

CLUSTERING OF GYROTACTIC ALGAE IN A TURBULENT OCEAN

Filippo De Lillo

Dipartimento di Fisica and INFN, Università di Torino

Turbulence drives microscale patches of motile phytoplankton

Durham, *et al.* Nature Comm. **4**, 2148 (2013).

Turbulent Fluid Acceleration Generates Clusters of Gyrotactic Microorganisms

De Lillo, *et al.* Phys. Rev. Lett. **112**, 044502 (2014).

Gyrotactic trapping in laminar and turbulent Kolmogorov flow

Santamaria, *et al.*, Phys. Fluids **26**, 111901 (2014).



Flowing Matter – COST Action MP1305

Flowing Matter – COST Action MP1305

FLOWING MATTER
ACROSS THE SCALES
ROME
XXIV-XXVII MARCH
A.D. MMXV

A.D. MMXV

PEOPLE INVOLVED

FD, Guido Boffetta

Dipartimento di Fisica and INFN, Università di Torino

Massimo Cencini

ISC-CNR Roma

for small scale clustering (1st part)

Roman Stocker, Michael Barry

*Ralph M. Parsons Laboratory, Department of Civil and
Environmental Engineering, MIT*

William Durham

Department of Zoology, University of Oxford

Eric Climent

*Institut de Mécanique des Fluides, Université de Toulouse
INPT-UPS-CNRS*

for thin gyrotactic trapping (2nd part)

Francesco Santamaria

Dipartimento di Fisica and INFN, Università di Torino



...and Chlamy

MOTIVATIONS

Phytoplankton is composed by one-celled organisms able to perform phototaxis

It is at the basis of the oceanic food web

It is the source of about 50% of the oxygen “produced” on the earth

It is fundamental for carbon cycle

Many phytoplankters are able to swim as a way to control their position in the water column
(some others control their buoyancy)

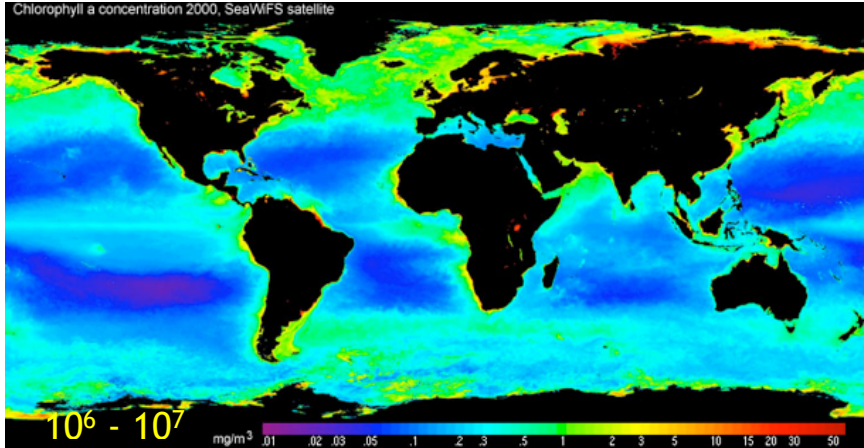
Doing so allows them to stay in the “photic” layer...

Phytoplankton is “patchy” at several scales which affects:

- exploitation of nutrients
- predation
- mating (when reproducing sexually)
- access to light (mutual shading...)

LARGE SCALE PATCHINESS

Plankton is “patchy” over many scales



Phytoplankton (chlorophyll) distribution on a global scale

Large scale



“ecological” causes influenced by flow (e.g., presence and distribution of nutrients)

Still, some large formations may have other origins (more about this later...)



Algal blooms (*N. scintillans* in NZ)

SMALL SCALE PATCHINESS

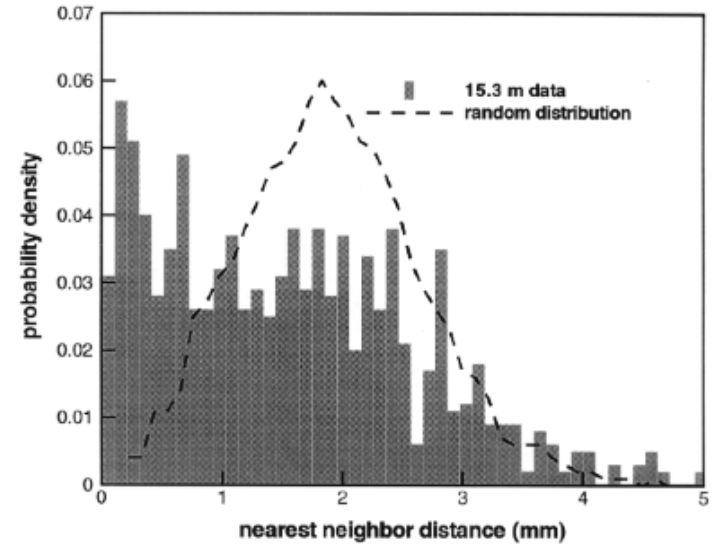


Figure 10. Measured nearest-neighbour distances and expected values from a random distribution.

E.Malkiel, O.Alquaddoomi, J.Katz
Meas. Sci. Technol. 10 (1999)

Patchiness at mm/cm-scale

Motile phytoplankton **more patchy** than non-motile one

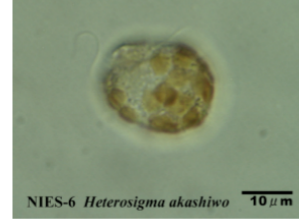
A fluid-dynamic explanation?

See also F Toschi’s and I Pagonabarraga’s works (and talks in this conference) for related phenomena

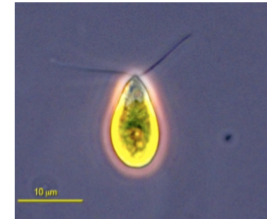
MODEL GYROTACTIC ALGAE

- “bottom heavy” swimmers, e.g. *Chlamydomonas*
- dilute -> no interaction, no feed-back on the fluid
- Translational and rotational diffusion negligible
- Modulus of the swimming velocity constant

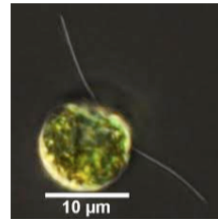
Heterosigma akashiwo



Dunaliella tertiolecta



Chlamydomonas reinhardtii

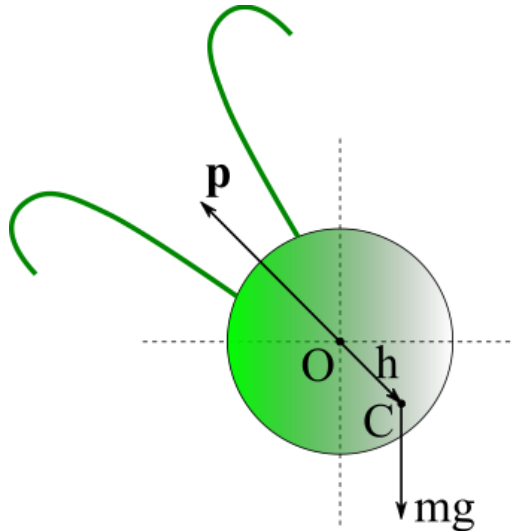


$$\frac{d\mathbf{X}}{dt} = \mathbf{u}(\mathbf{X}, t) + v_s \mathbf{p}$$

$$\frac{d\mathbf{p}}{dt} = \frac{1}{2B} \left[\hat{\mathbf{k}} - (\hat{\mathbf{k}} \cdot \mathbf{p}) \mathbf{p} \right] + \frac{1}{2} \boldsymbol{\omega} \times \mathbf{p} \quad |\mathbf{p}| = 1$$

GRAVITAXIS

fluid
vorticity



$$v_s \simeq 100 \mu\text{m/s}$$

$$B = \frac{3\nu}{hg} \simeq 1 \div 6 \text{ s}$$

ν kinematic viscosity

g gravitational acceleration

JO Kessler (Nature 1985)

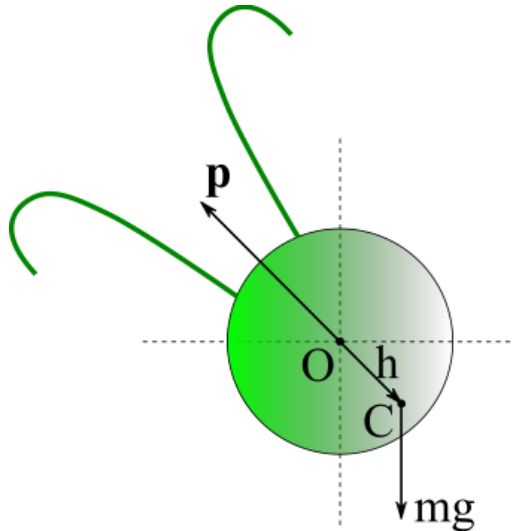
T Pedley and JO Kessler (Annu. Rev. Fluid. Mech. 1992)

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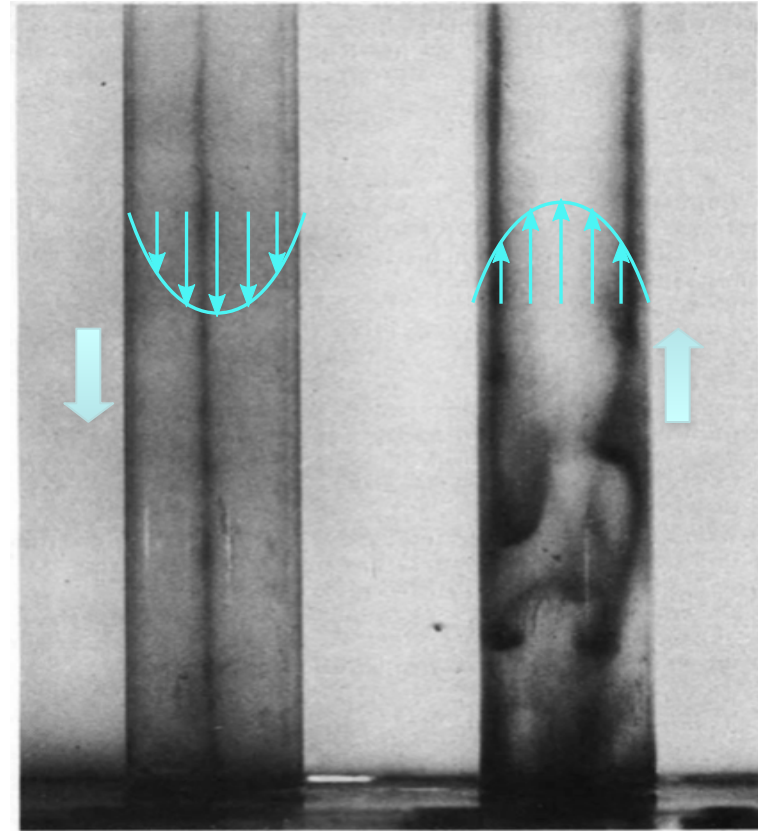


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JO Kessler (Nature 1985)

T Pedley and JO Kessler (Annu. Rev. Fluid. Mech. 1992)



Gyrotactic focusing in pipe flows

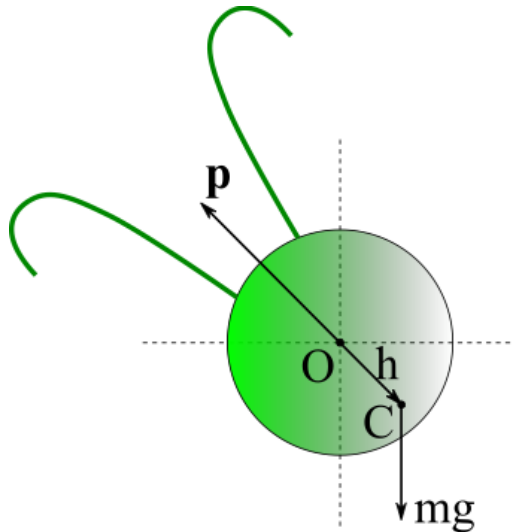
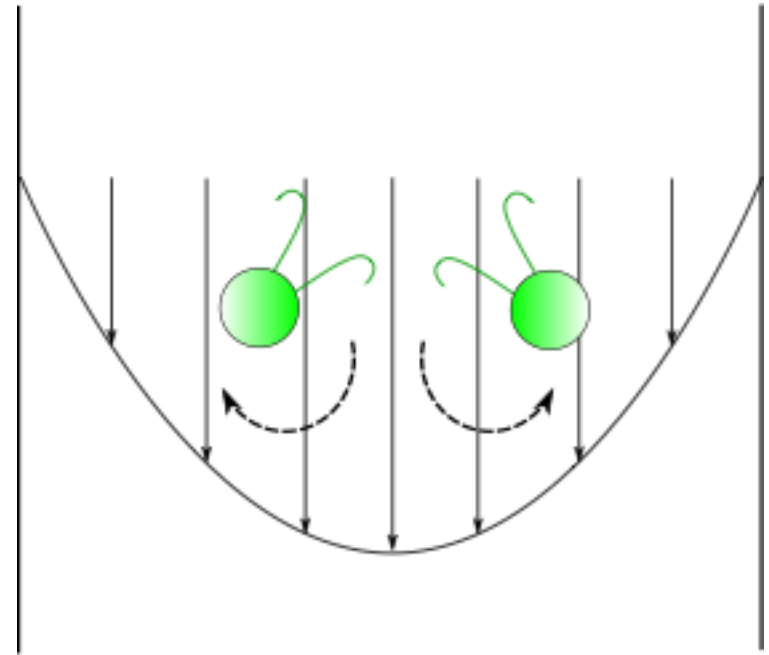
JO Kessler, Nature 313, 218 (1985)

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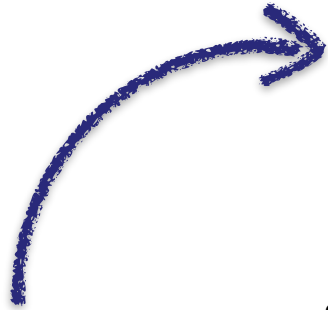
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IN THIS TALK...



