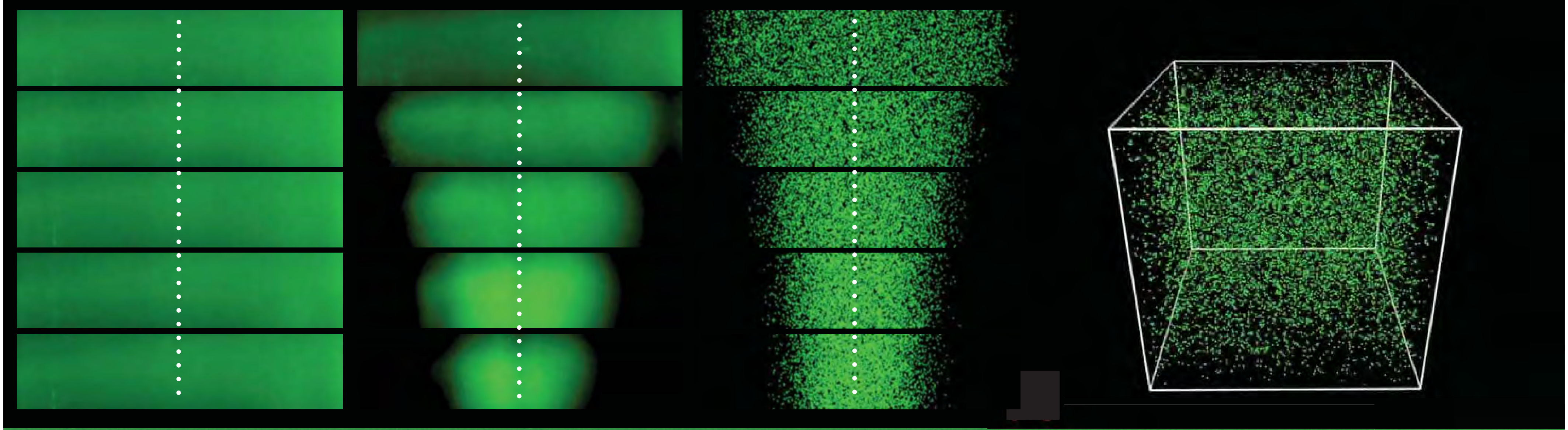

Gyrotactic phytoplankton in turbulent flows

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ISC institute for complex systems

NLOA: Nonlinear processes in oceanic and atmospheric flows, Madrid July 6-8 2016

General motivation

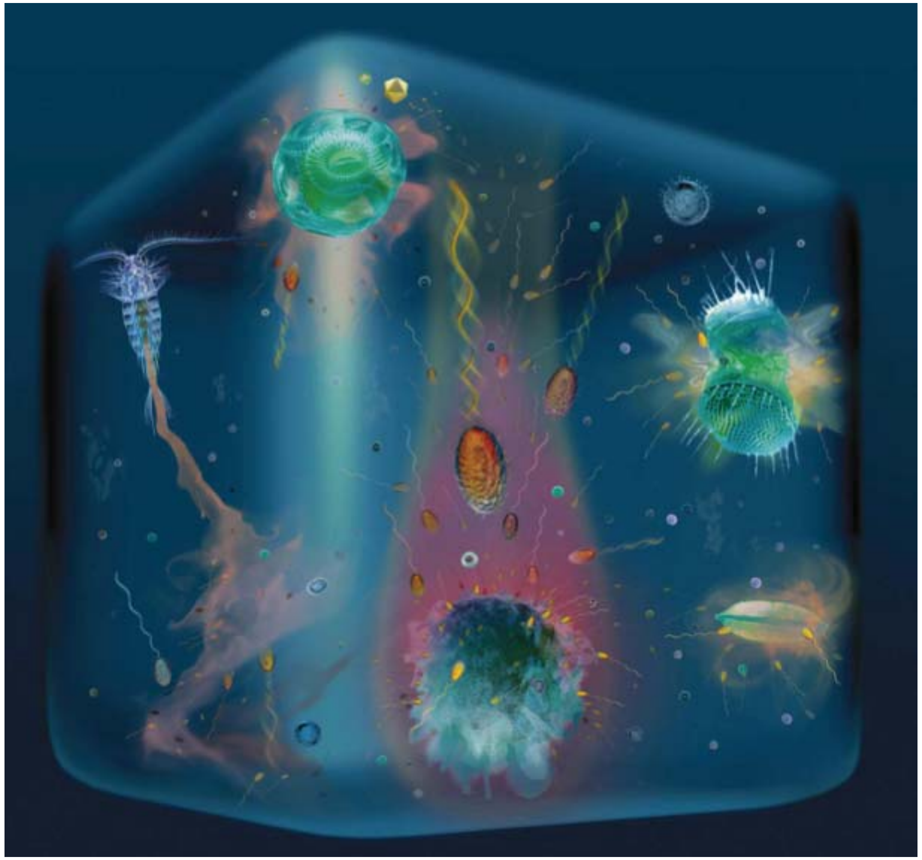
Marine microorganisms live in turbulent environments which mediate key processes including nutrient uptake, reproduction and predation.

