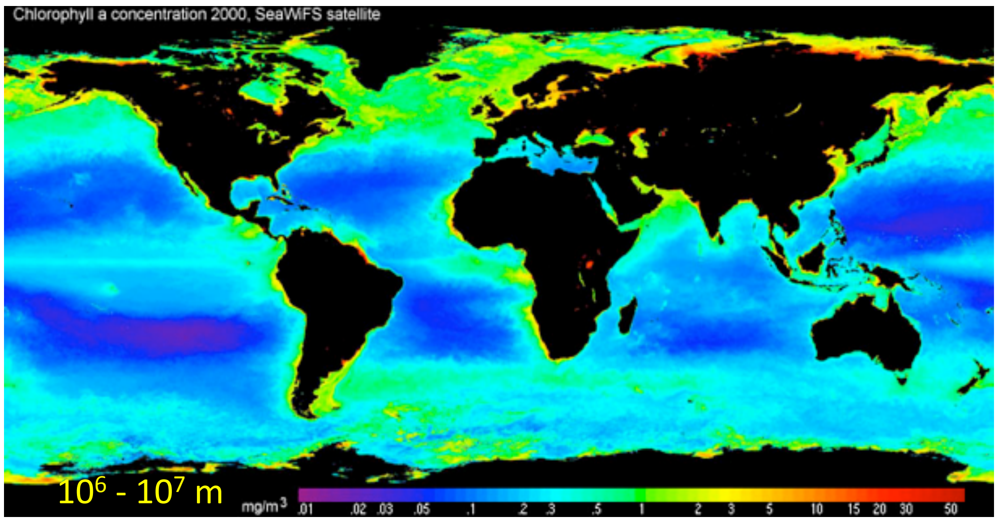
Ecological motivations

Ecology of phytoplankton

- plankton patchiness over many scales
- (toxic) algal blooms and "thin layers"



Red tide of harmful algae

Motile phytoplankton is found to be **more patchy** than non-motile one

Thin layers of *Heterosigma akashiwo* near Shannon Point (WA)

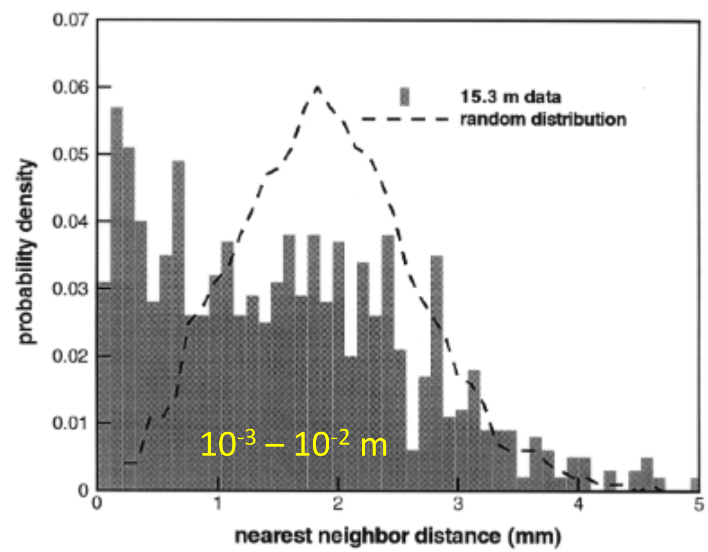


Figure 10. Measured nearest-neighbour distances and expected values from a random distribution.

Outline

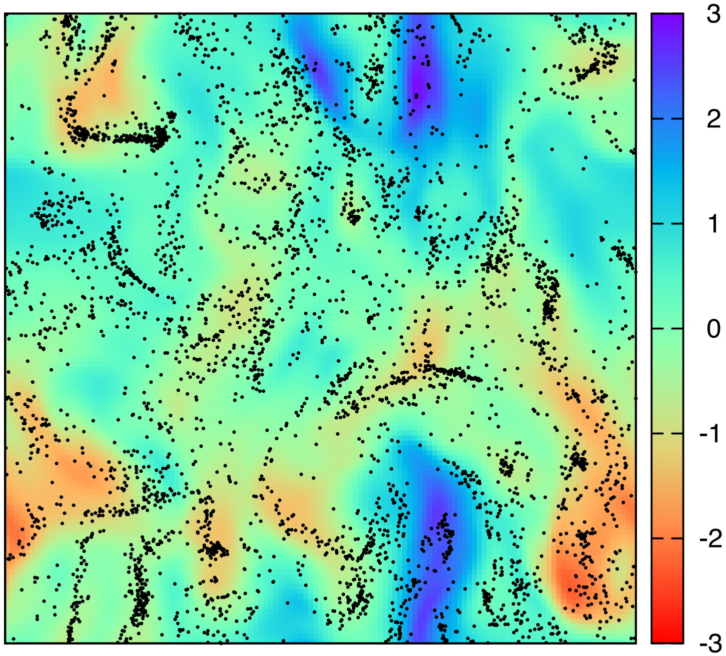
Understand how the combined effect of swimming and turbulence generates patchiness in plankton distribution

Models of gyrotactic swimmers (with refinements)

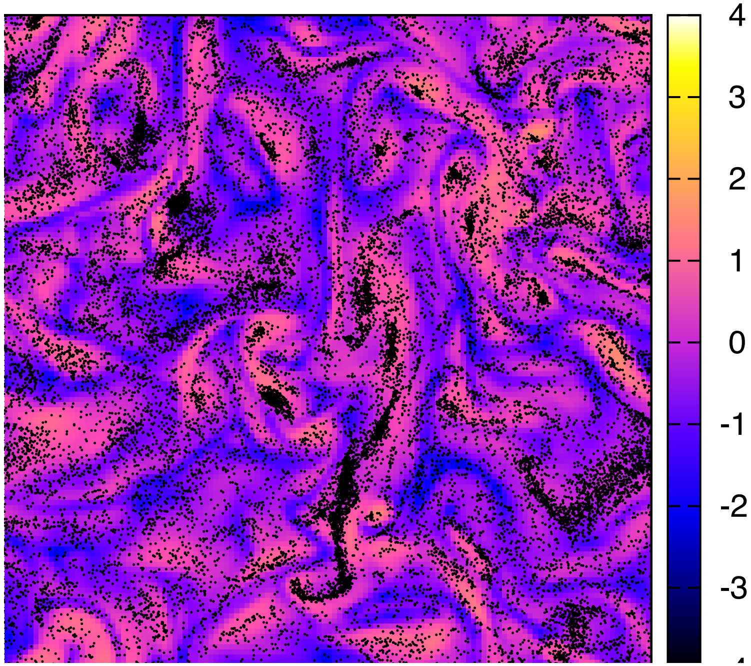
Experimental verification

Direct Numerical Simulations of turbulent flows

moderate turbulence



intense turbulence



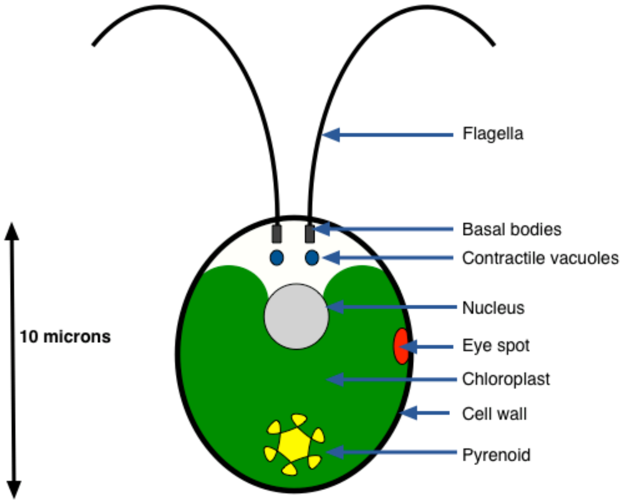
Phytoplankton: living in a flow

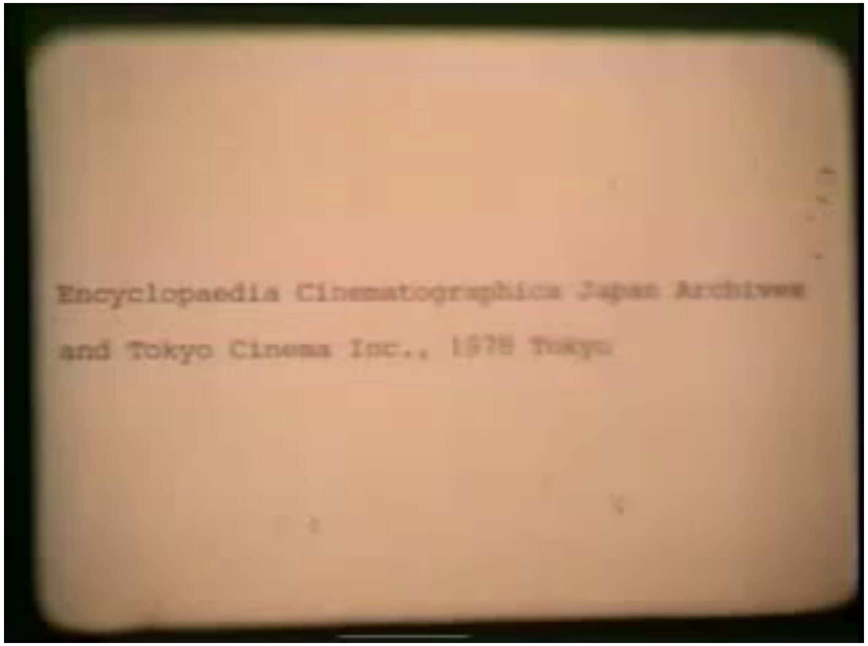
- unicellular organisms of many forms and sizes between 1 and 100 μm
- about 5000 species
- about 50% of photosynthetic activity on Earth
- at the basis of the marine food web
- harmful algal blooms from toxic species
- many species are able to swim
- patchiness at different scales