Small scale patchiness

scales: mm to cm

Role of
turbulence in:

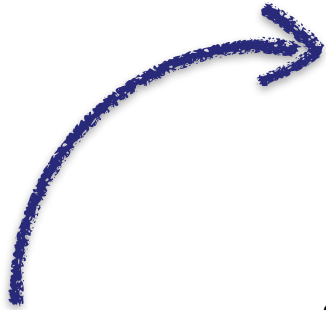


Thin Phytoplankton Layers (formation and dissolution)

scales: some 10 cm to some m
vertically

up to some km
horizontally

IN THIS TALK...



Small scale patchiness

scales: mm to cm

**Role of
turbulence in:**



**Thin Phytoplankton Layers
(formation and dissolution)**

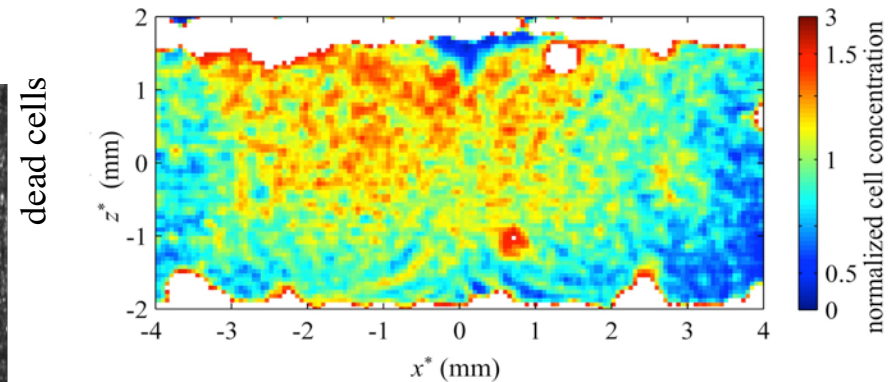
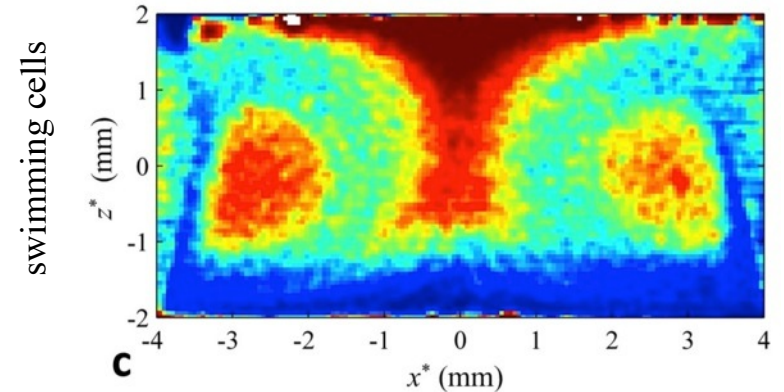
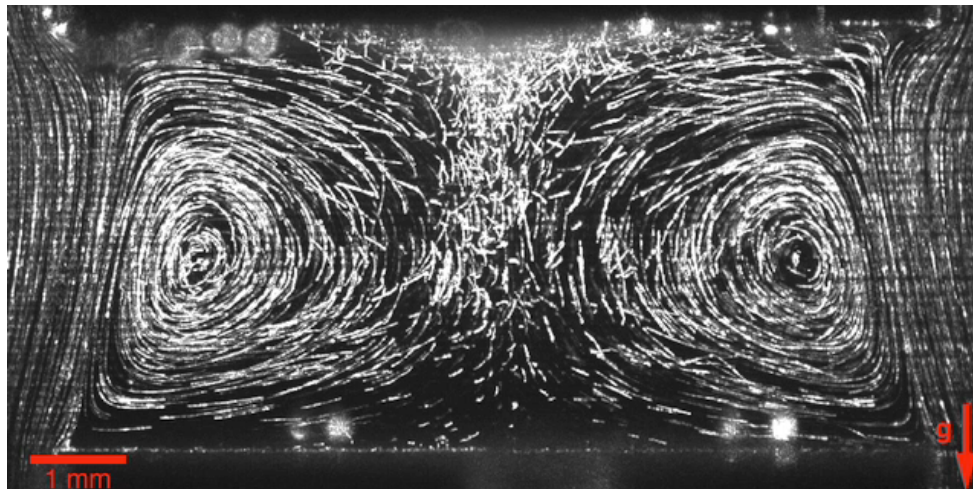
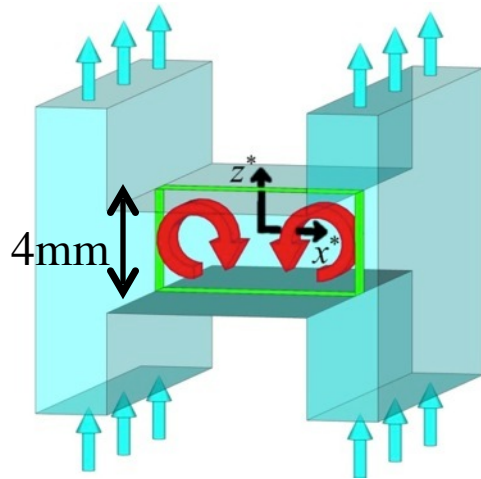
scales: some 10 cm to some m
vertically

up to some km
horizontally

EXPERIMENT IN VORTICAL FLOW

Durham *et al.* Nature Comm. **4**, 2148 (2013)

Steady vortical flow in microfluidic apparatus (at MIT) Density of *Heterosigma akashiwo*



Cells accumulate in the downwelling region and slightly in the vortex cores

numerical simulation

What happens in real turbulent flows ?

DIRECT NUMERICAL SIMULATIONS

Durham *et al.* Nature Comm. **4**, 2148 (2013)

Simulation of the complete set of equations
Resolutions up to 256^3

Three dimensionless numbers

$$\text{Re} = \frac{UL}{\nu} \quad \Phi = \frac{v_s}{u_\eta} \quad \Psi = B\omega_{\text{rms}}$$

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

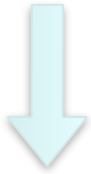
$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(\mathbf{x}, t) + v_s \mathbf{p}$$

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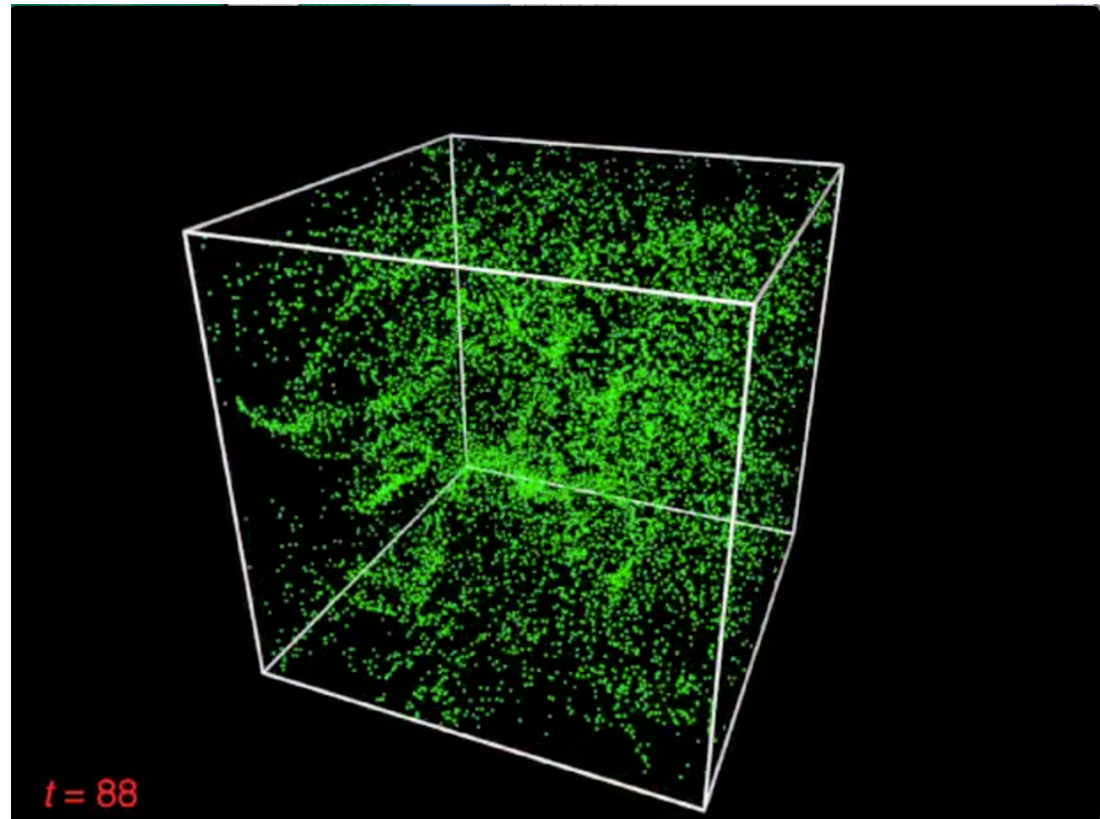
A dissipative dynamical system

Phase space contraction rate

$$\sum_{i=1}^d \frac{\partial \dot{X}_i}{\partial X_i} + \frac{\partial \dot{p}_i}{\partial p_i} = -\frac{d-1}{2v_o} gp_z$$



Clustering on a **fractal set**



DIRECT NUMERICAL SIMULATIONS

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

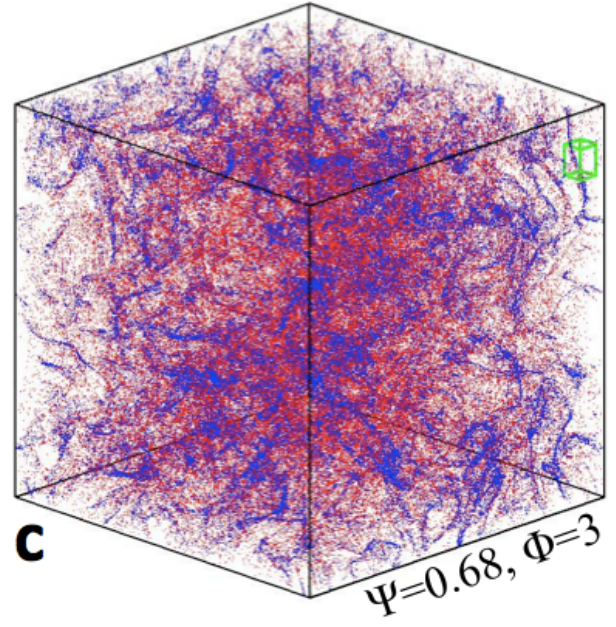
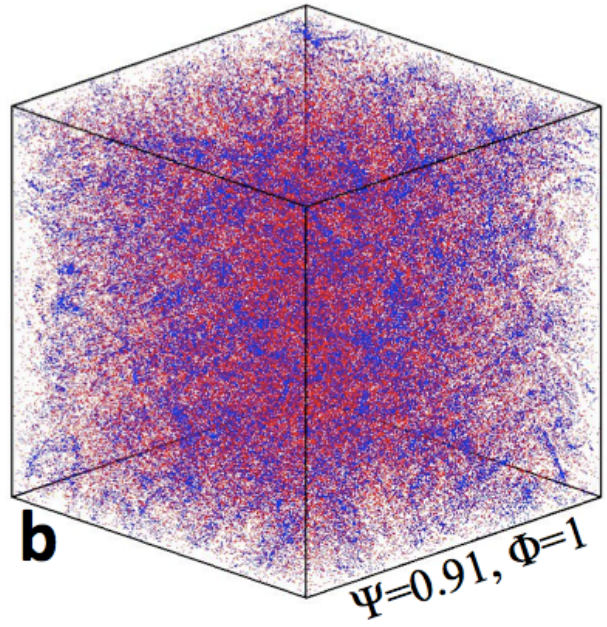
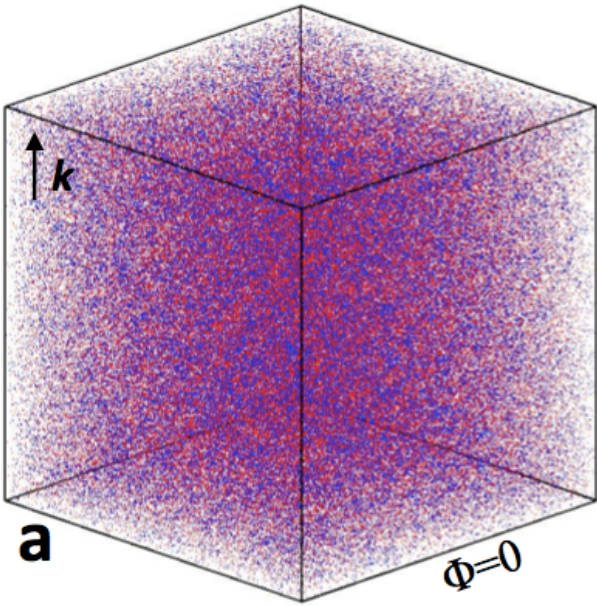
$$\eta = (\nu^3/\epsilon)^{1/4} \simeq 2 \text{ mm}$$