Turbulence generates heterogeneous distribution of nutrients at very small scales and influences the encounter rates which are important to reproduction and predation.

What is the evolutionary response of microbes, how they adapt to the turbulent environment?

In spite of their name many planktonic microorganisms are able to swim (e.g. bacteria, dinoflagellates microalgae, most of zooplankton) typically with some taxis (chemo,photo,gyro).

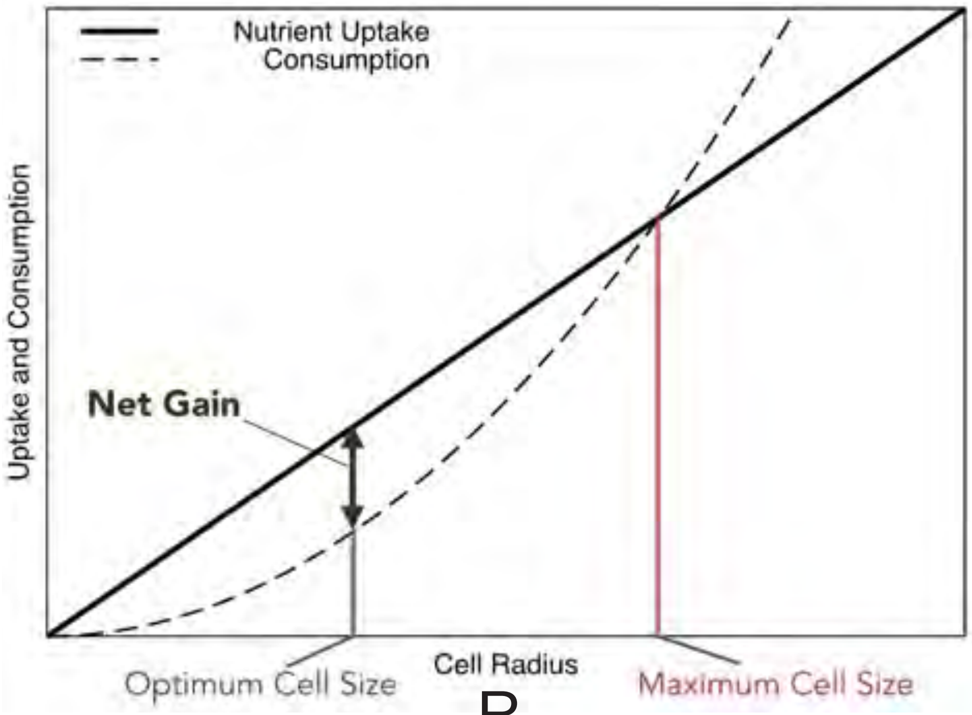
What are the advantages of motility?



(courtesy of R. Stocker)

Swimming and Feeding in turbulence

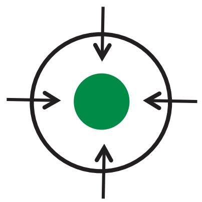
From T. Kiørboe



R

$$Q_D \propto R$$ diffusive uptake

$$M \propto R^{\alpha}$$ metabolic rate (α>1)



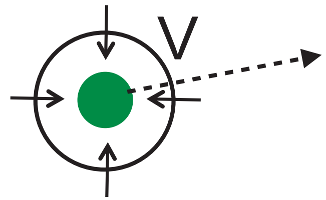
Beyond the optimal cell size (a few μm) turbulence and/or motility can help