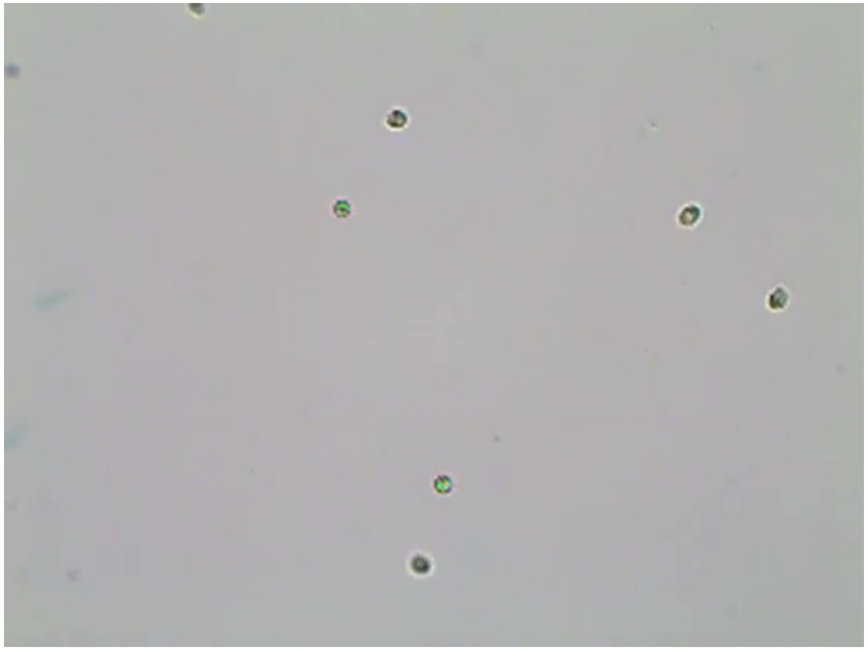
Turbulence mediates many processes crucial to the ecology of phytoplankton,
including motility, nutrient uptake, and cell-cell encounters.

Swimming algae

The genus Chlamydomonas, unicellular flagellate, a model organism for molecular biology.







Both sexual and asexual reproduction

Eyespot: light receptor for phototactic (and photophobic) behaviors (cell rotates at about 2 Hz to detect direction)

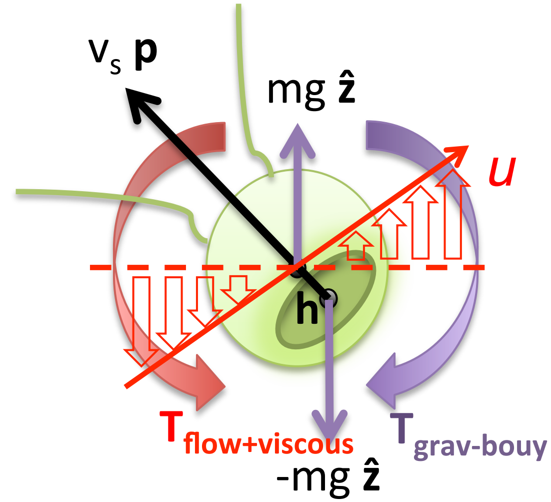
Good swimmers: about 10 body-length per second

Slightly heavy, unbalanced weight (bottom heavy due to chloroplast distribution): they naturally swim against gravity (gyrotaxis)

Gyrotactic model for bottom-heavy cells

$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x},t) + v_s\mathbf{p}$$

$$\frac{d\mathbf{p}}{dt} = -\frac{1}{2v_o}\left[\mathbf{A} - (\mathbf{A}\cdot\mathbf{p})\mathbf{p}\right] + \frac{1}{2}\omega\times\mathbf{p}$$



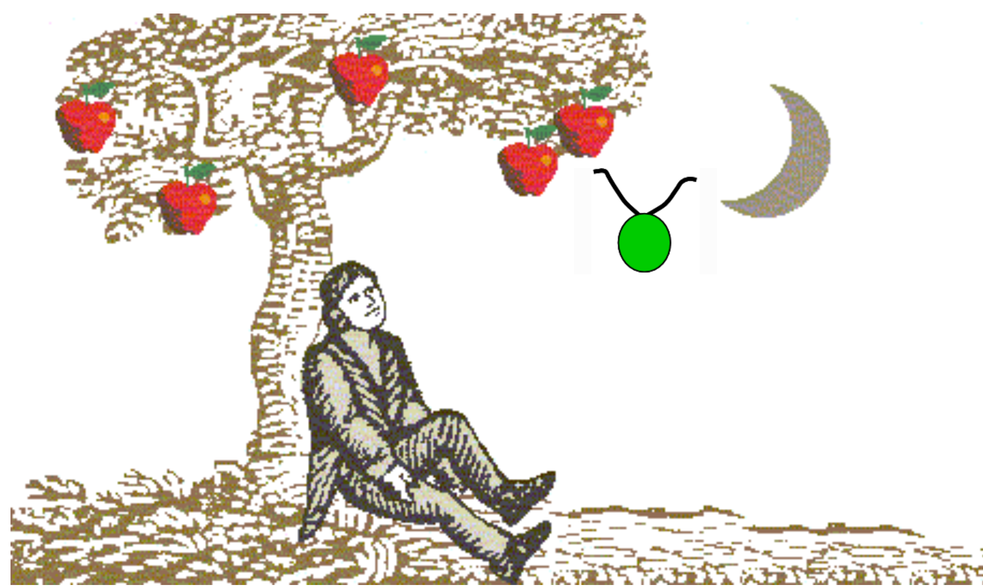
$$\mathbf{A} = \mathbf{g} - \mathbf{a}(\mathbf{x},t)$$

$$v_s \simeq 100\,\mu m\,s^{-1}$$

$$v_0 = \frac{3\nu}{h} = O(10)\,m\,s^{-1}$$

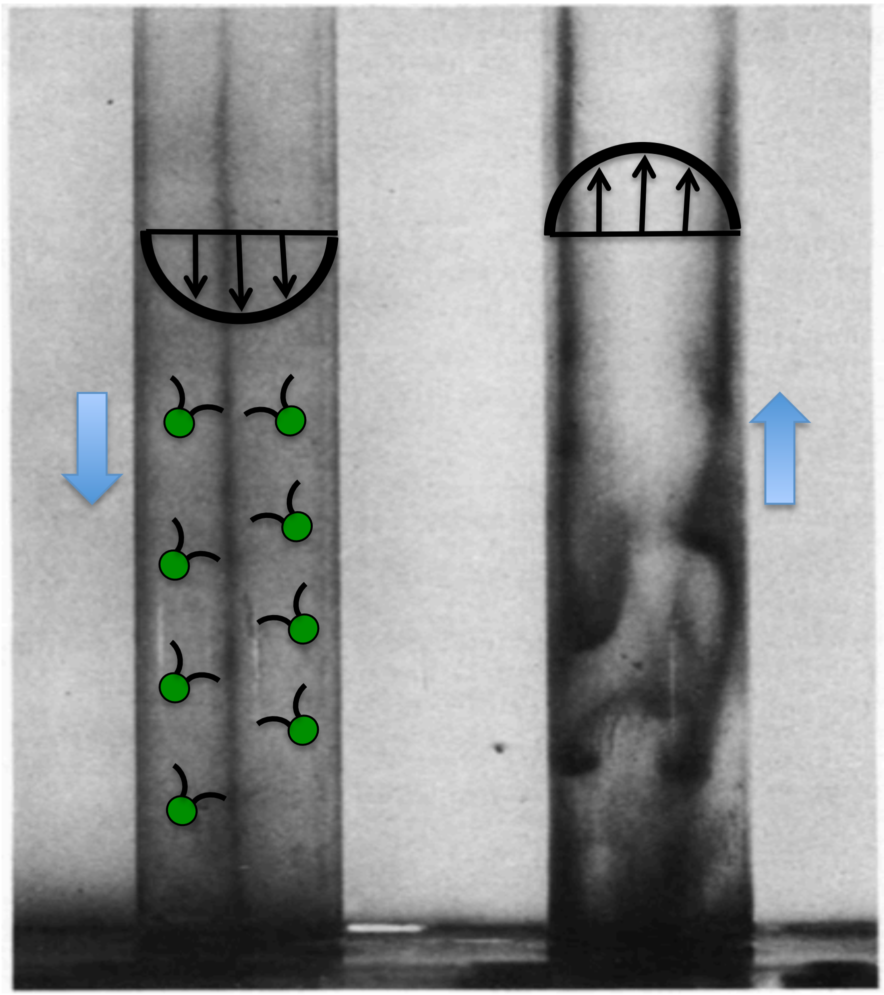
When $\mathbf{A} = \mathbf{g}$

$$\frac{v_0}{g} \equiv B = O(1)\,s$$



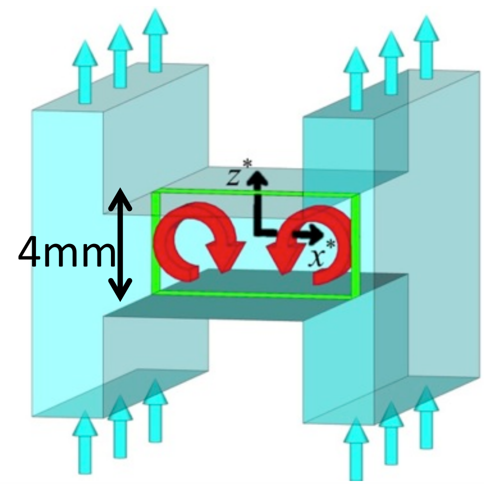
JO Kessler, Nature **313**, 218 (1985)
T.J. Pedley, J.O. Kessler, Proc. Roy Soc. B **231** (1987)