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

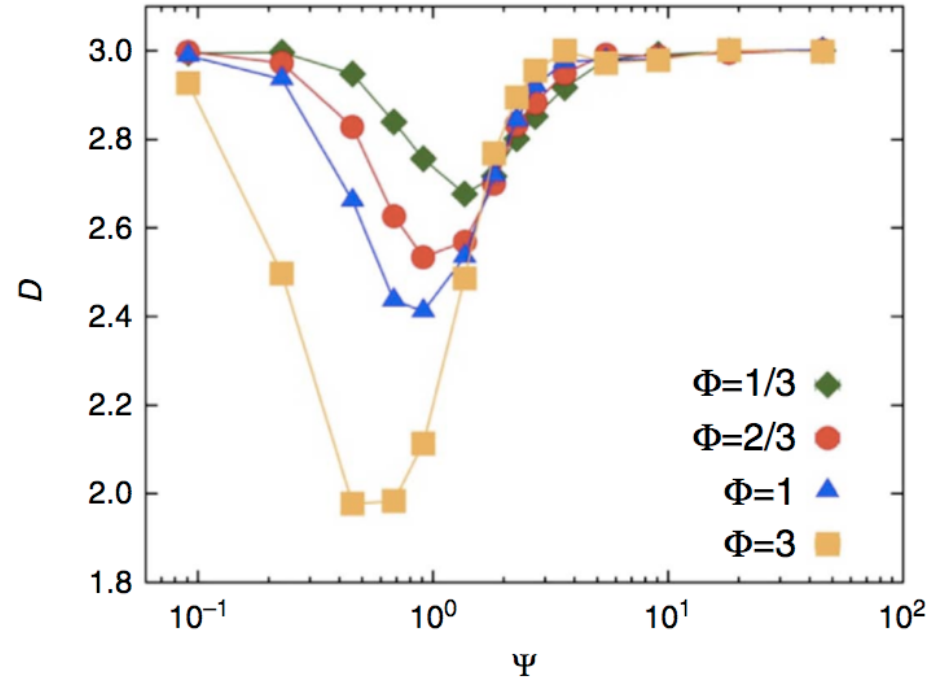
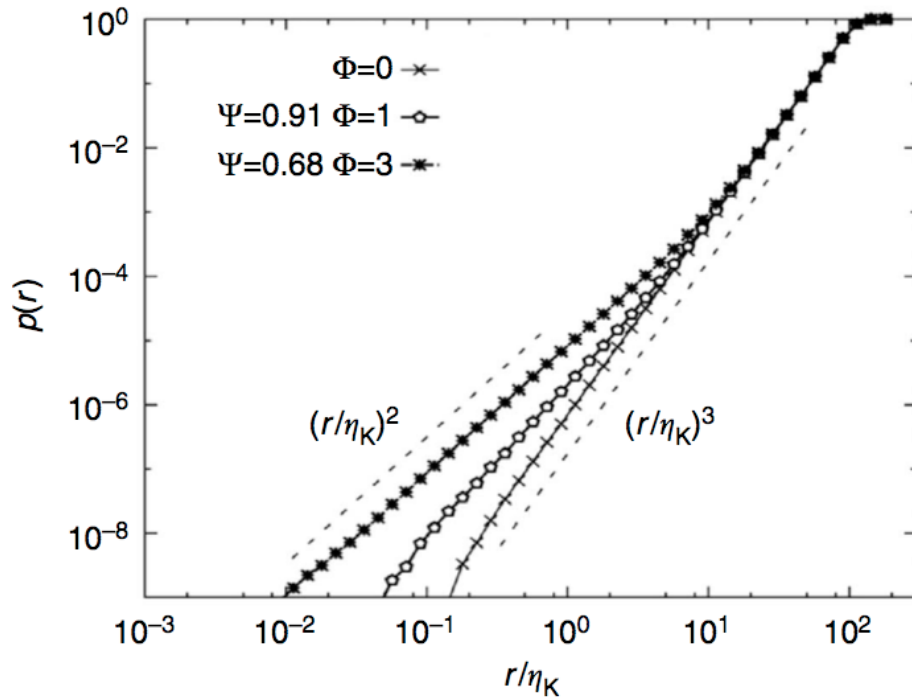
$$u_k = (\nu\epsilon)^{1/4} \simeq 0.5 \text{ mm/s}$$

$$\Phi = \frac{v_s}{u_\eta} \simeq 0.4$$
$$\Psi = \omega_{\text{rms}} B \simeq 0.3$$

$Re_\lambda = 65$
 10^6 cells
 $n > 2\langle n \rangle$



FRACTAL CLUSTERING



$p(r)$: probability to have two cells closer than r

$p(r) \sim r^D$, D : correlation dimension

Clustering is maximum where D is minimum

$$\Phi = \frac{v_s}{u_\eta}$$

$$\Psi = B\omega_{\text{rms}}$$

FRactal Clustering

D : correlation dimension

Clustering is maximum (D minimum)

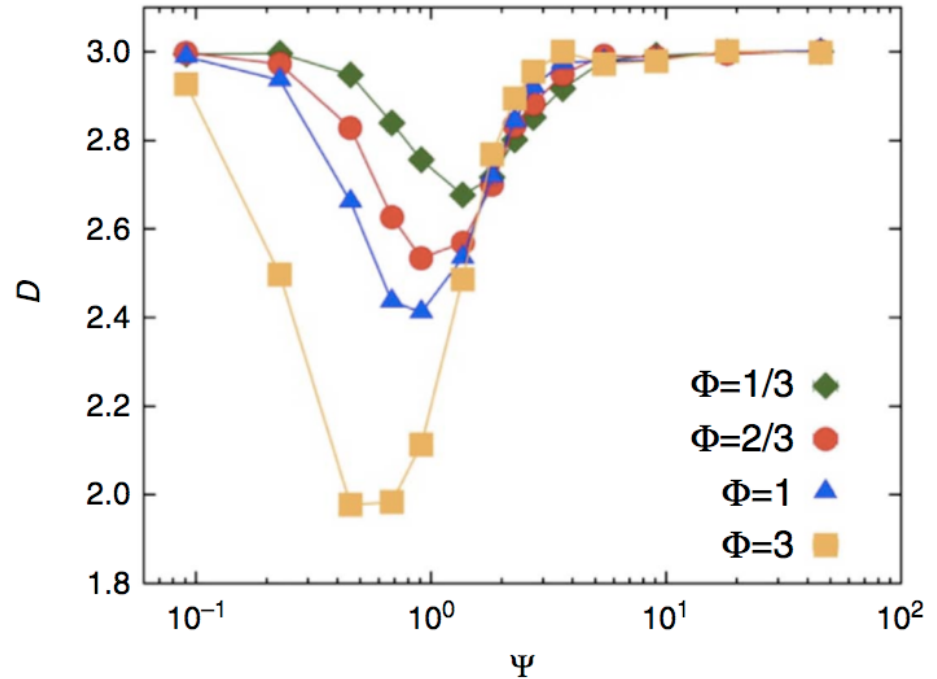
for $\Psi \simeq 1$ and increases with Φ

Homogeneous distribution in both limits

$\Psi \rightarrow 0$ (vertical swimming)

and

$\Psi \rightarrow \infty$ (random directions)



$$\Phi = \frac{v_s}{u_\eta}$$

$$\Psi = B\omega_{\text{rms}}$$

See also Bernhard Mehlig's talk and his paper

K. Gustavsson, *et al.* arXiv:1501.02386 [physics.flu-dyn] (2015)

PREDICTION FOR SMALL Ψ (fast orientation)

Dimensionless form of equations for swimmers

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

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

For small Ψ , at first order we have

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

passive tracers in an effective velocity field

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

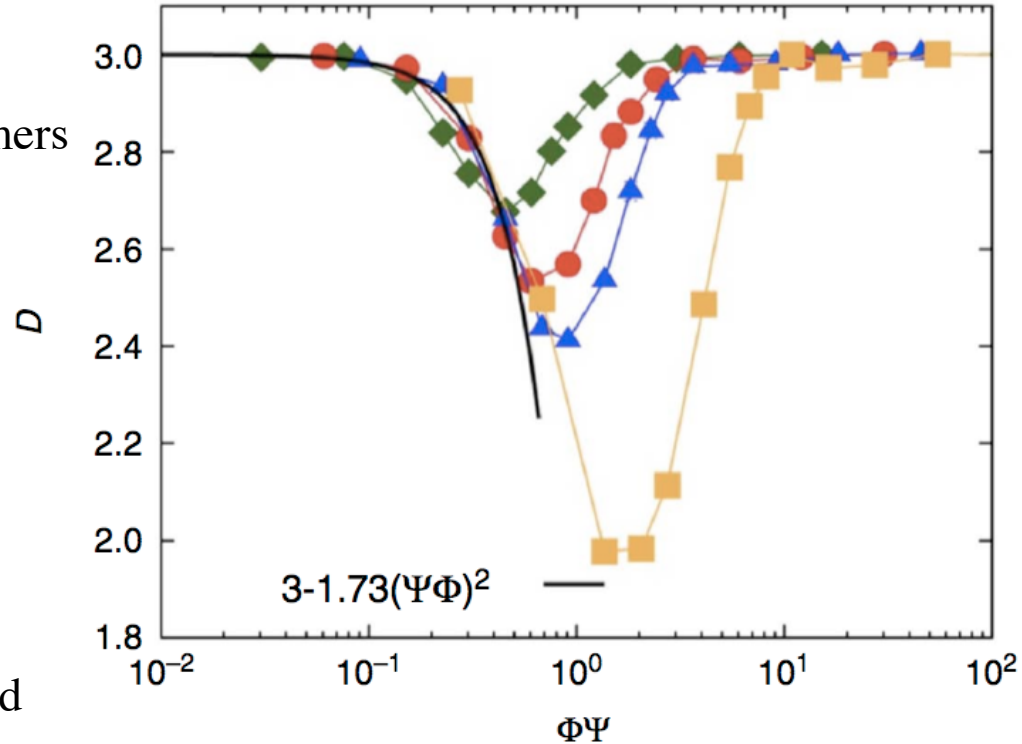
with divergence

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

Fractal codimension
and therefore

$$3 - D \propto (\Phi \Psi)^2$$

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



For a weakly compressible flow

$$\mathbf{v} = \mathbf{u} + \alpha \mathbf{w} \quad \nabla \cdot \mathbf{w} \neq 0$$

$$\nabla \cdot \mathbf{u} = 0$$

$$d - D \propto \alpha^2$$

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 \mathbf{v}

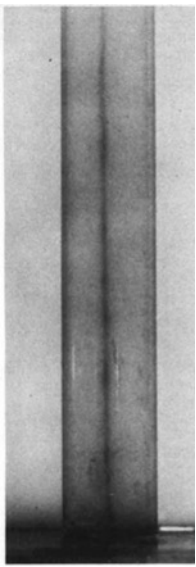
$$\nabla \cdot \mathbf{v} = \Phi \nabla \cdot \mathbf{p} = -\Psi \Phi \nabla^2 u_z$$