Sherwood number measures effective uptake over diffusive uptake

Swimming increases uptake

$$Sh \equiv \frac{Q}{Q_D} = \frac{1}{2}[1 + (1 + 2Pe)^{1/3}]$$

$$Pe = VR/D$$



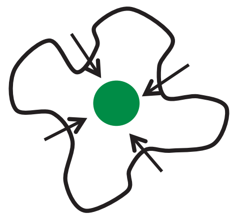
Turbulence increases uptake

$$Sh = 1 + 0.29Pe^{1/2} \qquad Pe \ll 1$$

$$Sh = 0.55Pe^{1/3} \qquad Pe \gg 1$$

$$Pe \propto \frac{\gamma R^2}{D}$$

γ shear rate



more effective for larger cells

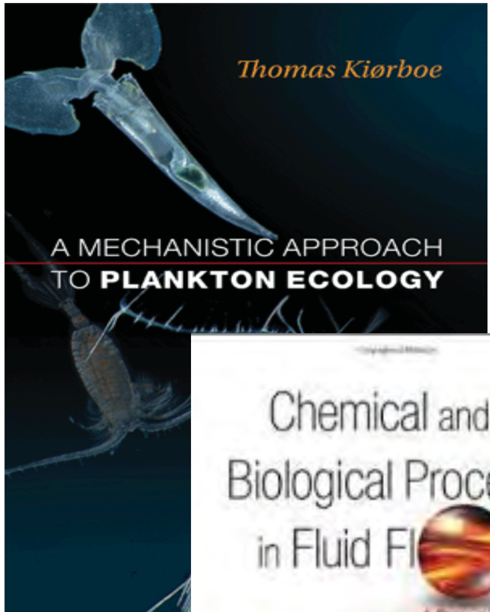
T. Kiorboe (2008) L. Karp-Boss *et al (1996)*

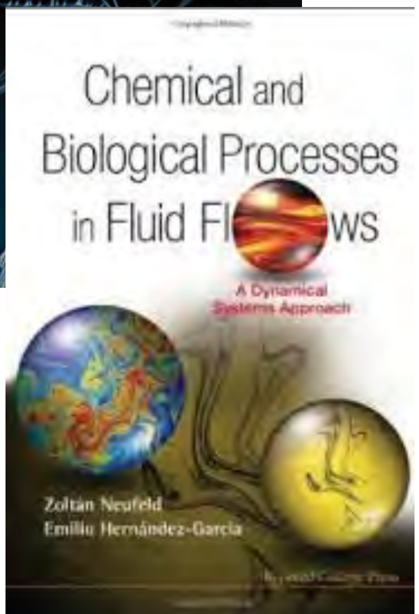
Key issue

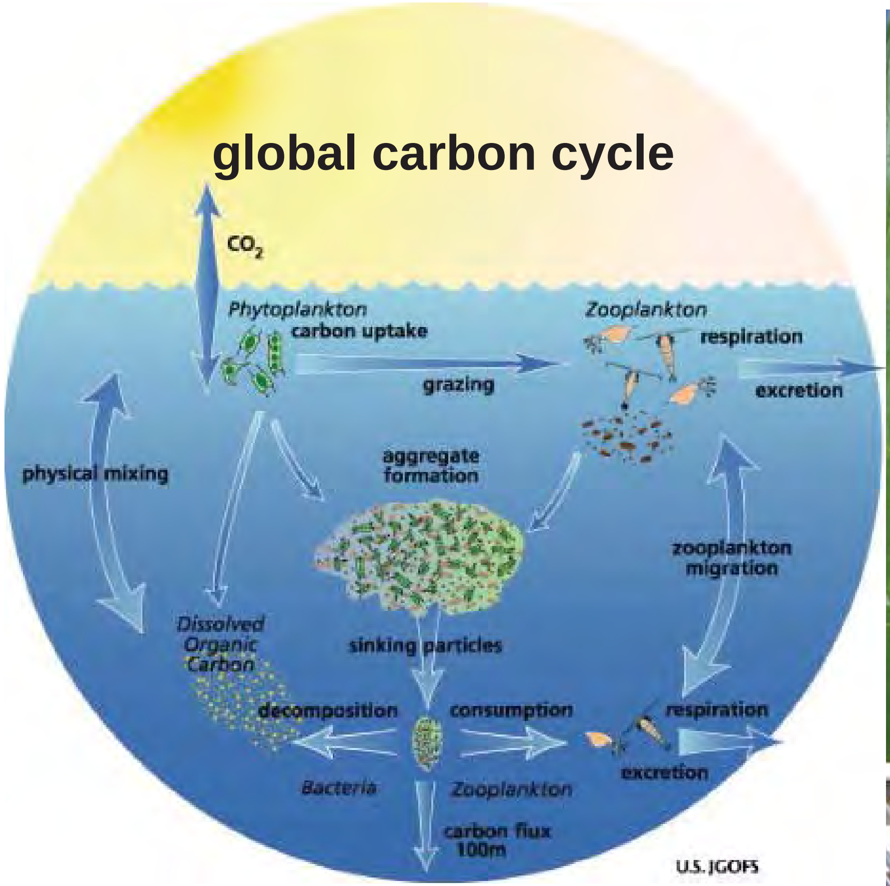
In labs microorganisms are typically studied in still fluids, in natural habitats, they move by

swimming & fluid transport

understanding such an interplay is key to marine ecology, global bio-chemical cycles, and applications (e.g. food industry, biofuel production, etc.)