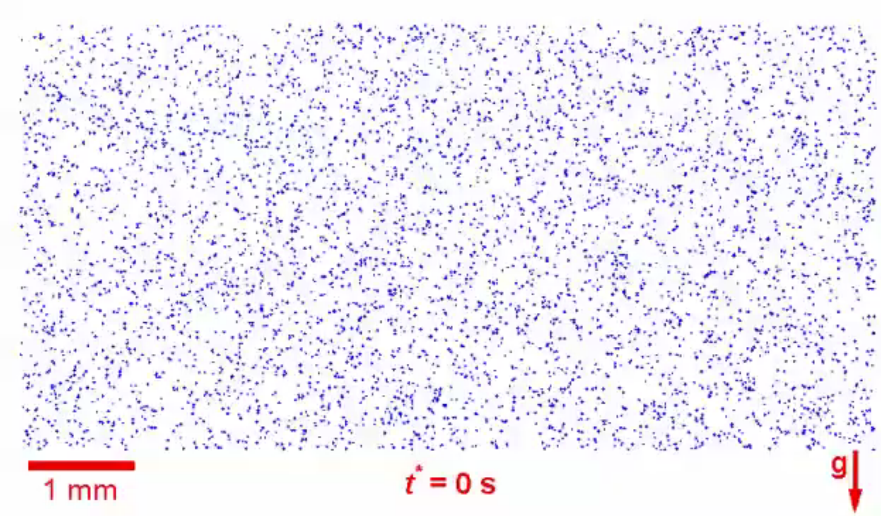
Gyrotactic focusing in (laminar) pipe flows



$$a = 0$$

$$\frac{d\mathbf{p}}{dt} = -\frac{1}{2v_o}\left[\mathbf{g} - (\mathbf{g}\cdot\mathbf{p})\mathbf{p}\right] + \frac{1}{2}\omega \times \mathbf{p}$$





JO Kessler, Nature **313**, 218 (1985)

Acceleration in turbulence

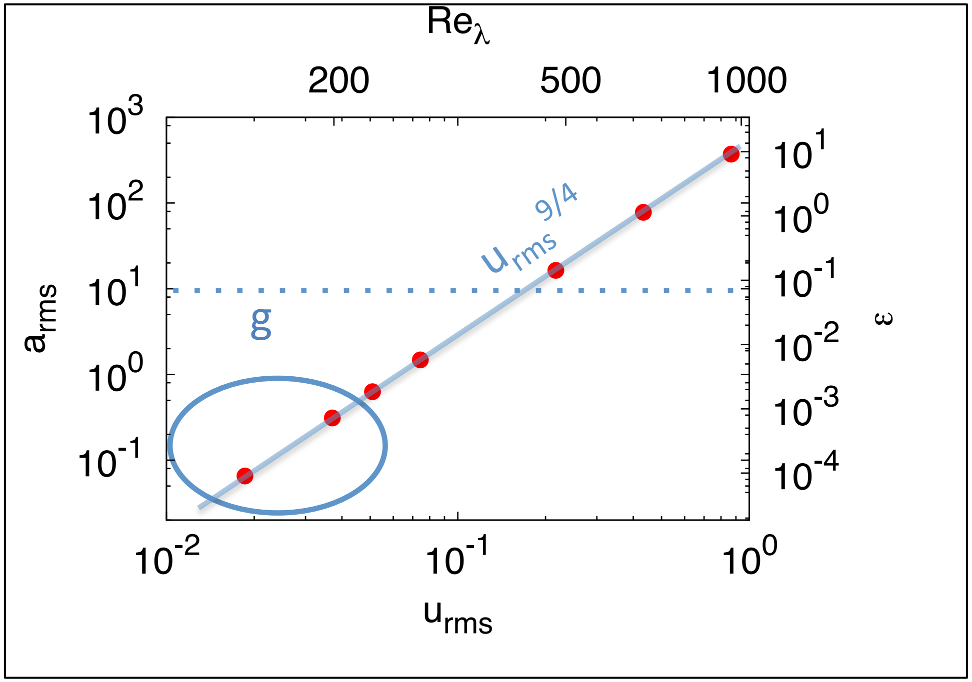
$$\langle a^2 \rangle = a_0 \epsilon^{3/2} \nu^{-1/2}$$

with $a_0 \simeq 5-6$ and $\nu_{H_2O} \simeq 10^{-6} m^2 s^{-1}$

Kinetic energy dissipation in the oceanic mixing layer $\epsilon \leq 10^{-4} m^2 s^{-3}$ which means

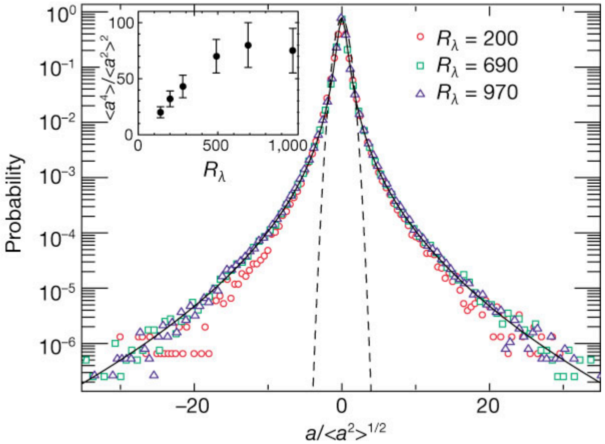
$$a_{rms} \simeq 0.1\, ms^{-2} \ll g$$

Laboratory experiments

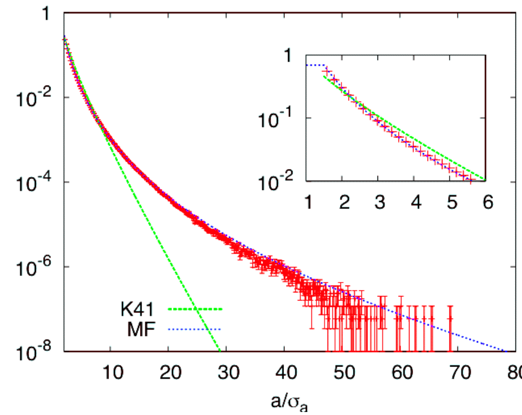


from Voth *et al*, JFM **469**, 121 (2002)

Experimental and numerical data show that local acceleration in turbulence is extremely intermittent with PDF with very wide tails



La Porta *et al*, Nature **409**, 1017 (2001)



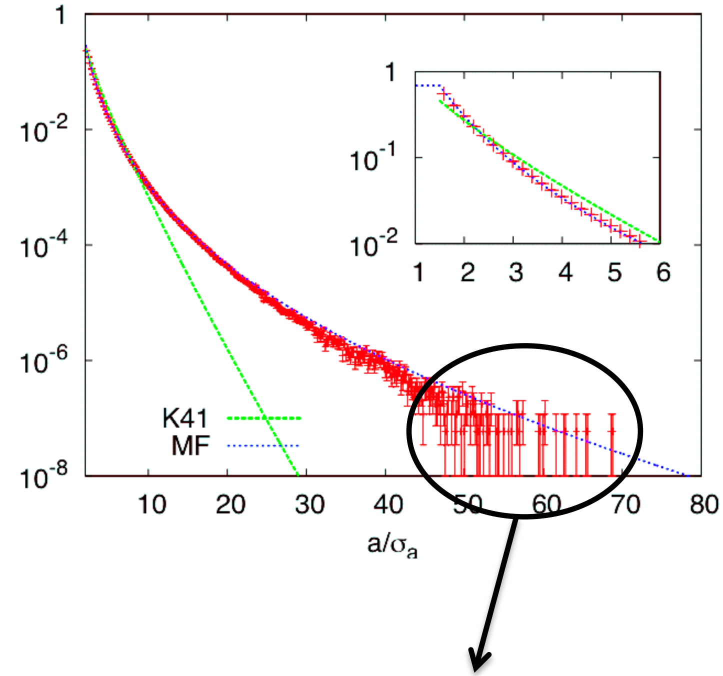
Biferale *et al*, Phys. Rev. Lett. **93**, 064502 (2004)

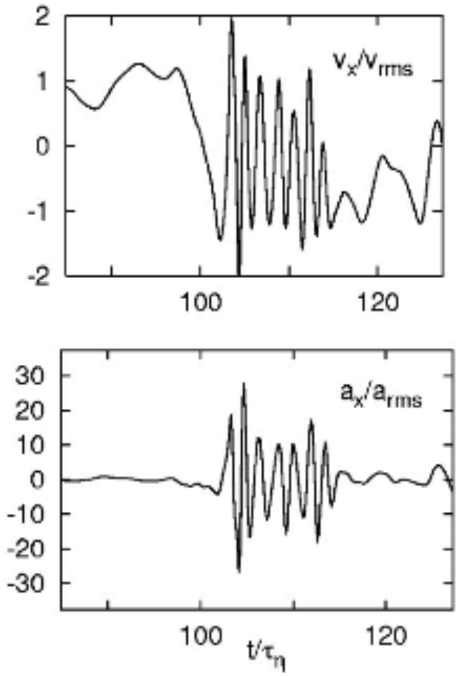
Even if $a_{rms} < g$, locally fluid acceleration can locally exceed gravity

Origin of extreme accelerations: turbulent vortices

Trapping of particles in small scale vortices

Frequency in vortex $\simeq \tau_\eta^{-1}$
Trapping time $10 - 20\tau_\eta$





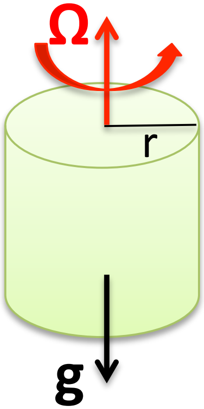
Biferale, Boffetta, Celani, Devenish, Lanotte, Toschi
Phys. Rev. Lett. **93**, 064502 (2004)

The effects of fluid accelerations: a toy model for a vortex

$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x},t) + v_s\mathbf{p}$$

$$\frac{d\mathbf{p}}{dt} = -\frac{1}{2v_o}\left[\mathbf{A} - (\mathbf{A}\cdot\mathbf{p})\mathbf{p}\right] + \frac{1}{2}\omega \times \mathbf{p} \qquad \mathbf{A} = \mathbf{g} - \mathbf{a}(\mathbf{x},t)$$