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

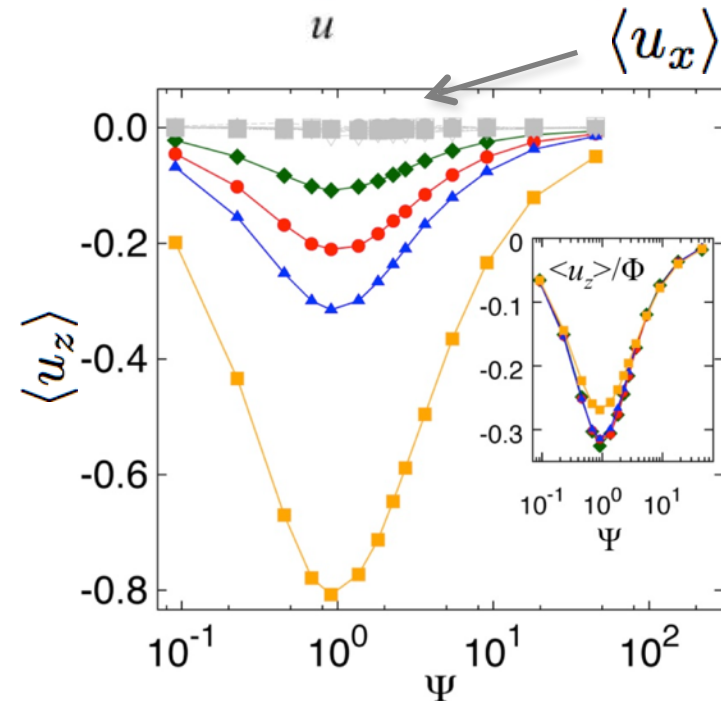
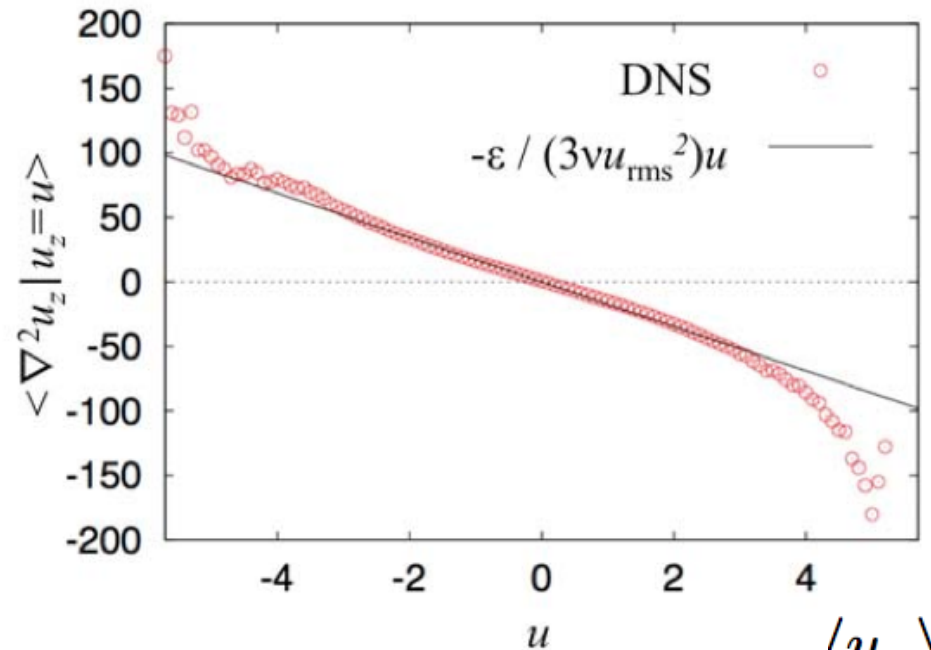
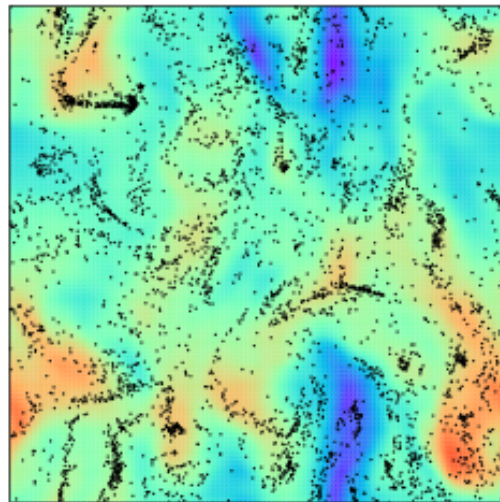
In homogeneous, isotropic turbulence

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

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

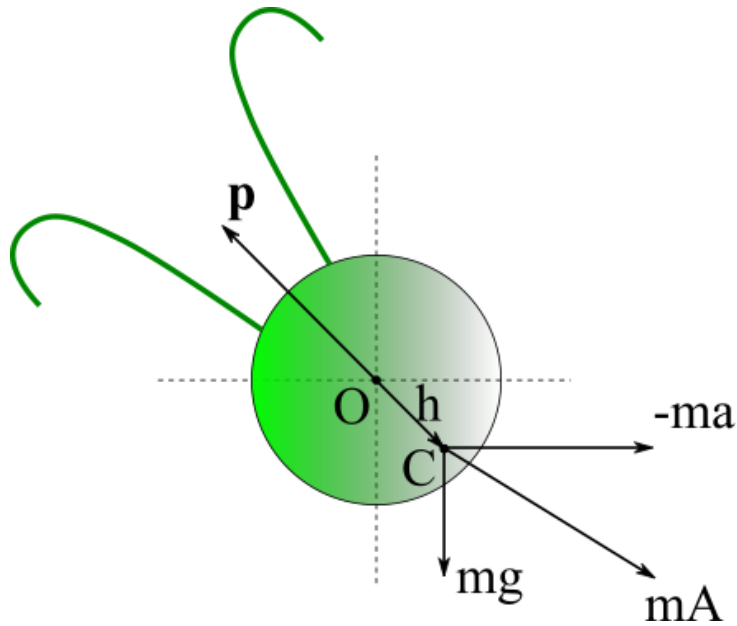


Swimming cells
accumulate in
downwelling
regions,
where $u_z < 0$



WITH LARGE ACCELERATIONS

De Lillo *et al.* Phys. Rev. Lett. **112**, 044502 (2014)



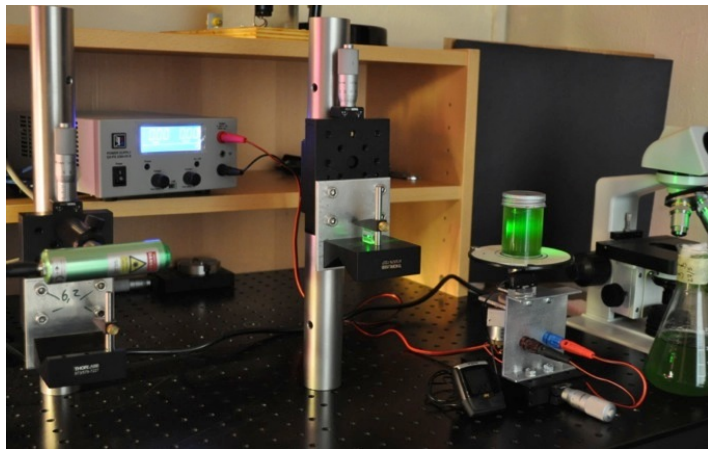
Gyrotactic algae should feel **inertial forces** too!

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

$$\frac{d\mathbf{p}}{dt} = -\frac{1}{2v_0} [\mathbf{A} - (\mathbf{A} \cdot \mathbf{p})\mathbf{p}] + \frac{1}{2}\boldsymbol{\omega} \times \mathbf{p}$$

$$\mathbf{A} = \mathbf{g} - \mathbf{a}$$

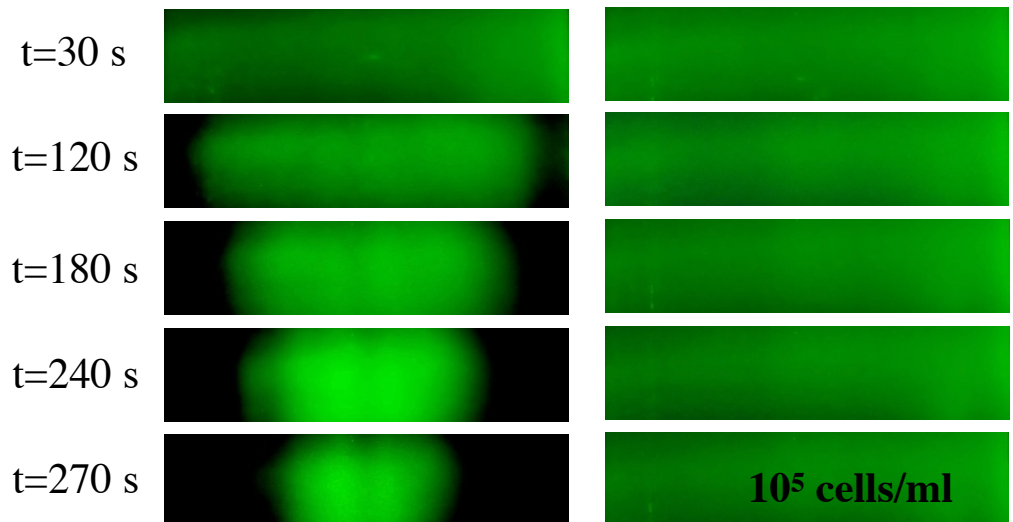
$$v_0 = 3\nu/h \quad B = \frac{v_0}{g} \simeq 1 \div 6 \text{ s}$$



Experiment in a rotating tank

r=2 cm
f=5 Hz

alive *C. augustae* dead

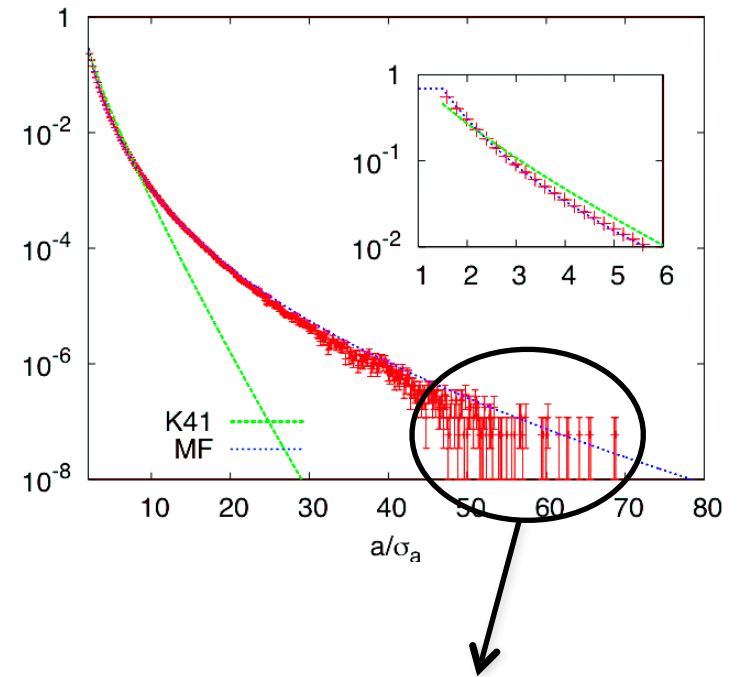
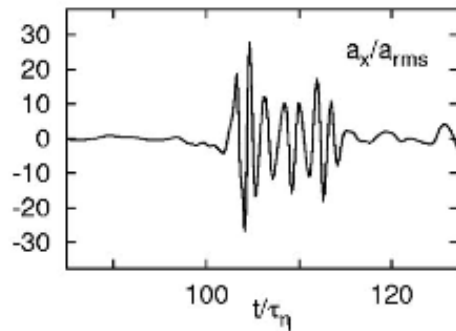
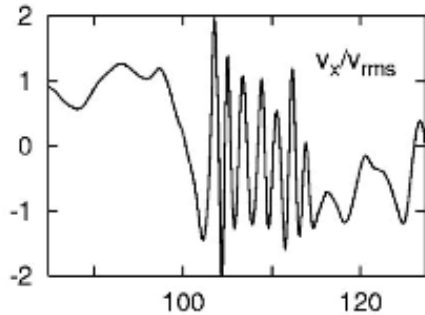


Accelerations in turbulence

Trapping of particles in **small scale vortices**

Frequency in vortex $\simeq \tau_\eta^{-1}$

Trapping time $10 - 20\tau_\eta$



WITH LARGE ACCELERATIONS

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$$\mathbf{A} = \mathbf{g} - \mathbf{a}$$

If $a_{\text{rms}} \gg g$

orientation is controlled by $\Psi_a = \frac{v_0 \omega_{\text{rms}}}{a_{\text{rms}}}$