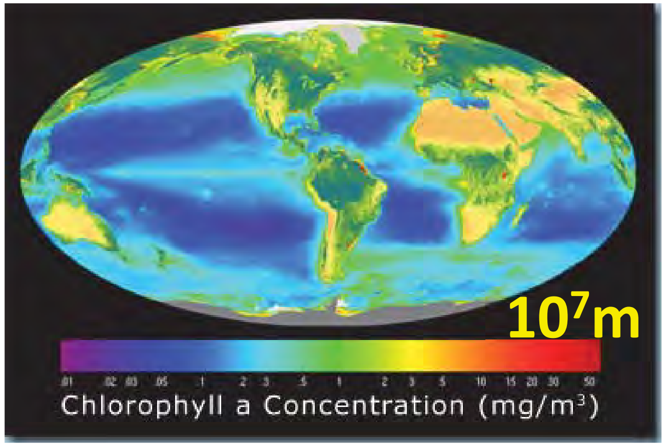






Phytoplankton patchiness
over many scales

Goals: Rationalizing some aspects of phytoplankton patchiness in terms of the interplay between motility and fluid motion within the framework of dynamical systems and fluid mechanics

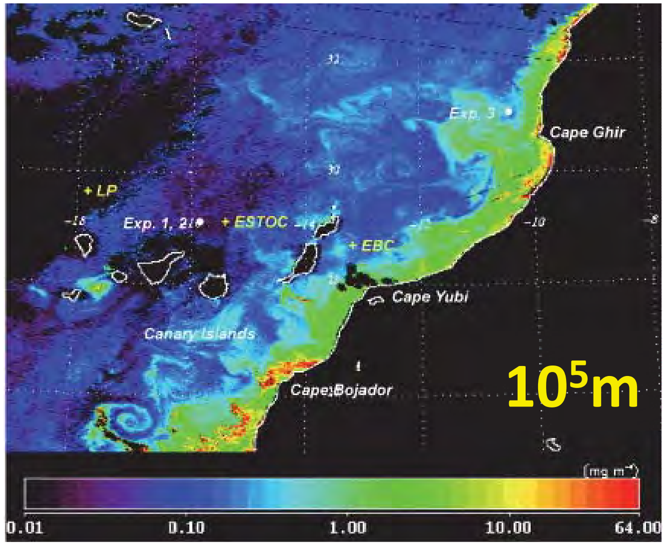


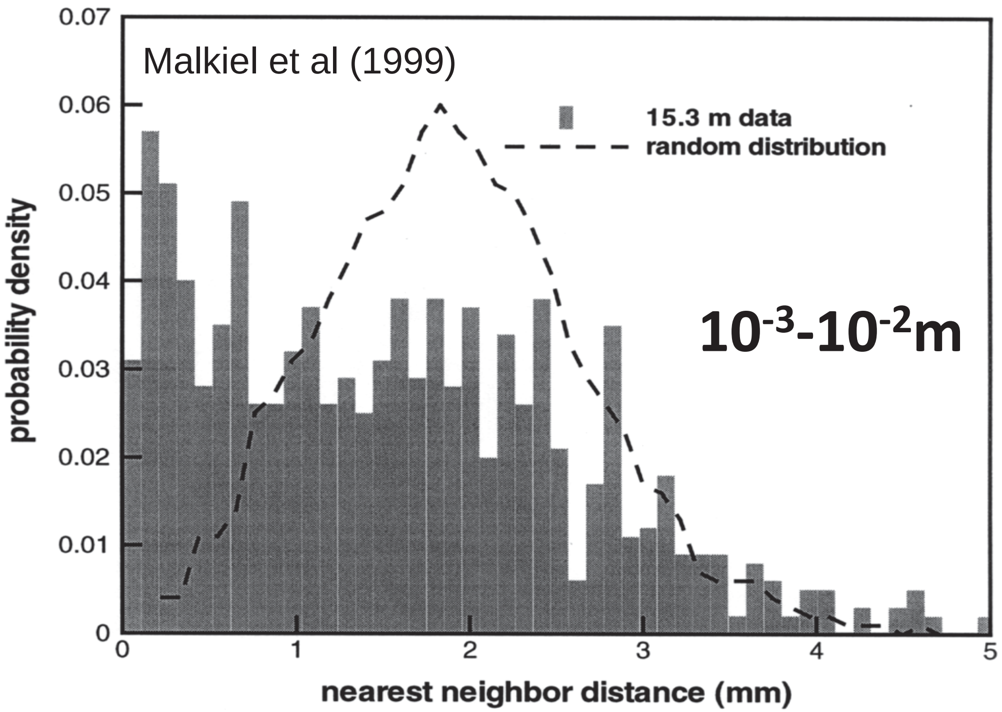
micro-patchiness correlates with motility

dinoflagellates (motile) more patchy than diatoms (non-motile)