Cylinder in solid body rotation



$$\mathbf{u}(\mathbf{x}) = (-\Omega y, \Omega x, 0) \qquad \omega = (0,0,2\Omega) \qquad \mathbf{a}(\mathbf{x}) = (-\Omega^2 x, -\Omega^2 y, 0)$$

equilibrium swimming direction (stationary) $\frac{d\mathbf{p}}{dt} = 0$

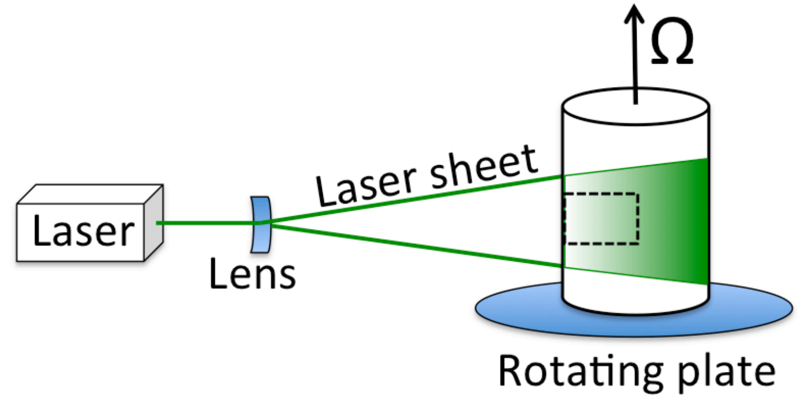
cylindrical coordinates $\begin{cases} \mathbf{p}_r = -\gamma \mathbf{r} \\ p_z = \sqrt{1-\gamma^2 r^2} \end{cases}$ $\gamma = \Omega^2/g$

gives the trajectory $r(t) = r(0)e^{-\gamma v_s t}$ cells concentrate around the axis

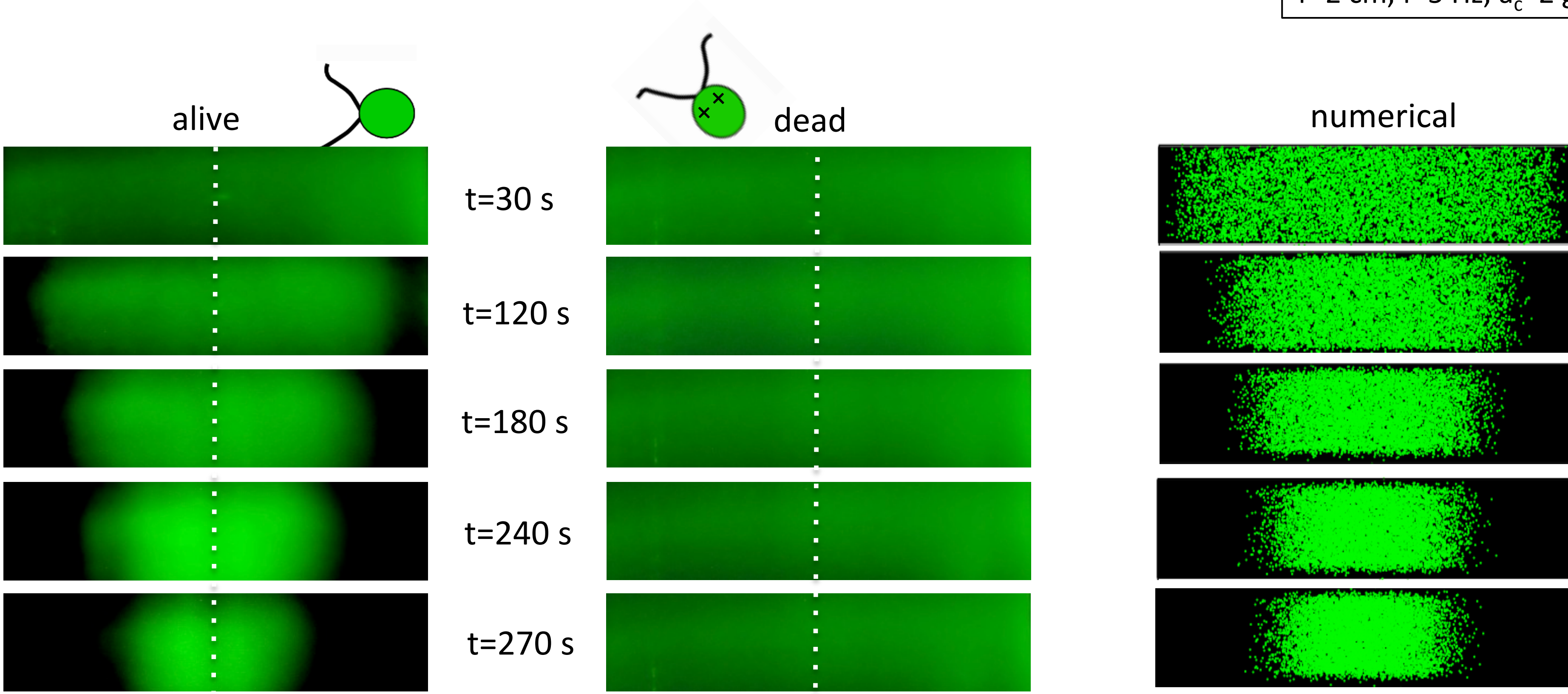
and $\mathbf{p}$ aligns asymptotically in the direction z

A toy model for a vortex

Simple experiment using solid body rotation as a proxy for a vortex.
As cells swim along local acceleration, they are expected to concentrate along the axis of rotation.



r=2 cm, f=5 Hz, $a_c \approx 2$ g



yes! but … in real turbulence ?

Simulations of turbulence

Simulation of the complete set of equations

Three dimensionless numbers

$$Re_\lambda = \frac{u_{rms}\lambda}{\nu}$$ controls the weight of turbulent acceleration $$\alpha \equiv \frac{a_{rms}}{g}$$

$$\Phi = \frac{v_s}{v_k}$$ swimming number

$$\Psi = \frac{\omega_{rms} v_o}{A_{rms}}$$ stability number

$$\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u}\cdot\nabla\mathbf{u} = -\nabla p + \nu\nabla^2\mathbf{u} + \mathbf{f}$$

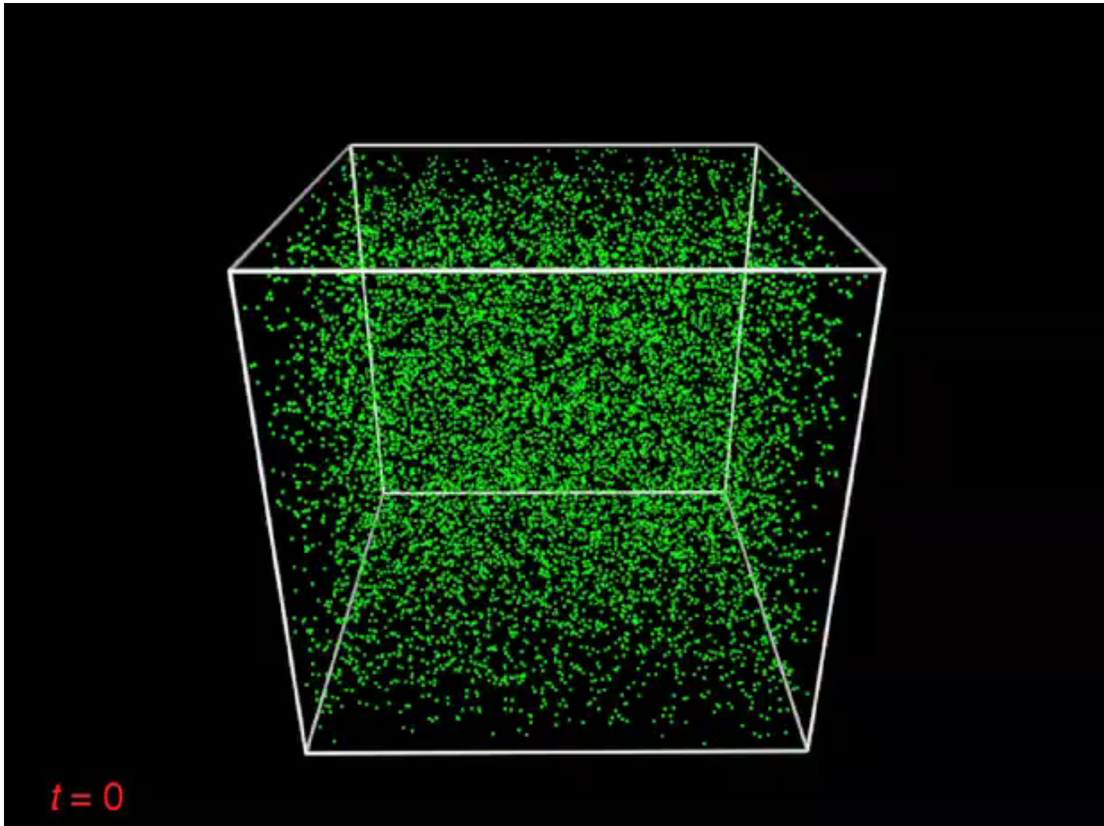
$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x},t) + v_s\mathbf{p}$$

$$\frac{d\mathbf{p}}{dt} = \frac{1}{2v_o}\left[\mathbf{A} - (\mathbf{A}\cdot\mathbf{p})\mathbf{p}\right] + \frac{1}{2}\omega\times\mathbf{p}$$

Gyrotactic swimmers as a dissipative system

$$\sum_{i=1}^{d}\left(\frac{\partial \dot{X}_i}{\partial X_i} + \frac{\partial \dot{\mathbf{p}}_i}{\partial \mathbf{p}_i}\right) = -\frac{d-1}{2v_o}\left(g\mathbf{p}_z + \mathbf{a}\cdot\mathbf{p}\right)$$

as **p** orients in the direction of local acceleration, swimming cells concentrate on a (fractal) subset of the phase space



Turbulence at small Reynolds numbers (a_{rms} << g)