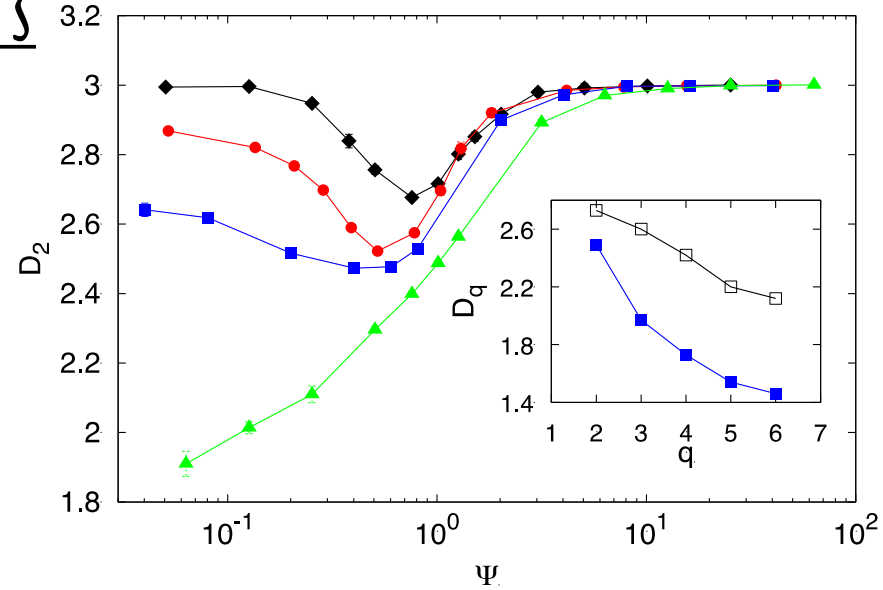
Phase-space contraction:

$$\sum_{i=1}^d \frac{\partial \dot{X}_i}{\partial X_i} + \frac{\partial \dot{p}_i}{\partial p_i} = -\frac{d-1}{2v_0} [g \cancel{\rho_z} + \mathbf{a} \cdot \mathbf{p}]$$

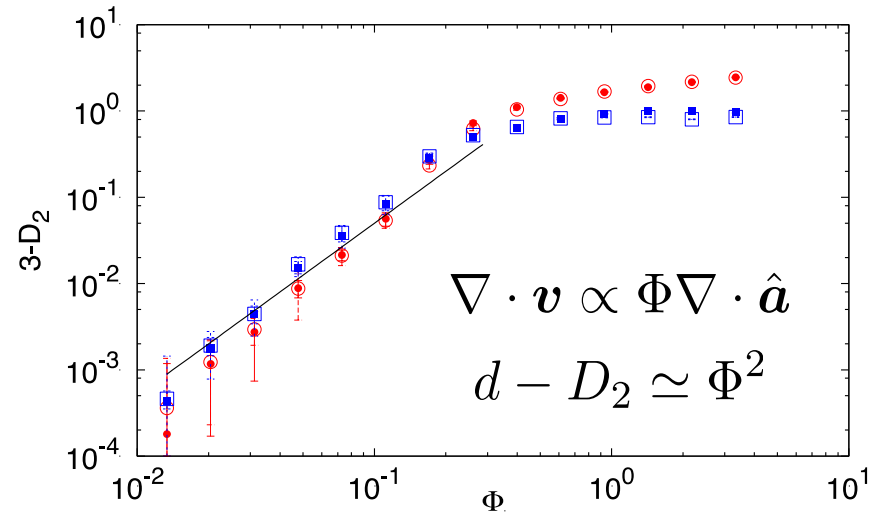
If $\Psi \ll 1$ \Rightarrow $\mathbf{p} \rightarrow \hat{\mathbf{a}} = \frac{\mathbf{a}}{|\mathbf{a}|}$

particle velocity: $\mathbf{v} \approx \mathbf{u} + v_s \hat{\mathbf{a}}$

Typical accelerations in the ocean are not large enough to observe this effect!



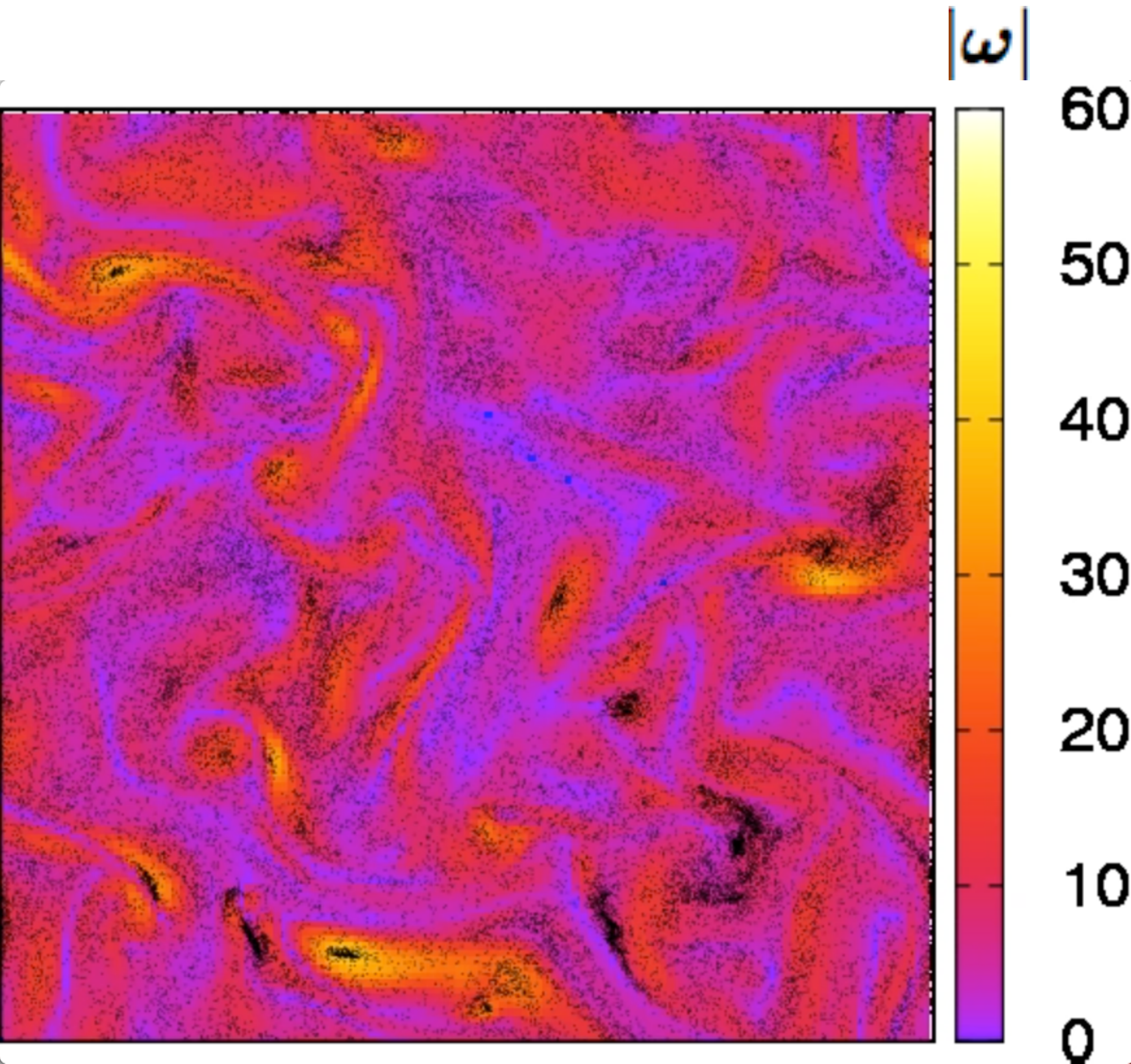
Black line \rightarrow $Re_\lambda = 62, \mathbf{A} = \mathbf{g}$
 $Re_\lambda = 20$ $Re_\lambda = 36$ $Re_\lambda = 62$



De Lillo, *et al.*

Phys. Rev. Lett. **112**, 044502 (2014).

WITH LARGE ACCELERATIONS



effective velocity:

$$v \approx u + v_s \hat{a}$$

So algae should
accumulate inside vortices
(like bubbles....)

$$\text{Re}_\lambda = 62$$

$$\Phi = 1$$

$$\Psi = 1.5$$

IN THIS TALK...



Small scale patchiness

scales: mm to cm

Role of
turbulence in:



**Thin Phytoplankton Layers
(formation and dissolution)**

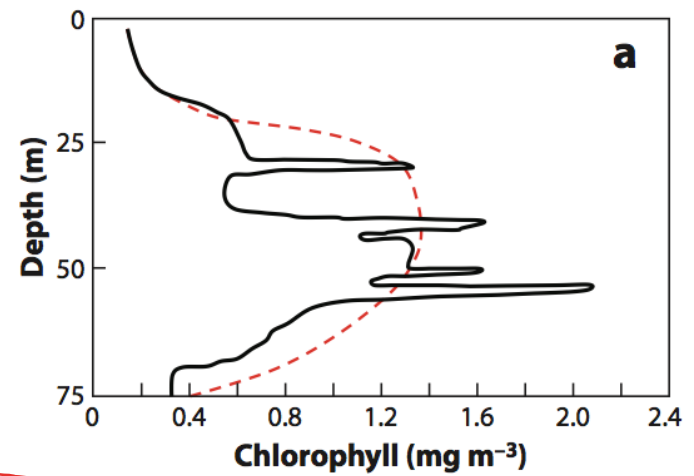
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vertically

up to some km
horizontally

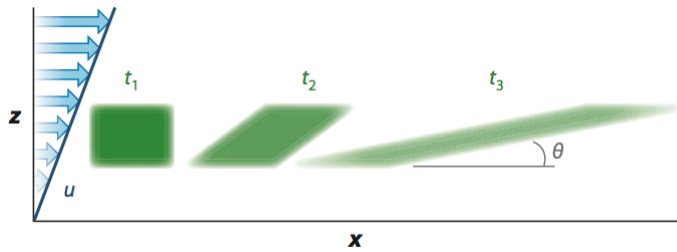
THIN PHYTOPLANKTON LAYERS

- Thin layers of high phytoplankton concentration.
- Vertical thickness cm to m
- Horizontal size up to km
- Persistence up to days

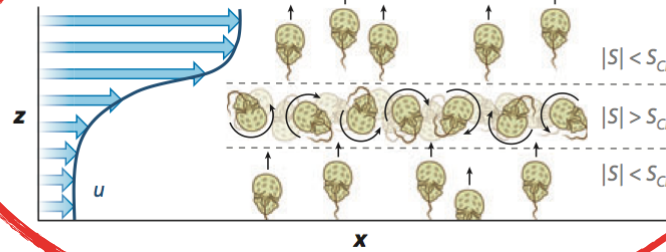
Some explanations....



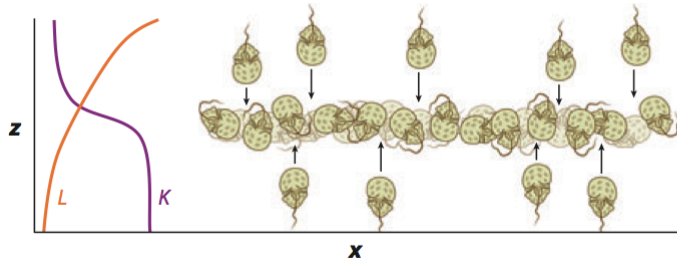
a Straining



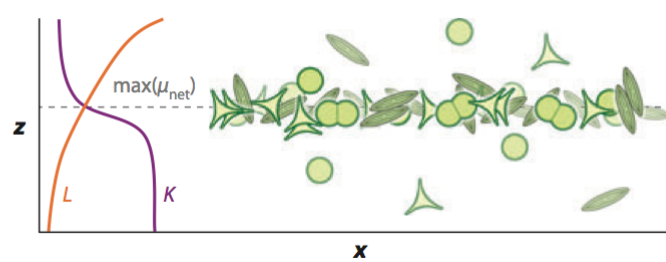
d Gyrotactic trapping



b Convergent swimming



e In situ growth



GYROTACTIC TRAPPING IN SHEAR FLOWS

W.M. Durham, J.O. Kessler and R. Stocker, *Science* **323**, 1067 (2009)

One possible explanation for the formation of layers at the bottom of the mixed layer, where vertical shear is present.