Typical conditions in the ocean mixing layer $\epsilon = 10^{-7}\, m^2\, s^{-3}$

$$\eta = (\nu^3/\epsilon)^{1/4} \simeq 2\, mm$$

$$\tau_k = (\nu/\epsilon)^{1/2} \simeq 3\, s$$

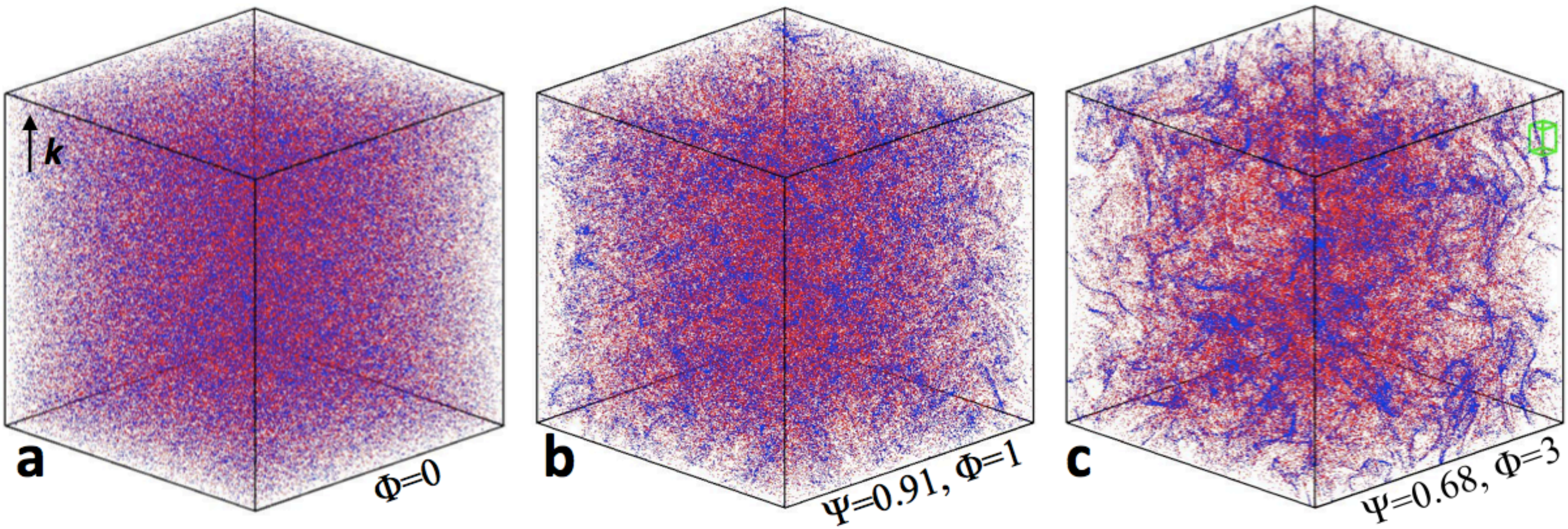
$$u_k = (\nu\epsilon)^{1/4} \simeq 0.5\, mm/s$$

$$a_{rms} = (\epsilon^3/\nu)^{1/4} \simeq 0.2\, mm/s^2$$

$$\Phi = \frac{v_s}{v_k} \simeq 0.4$$

$$\Psi = \frac{\omega_{rms} v_o}{g} \simeq 0.3$$

$Re_\lambda = 65$



$n > 2\langle n \rangle$

How clustering depends on parameters ?

Where do cells cluster ?

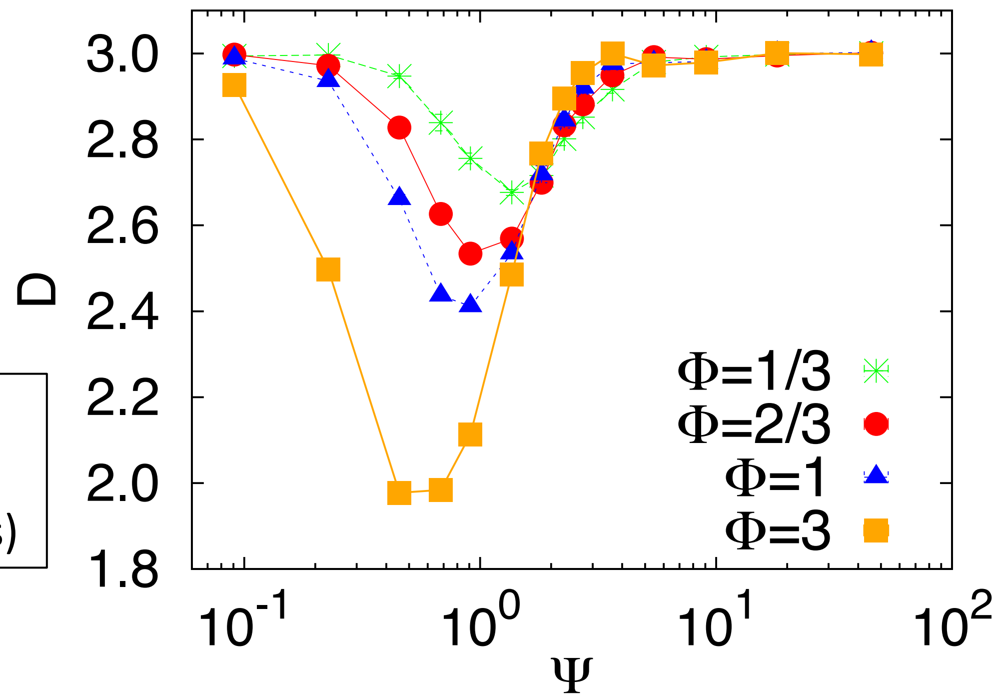
10^6 cells

Fractal clustering

$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x},t) + \Phi\mathbf{p}$$
$$\frac{d\mathbf{p}}{dt} = \frac{1}{2\Psi}\left[\mathbf{k} - (\mathbf{k}\cdot\mathbf{p})\mathbf{p}\right] + \frac{1}{2}\omega\times\mathbf{p}$$

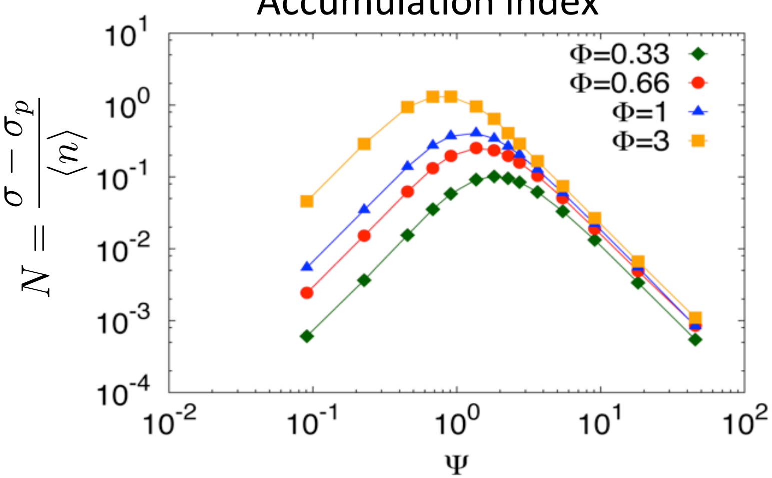
Homogeneous distribution in both limits $\Psi \to 0$ (uniform vertical swimming) and $\Psi \to \infty$ (swimming in random directions)

Correlation dimension



Clustering is maximum (D minimum) for $\Psi \simeq 1$ and increases with Φ

Accumulation index



$$N = \frac{\sigma - \sigma_p}{\langle n \rangle}$$

$$\sigma = \left(\langle n^2\rangle - \langle n\rangle^2\right)^{1/2}$$

swimming number	$\Phi = \frac{v_s}{v_k}$
stability number	$\Psi = \frac{\omega_{rms} v_o}{g}$

How clustering depends on Ψ

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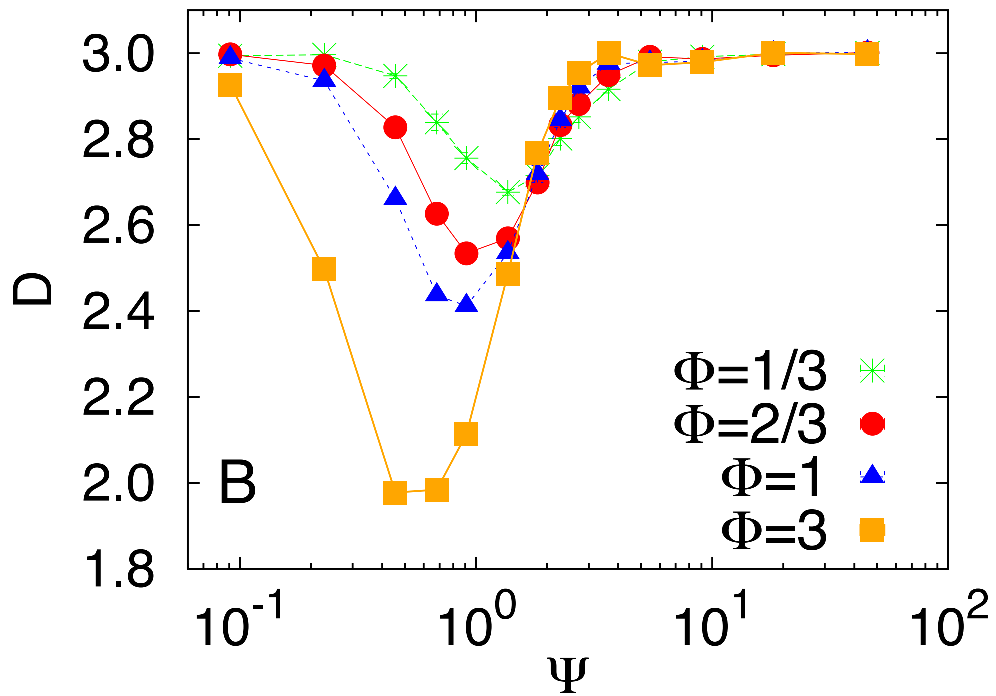

For small Ψ, at first order we have

$$\mathbf{p} = (\Psi\omega_y, -\Psi\omega_x, 1)$$

passive tracers in an effective velocity field

$$\mathbf{v} = \mathbf{u} + \Phi\mathbf{p}$$

with divergence

$$\nabla\cdot\mathbf{v} = \Phi\nabla\cdot\mathbf{p} = -\Psi\Phi\nabla^2 u_z$$

Fractal codimension $3 - D \propto (\nabla\cdot\mathbf{v})^2$

and therefore $D = 3 - a(\Phi\Psi)^2$

A weakly compressible velocity field

$$\boldsymbol{v} = \boldsymbol{u} + \delta\boldsymbol{w}$$

with $\nabla\cdot\boldsymbol{u} = 0 \quad \nabla\cdot\boldsymbol{w} \neq 0$

tracers cluster on a fractal set with codimension given by $d - D_2 \simeq \delta^2$

G Falkovich, A Fouxon, MG Stepanov, *Nature* **419**, 151-154 (2002).
I Fouxon, *Phys. Rev. Lett.* **108**, 134502 (2012).