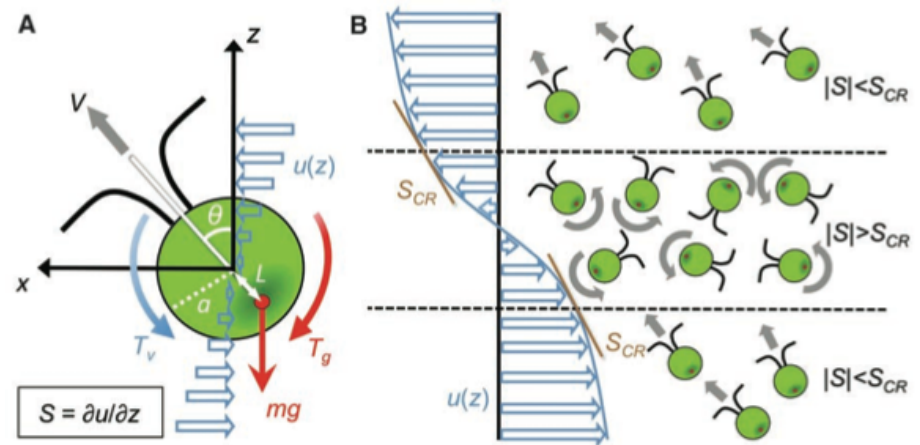
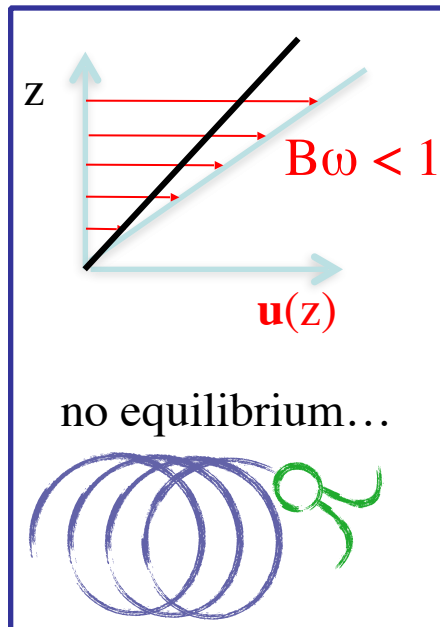
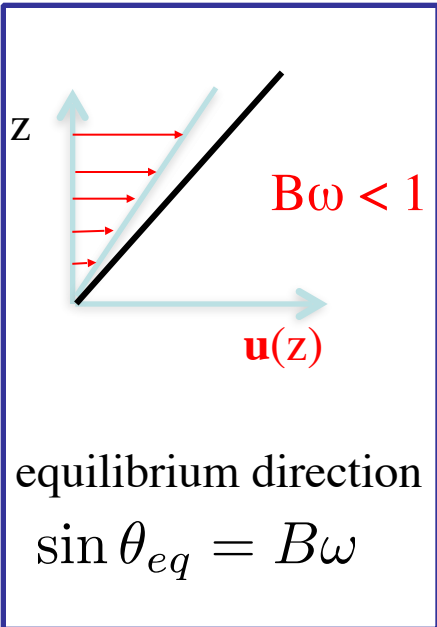
Trapping in a shear

$$\mathbf{u} = (u(z), 0, 0)$$

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

Equation for the angle

$$\dot{\theta} = \frac{1}{2}(\omega - B^{-1} \sin \theta) \quad \omega = \partial_z u(z)$$



GYROTACTIC TRAPPING IN SHEAR FLOWS

W.M. Durham, J.O. Kessler and R. Stocker, *Science* **323**, 1067 (2009)

One possible explanation for the formation of layers at the bottom of the mixed layer, where vertical shear is present.



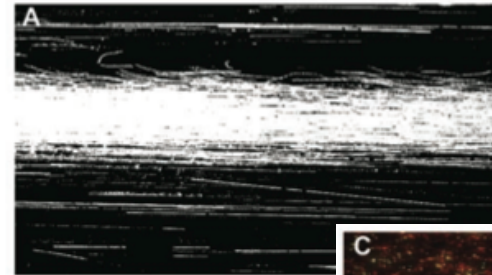
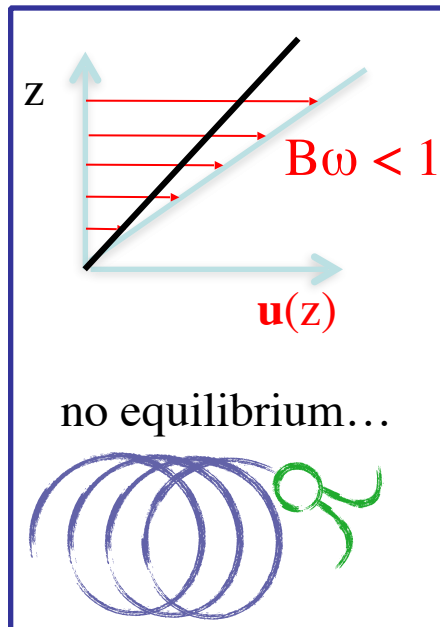
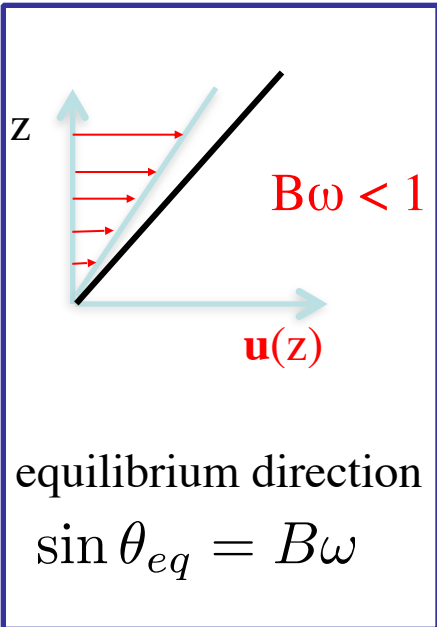
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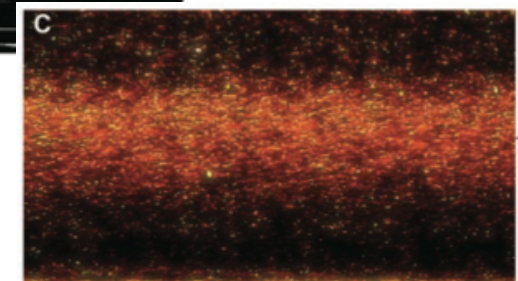
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C. rehinartii



H. akashiwo

Lab experiments
 by Durham *et al.*(2009)

WHAT ABOUT TURBULENCE?

KOLMOGOROV FLOW

Navier-Stokes equations for incompressible velocity field \mathbf{u}

$$\partial_t u_i + u_j \partial_j u_i = -\partial_i P + \nu \partial^2 u_i + g_i$$

Kolmogorov body force: $g_i = \delta_{i,1} F \cos z$

Stationary solution: $U_i = \delta_{i,1} U_0 \cos (Z/L)$

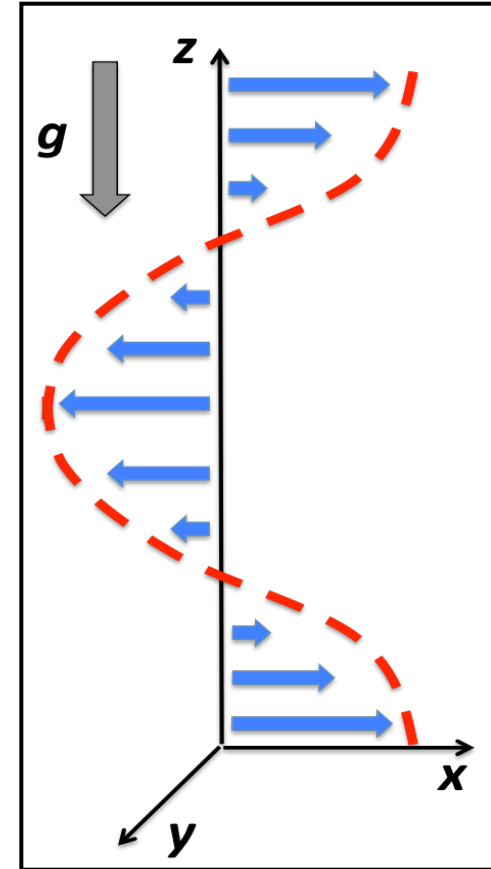
For $Re \equiv UL/\nu > \sqrt{2}$ the laminar solution is linearly unstable

For $Re \gg \sqrt{2}$ the flow becomes turbulent: DNS are necessary.

Why this flow?

because it is the simplest periodic shear flow

because the mean profile of the **turbulent** flow **is still a cosine**



G. I. Sivashinsky, *Physica D* (1985)

Musacchio and Boffetta, *Physical Review E* (2014)

SWIMMERS IN LAMINAR KOLMOGOROV FLOW

Santamaria *et al.*, Phys Fluids **26**, 111901 (2014).

$$\dot{Z} = \Phi p_z$$

$$\dot{p}_x = -\frac{1}{2\Psi} p_x p_z - \frac{1}{2} \sin Z p_z$$

$$\dot{p}_y = -\frac{1}{2\Psi} p_y p_z$$

$$\dot{p}_z = \frac{1}{2\Psi} (1 - p_z^2) + \frac{1}{2} \sin Z p_x$$

In analogy with the constant shear case we could expect

$\Psi < 1$ quasi-equilibrium solutions with $\dot{\mathbf{p}} = 0$ exist for all Z , **swimmers can escape**

$\Psi > 1$ for some Z rotation due to shear dominates, **swimmers are trapped**

$$\mathcal{C}(\mathbf{p}, Z) = p_y e^{Z/(2\Phi\Psi)}$$

$$\mathcal{H}(\mathbf{p}, Z) = \Phi e^{\frac{Z}{2\Phi\Psi}} \left[p_x - \frac{\Psi(2\Phi\Psi \cos Z - \sin Z)}{1 + 4\Phi^2\Psi^2} \right]$$

Two constants of motion

the system is integrable

If a swimmer is not trapped, Z is not limited, $p_y \rightarrow 0$

The system becomes 2D.

$$\dot{\theta} = \frac{1}{2\Psi} \cos \theta + \frac{1}{2} \sin Z$$

$$\dot{Z} = \Phi \sin \theta$$

$$\dot{\theta} = G(Z) \partial_Z \mathcal{H}$$

$$\dot{Z} = -G(Z) \partial_\theta \mathcal{H}$$

$$G(Z) = e^{-\frac{Z}{2\Phi\Psi}}$$

$G(Z)$: inverse integrating factor

A Zöttl, H Stark, *PRL* (2012)
for a similar approach for prolate cells in Poiseuille flow

SWIMMERS IN LAMINAR KOLMOGOROV FLOW

Conservation of \mathcal{H} implies that for large Z (**untrapped swimmers**)

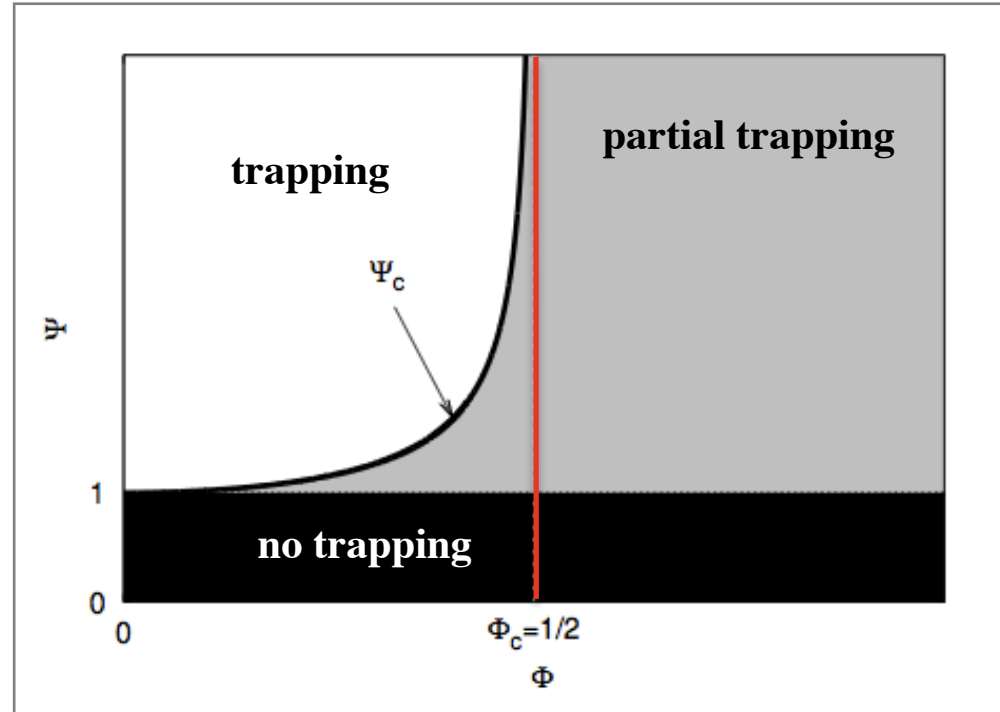
$$p_x = \frac{\Psi(2\Phi\Psi \cos Z - \sin Z)}{1 + 4\Phi^2\Psi^2}$$

This defines a $\Phi_c = \frac{1}{2}$

$\Phi < \Phi_c$ solutions for $\Psi \leq \Psi_c = (1 - 4\Phi^2)^{-1/2}$

$\Phi > \Phi_c$ solutions for any Ψ

$$\mathcal{H}(\mathbf{p}, Z) = \Phi e^{\frac{Z}{2\Phi\Psi}} \left[p_x - \frac{\Psi(2\Phi\Psi \cos Z - \sin Z)}{1 + 4\Phi^2\Psi^2} \right]$$