How clustering depends on Ψ

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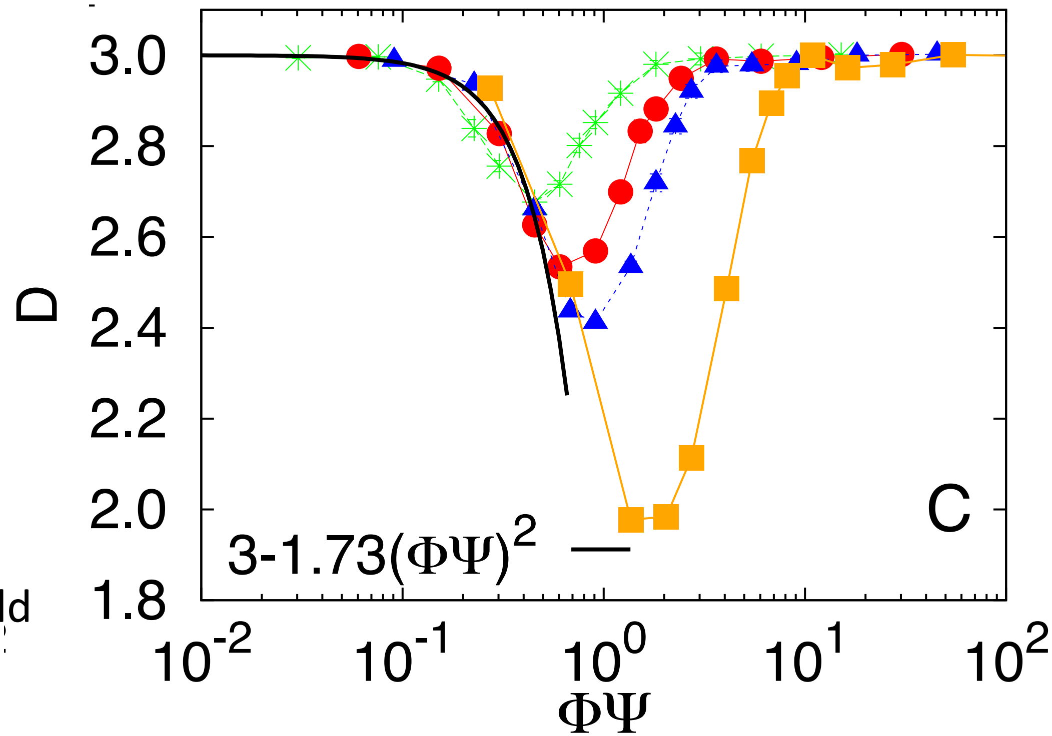

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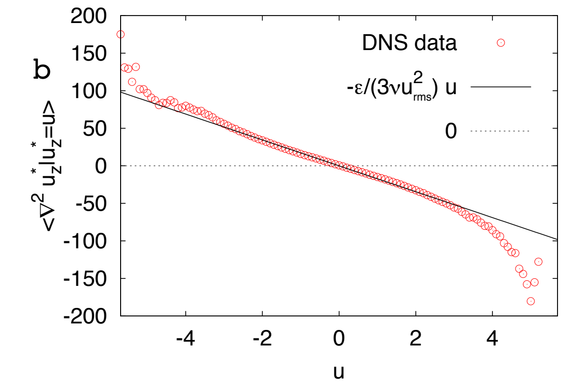
G Falkovich, A Fouxon, MG Stepanov, *Nature* **419**, 151-154 (2002).
I Fouxon, *Phys. Rev. Lett.* **108**, 134502 (2012).

Where do cells cluster ?

Swimmers as tracers transported by a weakly compressible flow

$$\nabla \cdot \mathbf{v} = \Phi \nabla \cdot \mathbf{p} = -\Psi \Phi \nabla^2 u_z$$

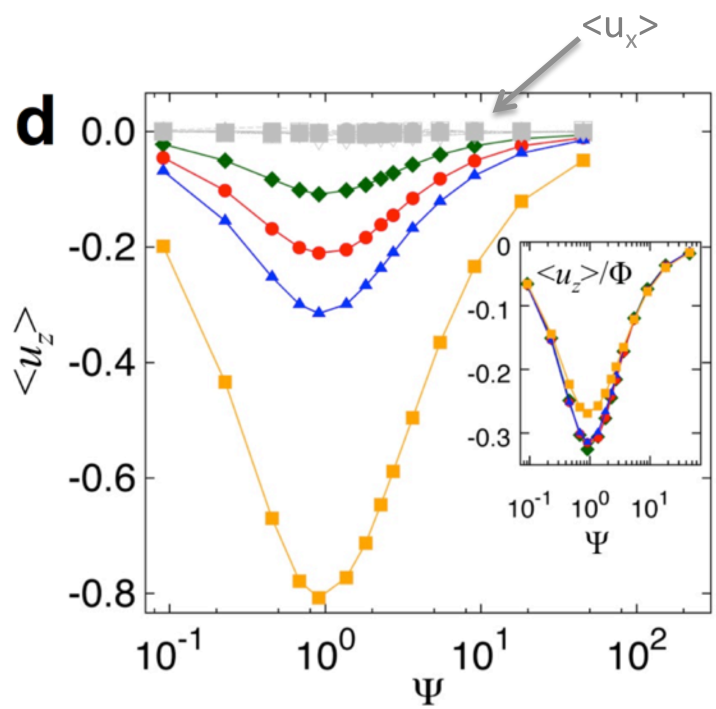
concentrate on regions where $\nabla^2 u_z > 0$

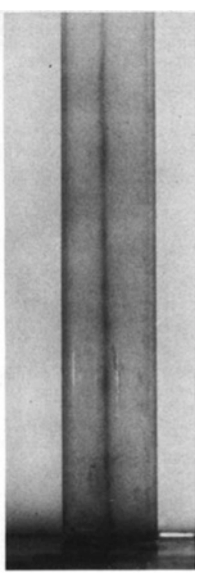


In homogeneous, isotropic turbulence

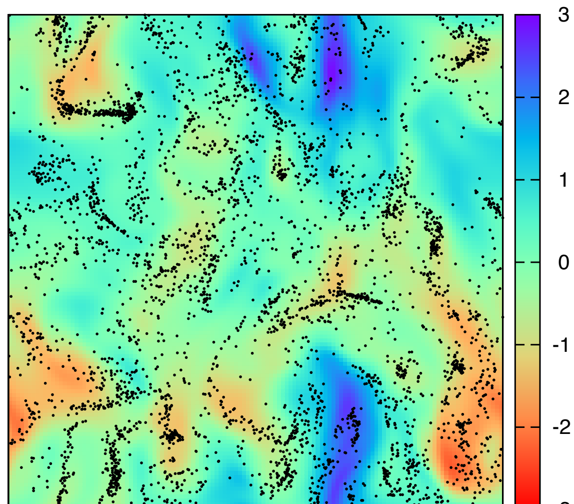
$$\epsilon = \nu \langle (\nabla \mathbf{u})^2 \rangle = -3\nu \langle u_z \nabla^2 u_z \rangle$$

and therefore $\nabla^2 u_z > 0$ means $u_z < 0$





Swimming cells accumulate in downwelling regions, where $u_z < 0$



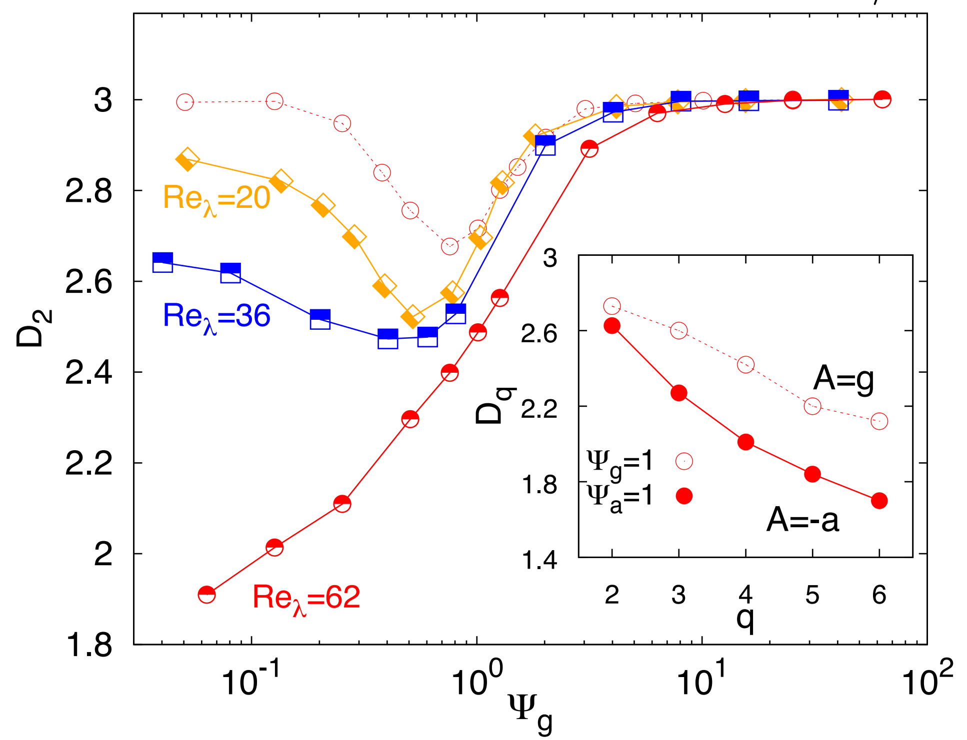
Clustering at increasing Reynolds numbers

$\Phi = 1/3$

- Clustering increases with Reynolds
- Minimum of D disappears for large Re (when α≈1)

$$\alpha \equiv \frac{a_{rms}}{g}$$

$\alpha = 0.34$	$Re_\lambda = 20$
$\alpha = 0.50$	$Re_\lambda = 36$
$\alpha = 0.84$	$Re_\lambda = 62$



Turbulent accelerations enhance cell clustering

At small Ψ the swimming direction aligns towards strong acceleration regions which are not uniform

What is the role of fluid acceleration ?