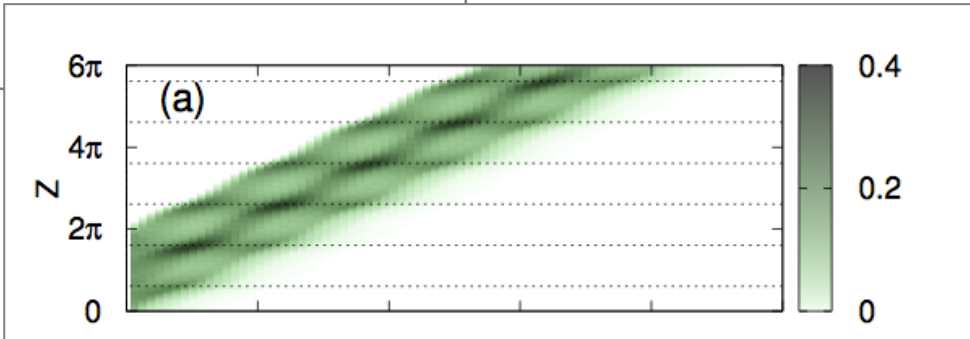
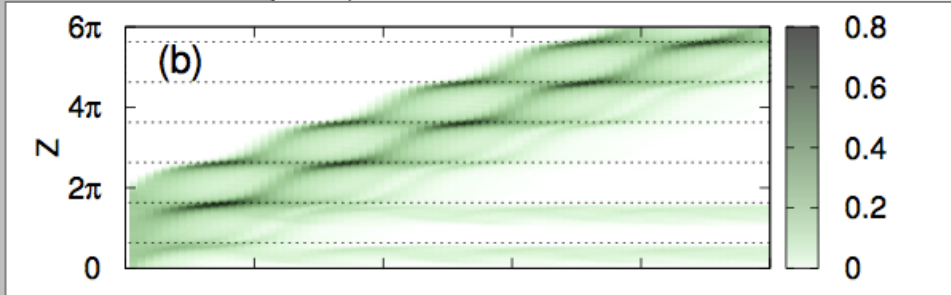
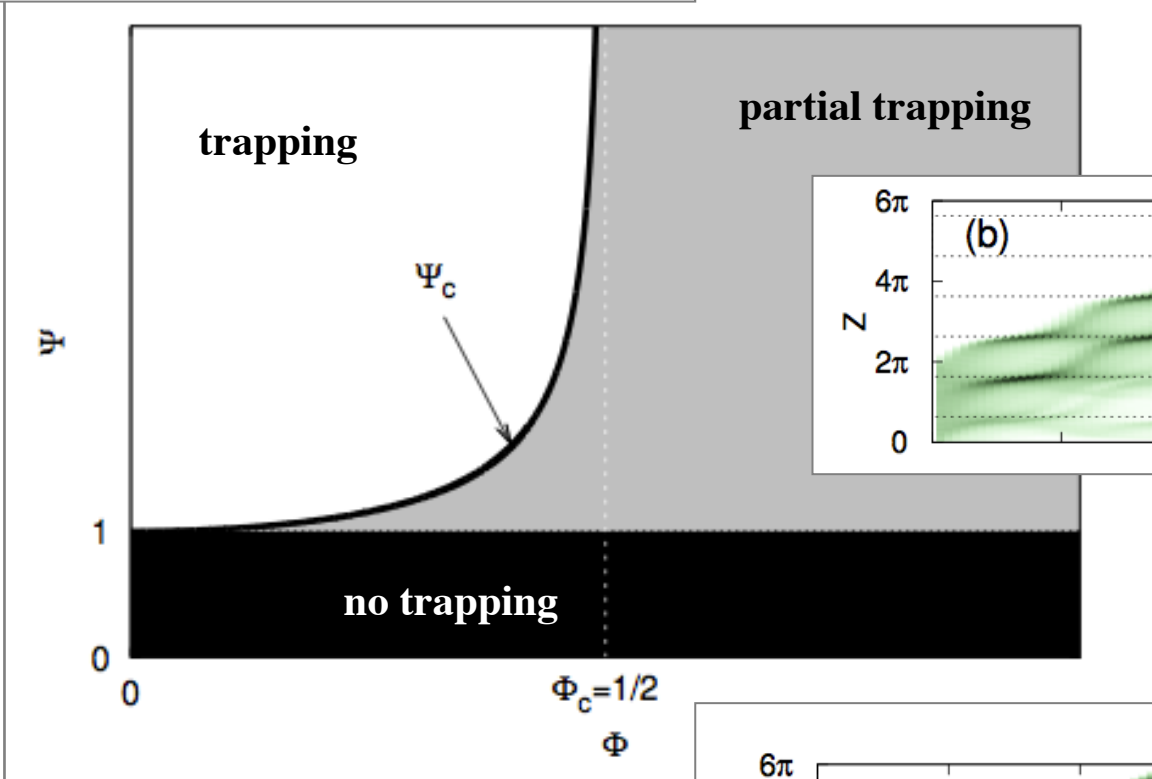
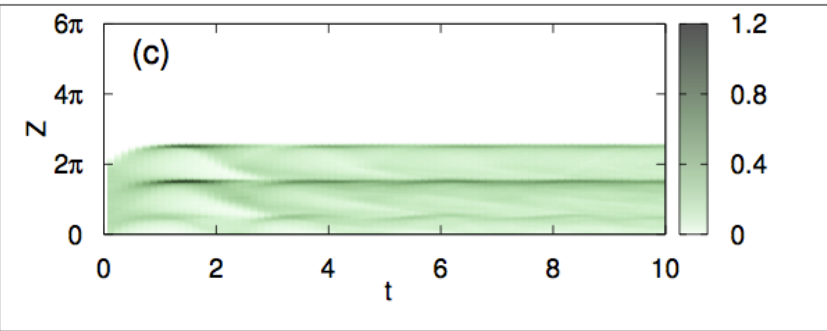


swimming number

$$\Phi = v_s/U_0$$

$$\Psi = BU_0/L$$

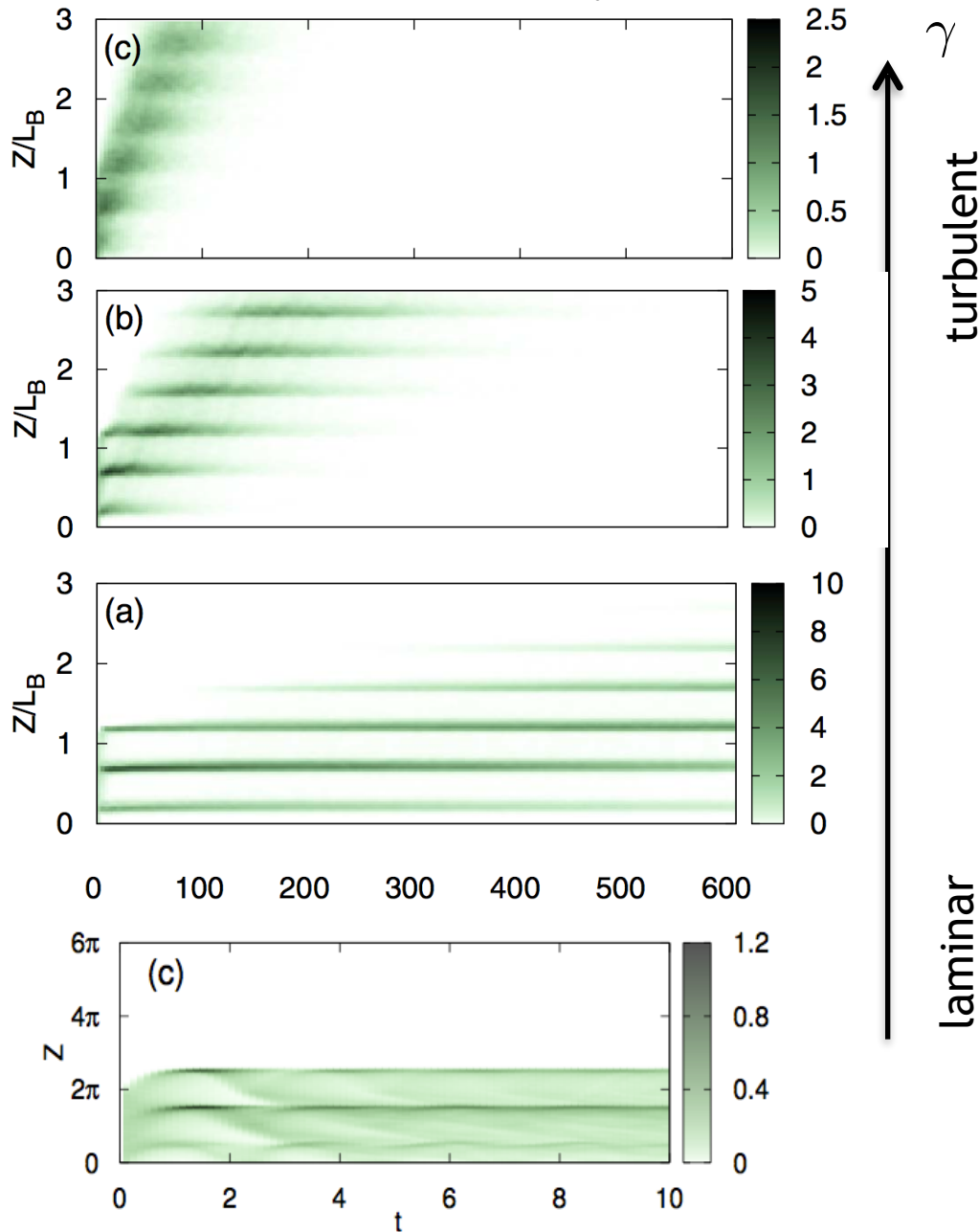
stability number



$$\Psi_c = (1 - 4\Phi^2)^{-1/2}$$

SWIMMERS IN TURBULENT KOLMOGOROV FLOW

Santamaria *et al.*, Phys Fluids **26**, 111901 (2014).



Effective diffusion due to turbulence **makes trapping transient**

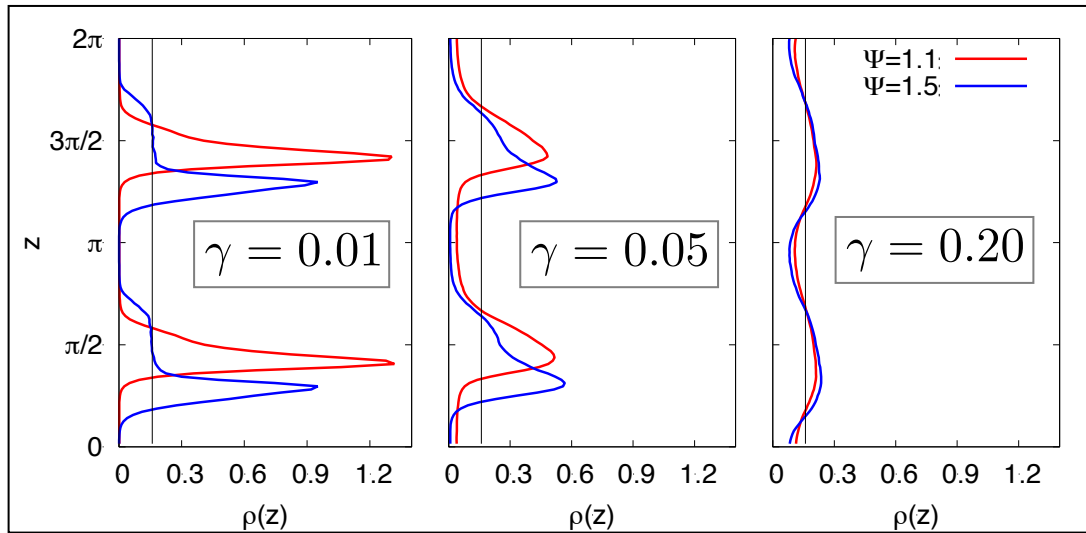
Technical note: in a turbulent Kolmogorov flow the relative intensity of fluctuations is constant. We change it by decomposing the velocity field

$$\mathbf{u} = \langle \mathbf{u} \rangle + \gamma \mathbf{u}'$$

From now on we consider only conditions that would give trapping in a laminar flow