Clustering in the limit g=0

$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x},t) + \Phi\mathbf{p}$$

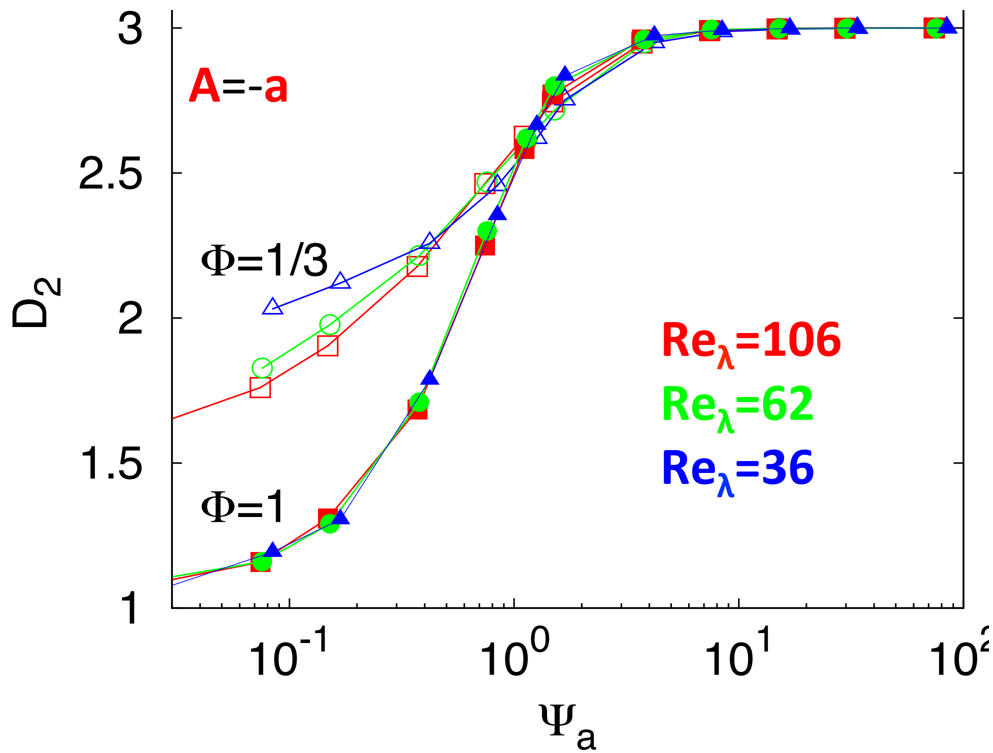
$$\frac{d\mathbf{p}}{dt} = \frac{1}{2\Psi}\left[\mathbf{a} - (\mathbf{a}\cdot\mathbf{p})\mathbf{p}\right] + \frac{1}{2}\omega \times \mathbf{p}$$

To understand the role of acceleration we consider the case $a_{rms} \gg g$ and take $g=0$

clustering increases with cell stability i.e when $\Psi \ll 1$

clustering increases with swimming speed i.e with Φ

weak (if any) dependence on Re_λ



what is driving clustering? where do cells go?

Predictions for small Ψ

$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x},t) + \Phi\mathbf{p}$$

$$\frac{d\mathbf{p}}{dt} = \frac{1}{2\Psi}\left[\mathbf{a} - (\mathbf{a}\cdot\mathbf{p})\mathbf{p}\right] + \frac{1}{2}\omega\times\mathbf{p}$$

$\Psi \ll 1$, **p** is mainly aligned with **a**.

Effective velocity for swimmers $\mathbf{v} \simeq \mathbf{u} + \Phi\hat{\mathbf{a}}$

a compressible field with

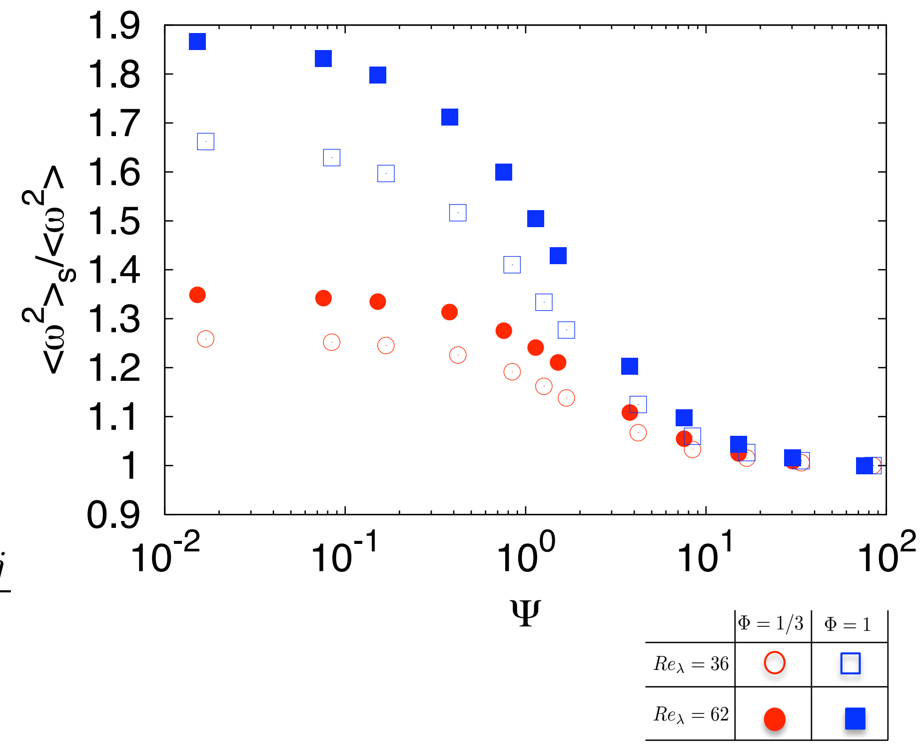
$$\nabla\cdot\mathbf{v} \simeq \Phi\nabla\cdot\hat{\mathbf{a}}$$

Clearly $\nabla\cdot\hat{\boldsymbol{a}} \not\propto \nabla\cdot\boldsymbol{a}$ however their sign is strongly correlated. Swimmers accumulate where

$$\nabla\cdot\mathbf{a} < 0$$

$$\boldsymbol{\nabla}\cdot\boldsymbol{a} = \sum_{ij}(\hat{S}_{ij}^2 - \hat{\Omega}_{ij}^2)$$

$$\hat{S}_{ij} = \frac{\partial_j u_i + \partial_i u_j}{2} \qquad \hat{\Omega}_{ij} = \frac{\partial_j u_i - \partial_i u_j}{2}$$

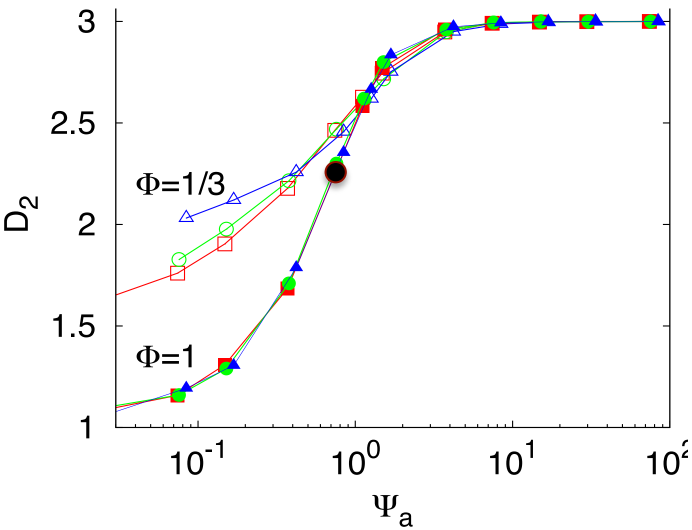


$\nabla\cdot\mathbf{a} < 0$ corresponds to large vorticity regions

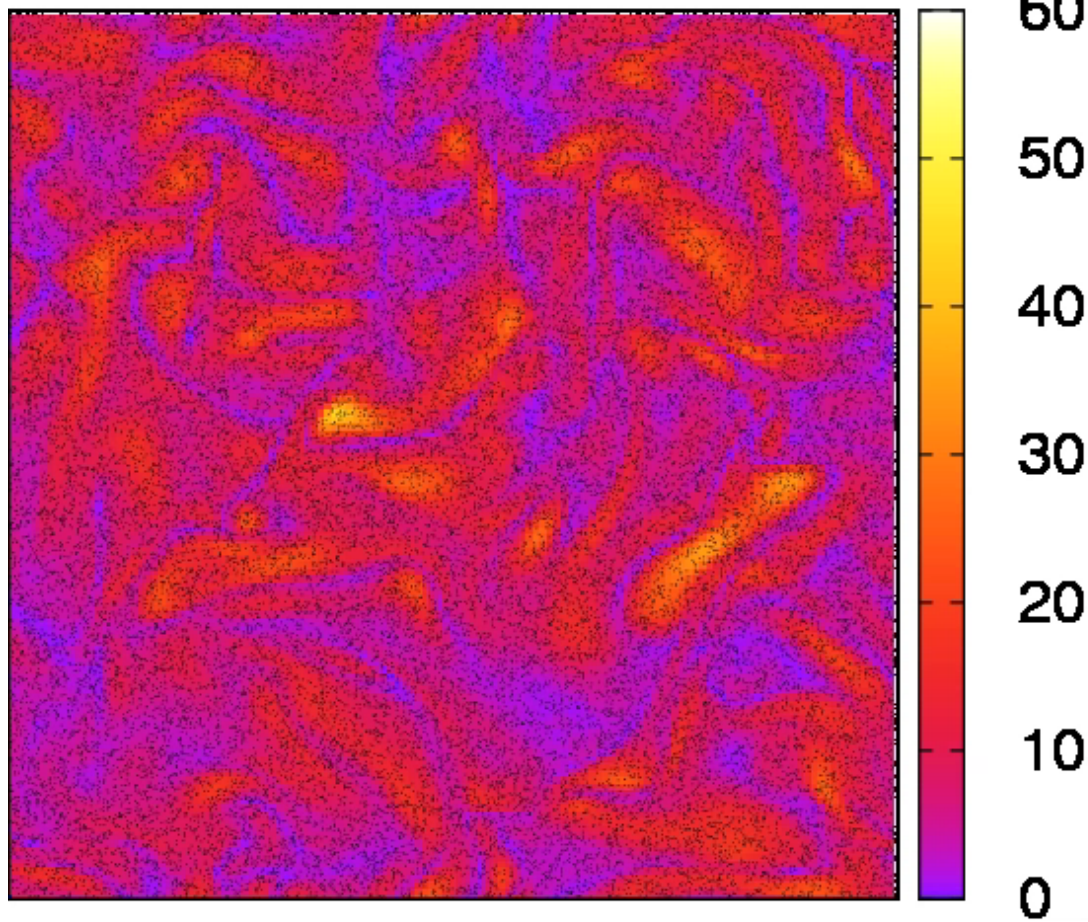
Swimmers concentrate in vortices (like light particles)

$\langle \dots \rangle_s$ average at swimmer positions

Swimmers concentrate in vortices



$$Re_\lambda = 62$$
$$\Psi = 1.5$$
$$\Phi = 1$$



Section of $\ln \frac{|\omega|}{\omega_{rms}}$

A prediction for D_2

Clustering is more efficient for faster swimmers

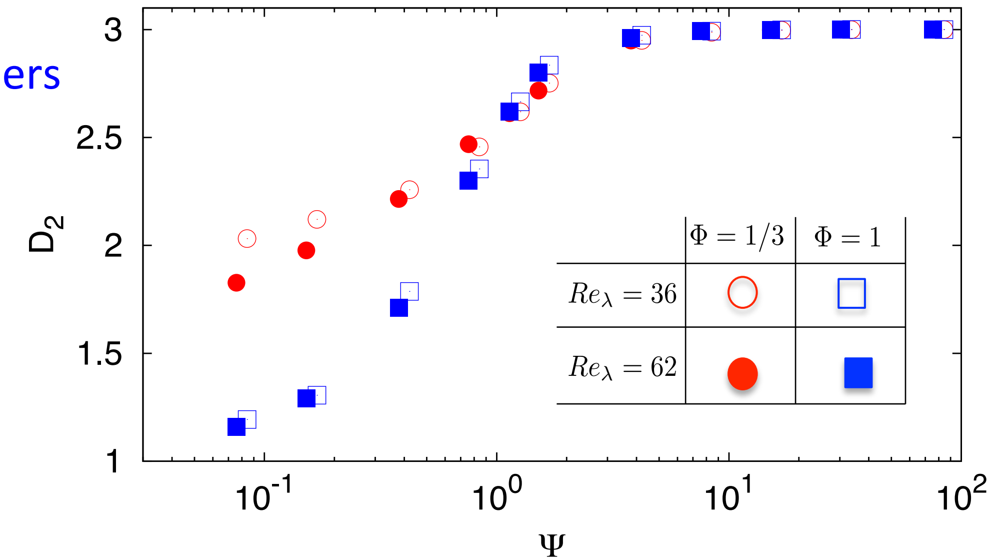
How does D_2 depends on Φ ?

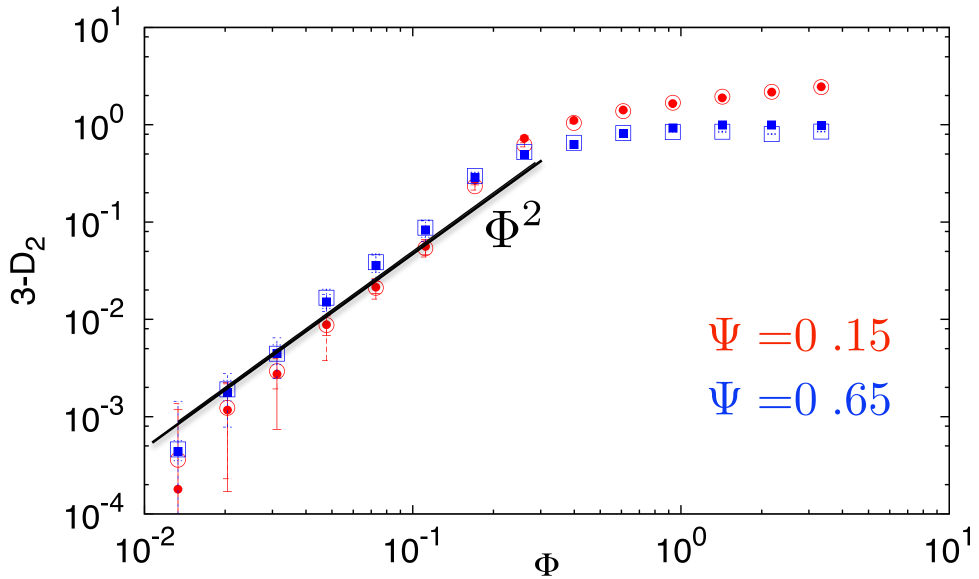
Effective velocity for swimmers

$$\mathbf{v} \simeq \mathbf{u} + \Phi\hat{\mathbf{a}}$$

with $\nabla \cdot \boldsymbol{v} \propto \Phi \nabla \cdot \hat{\boldsymbol{a}}$

$$3 - D_2 \simeq \Phi^2$$

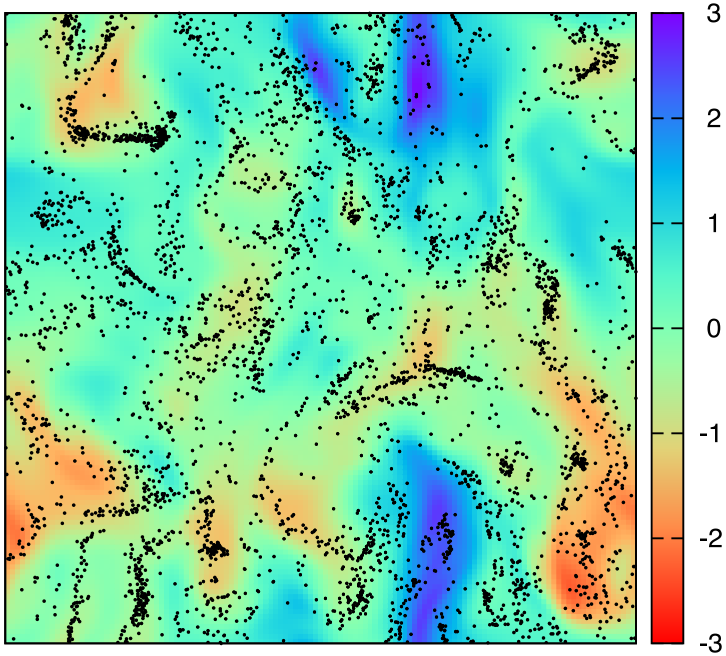




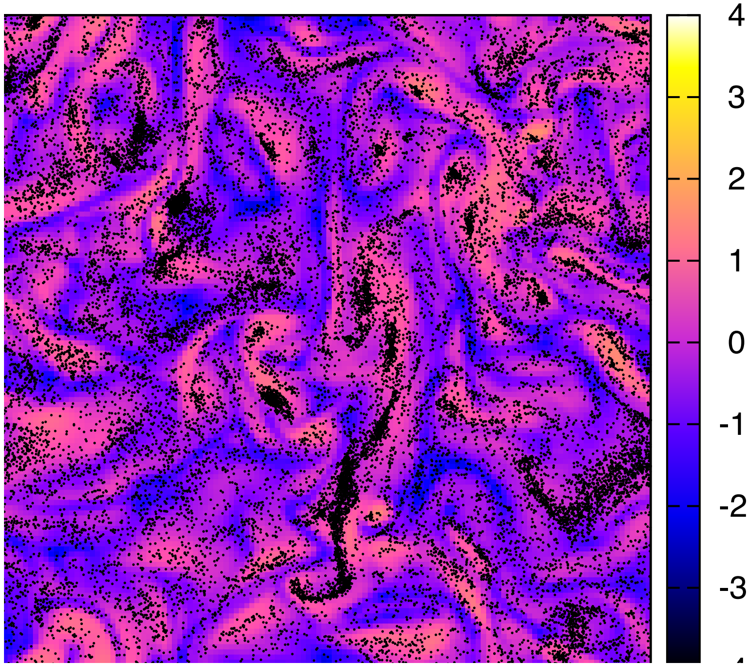
Conclusions

Combination of swimming and turbulence generates small scale patchiness in plankton distribution

Small Reynolds numbers (ocean)



Large Reynolds numbers (laboratory)



accumulation in downwelling regions

accumulation in high vorticity regions

Effects of clustering on nutrient uptake and predator feeding