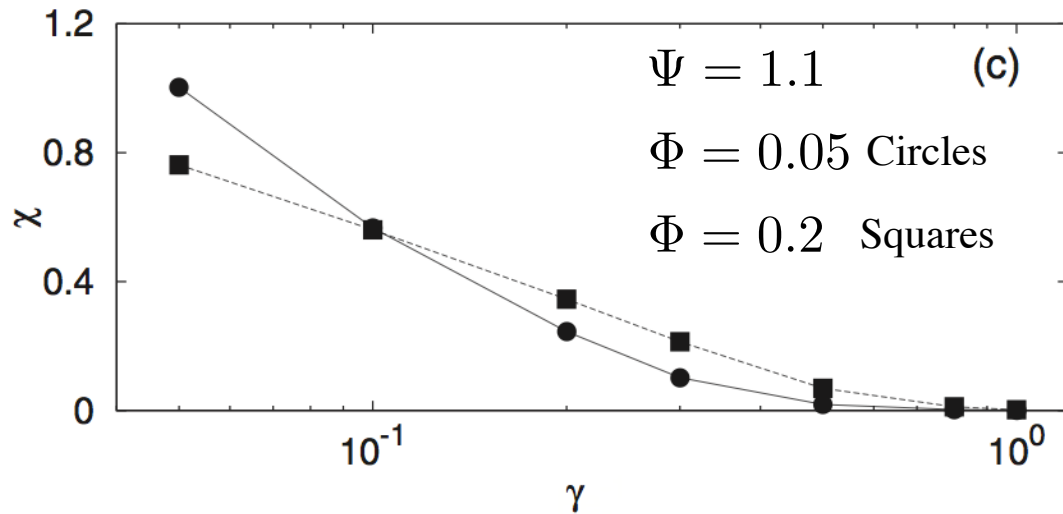
$$\Psi > \Psi_c$$

DENSITY PROFILES



$$\Phi = 0.05$$

Turbulence intensity

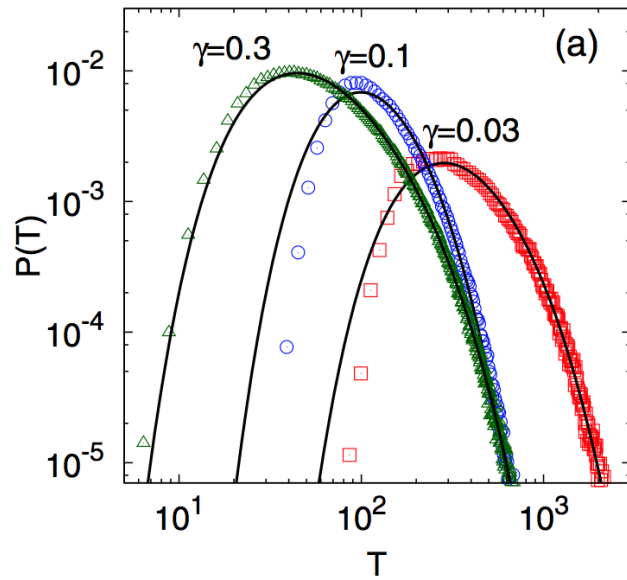


$$\chi = \frac{1}{\rho_0} \sqrt{\langle (\rho - \rho_0)^2 \rangle}$$

$$\gamma > 0.5 \Rightarrow \chi \simeq 0$$

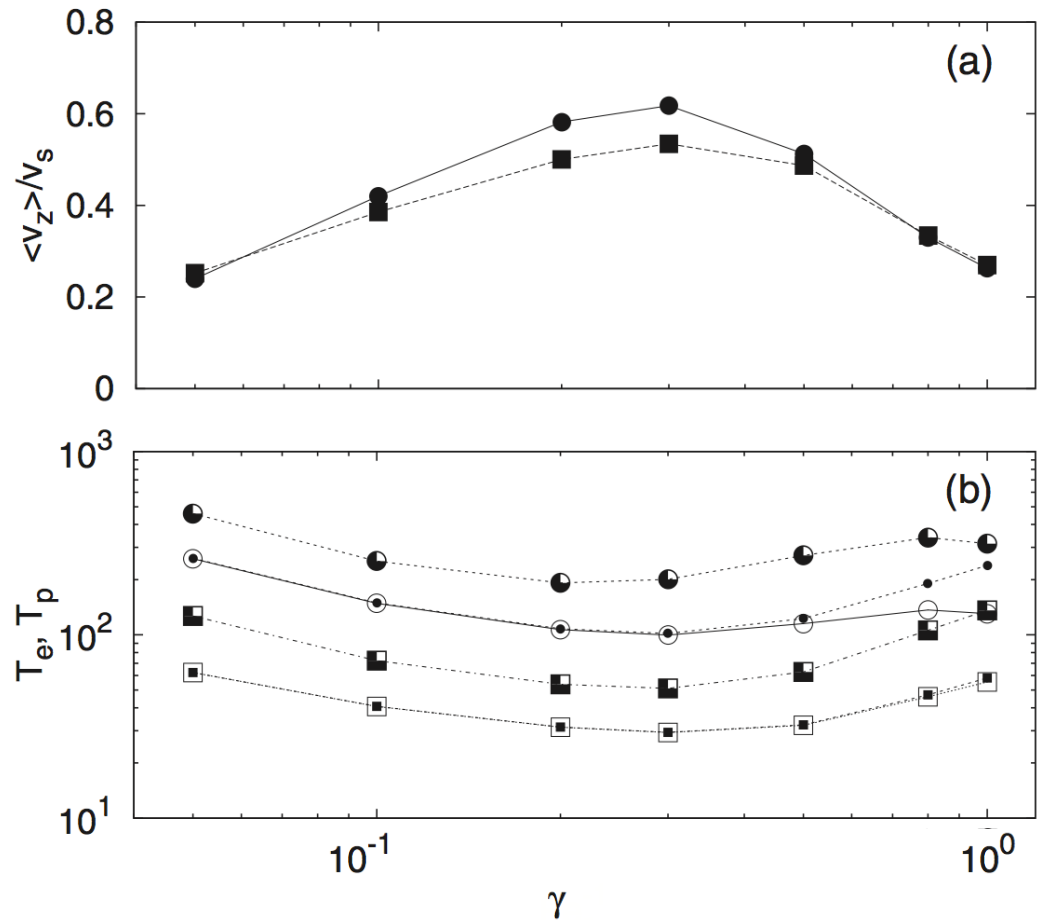
HOW LONG DO LAYERS LAST?

Exit time: time to swim half a period upwards



Exit time distribution compared with an **inverse gaussian** (i.e. the shape for a pure diffusion with drift)

If typical parameters for the ocean are used
hours $< T_p <$ days



$\Phi = 0.05$ Circles

$\Phi = 0.2$ Squares

\circ \square $\langle T \rangle$

\bullet \blacksquare $\pi / \langle V_z \rangle$

$$\int_0^{T_p} p(T) dT \approx 0.9$$

\bullet \blacksquare T_p

CONCLUSIONS

- We consider a simple model for gyrotaxis
- We studied the effects of turbulence on small scale patchiness and on the formation of thin phytoplankton layers
- Indications that **turbulence can induce small scale clustering** of swimming algae
- Gyrotactic algae tend to **cluster on downwelling regions**
- Clustering **controlled by the orientation time**
- Effects of fluid acceleration can be dramatic...but not in the ocean

Durham, *et al.* Nature Comm. **4**, 2148 (2013).

De Lillo, *et al.* Phys. Rev. Lett. **112**, 044502 (2014).

- **Analytical conditions** for the **formation of TLs** in laminar Kolmogorov flow can be derived
- Turbulence causes layers to **dissolve in a finite time**. We discussed some estimates of the **lifetime of layers**, with the correct orders of magnitude.

Santamaria *et al.*, Phys Fluids **26**, 111901 (2014).

Grazie!

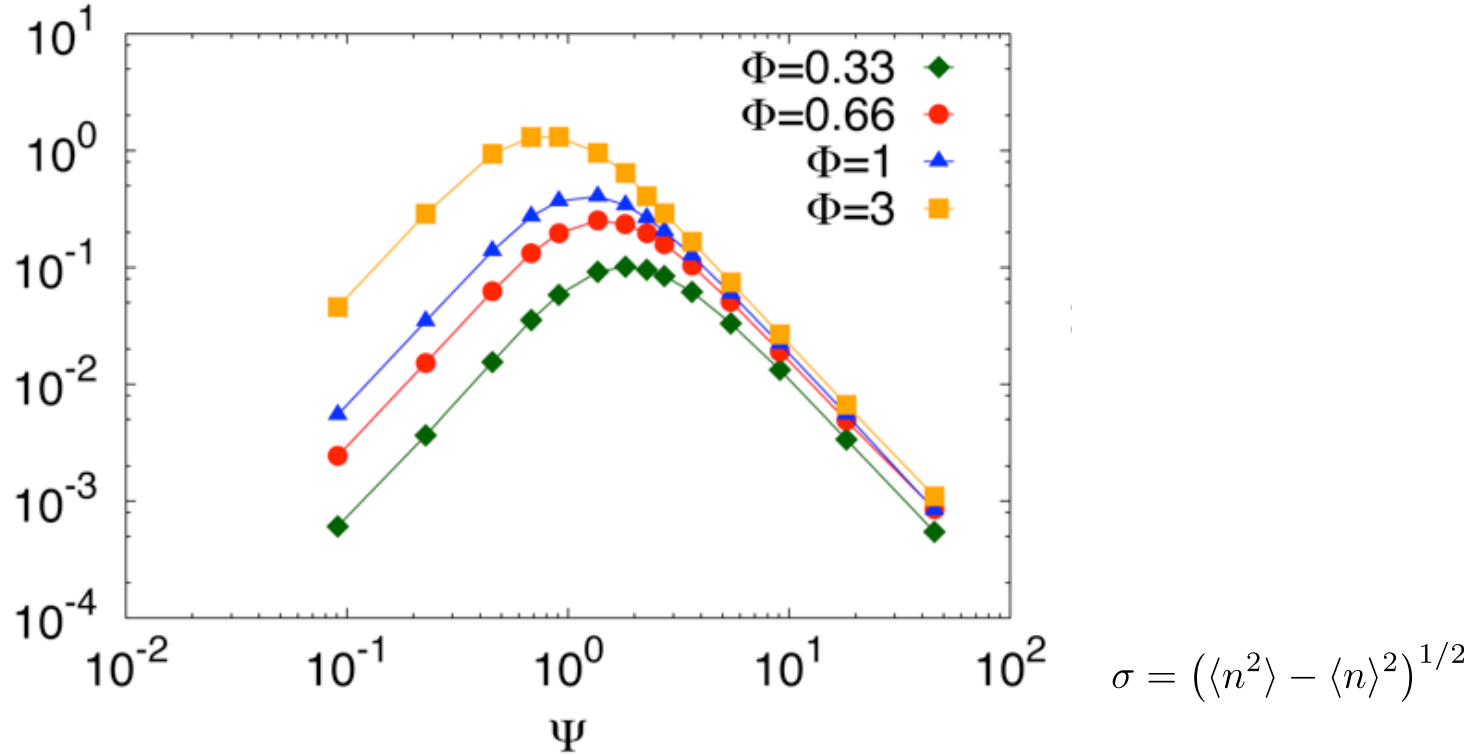


...and thanks to Chlamy!

Accumulation index

Another measure of clustering: the deviation from a Poisson distribution

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



N is related to the fractal dimension indeed if $3 - D_2 \ll 1$ one can show that

$$N \approx \frac{(3 - D_2) \langle n \rangle^{1/2}}{2} \ln \left(\frac{L_B}{\Lambda} \right)$$

A turbulence primer....

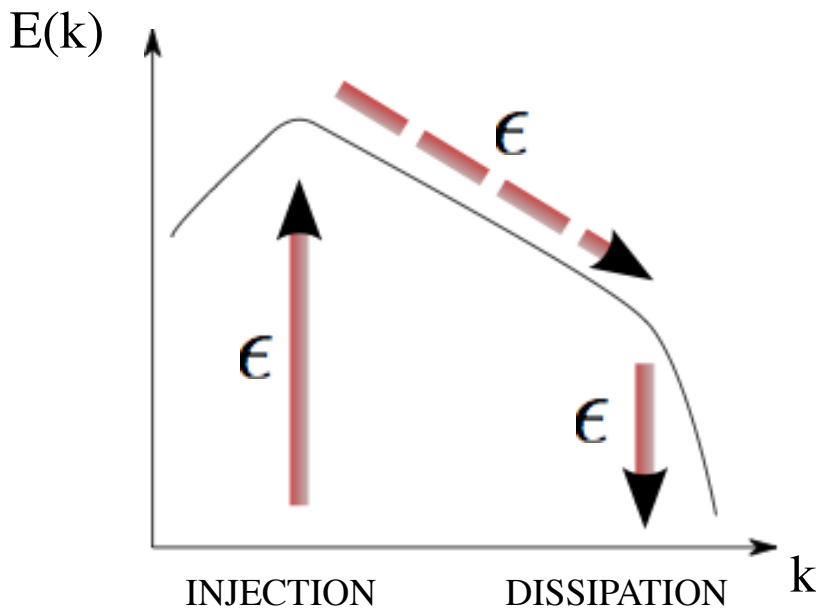
What we mean by turbulence (your neighbour might give a different definition):

-a solution of the Navier-Stokes equation at large Re

$$\text{Re} = \frac{UL}{\nu}$$

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

-“more than chaotic”: many active scales



$$\epsilon = \frac{U^3}{L} = \frac{u_\eta^3}{\eta} \quad \text{Energy flux across scales}$$

constant in the inertial range

η dissipative scale

(Kolmogorov's scale)

u_η typical velocity at scale η

τ_η typical eddy-turn-over time at scale η

$$\eta = \left(\frac{\nu^3}{\epsilon} \right)^{\frac{1}{4}} \quad \tau_\eta = \left(\frac{\nu}{\epsilon} \right)^{\frac{1}{2}}$$

Important for what follows: small scales are determined by ν and ϵ only!

$$u_\eta = (\nu\epsilon)^{1/4}$$