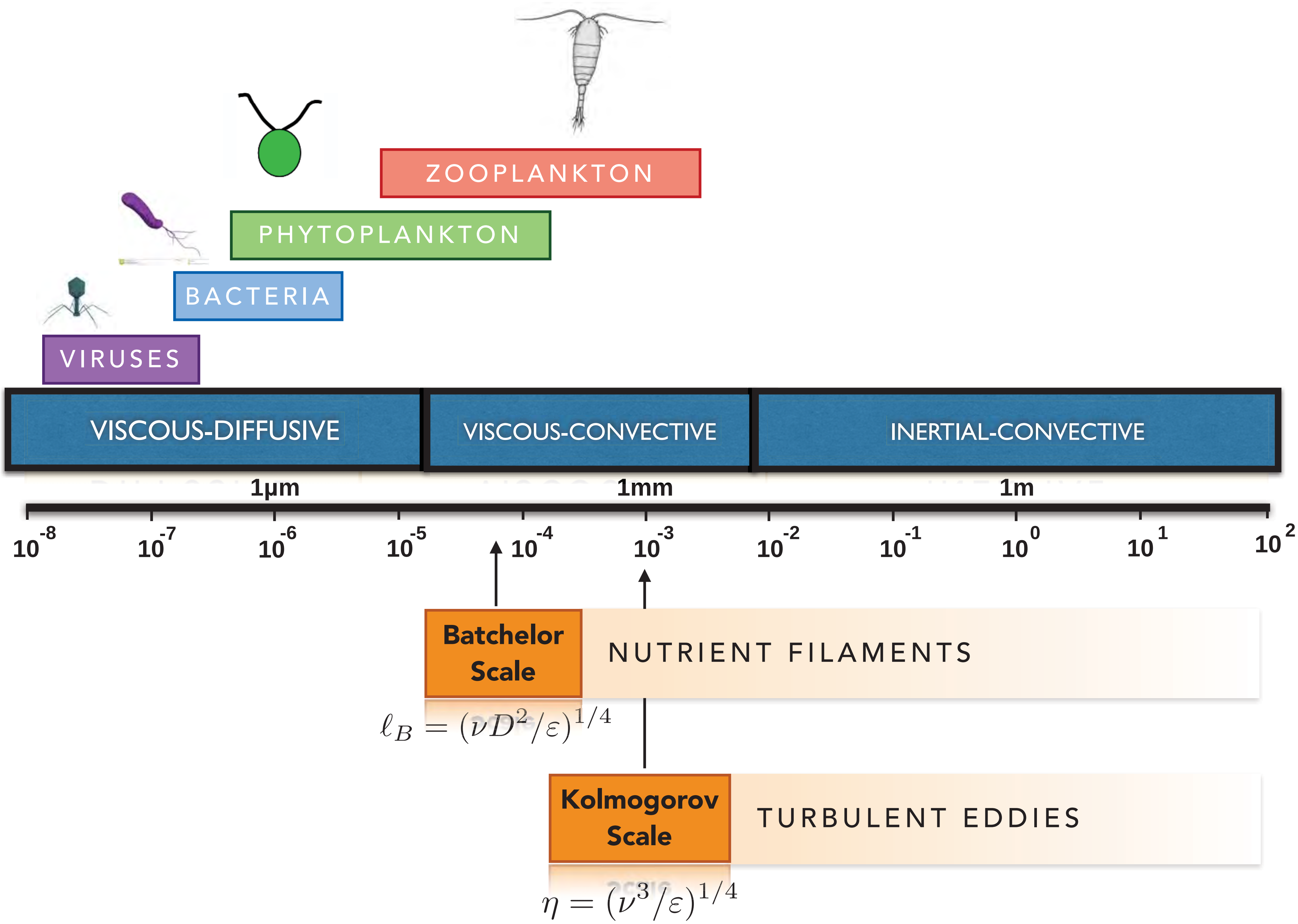
in situ techniques:

- 3D holography Malkiel et al (1999)
- Syringe arrays Moursiten et al. (2003)
- video-microscopy Gallagher et al (2004)

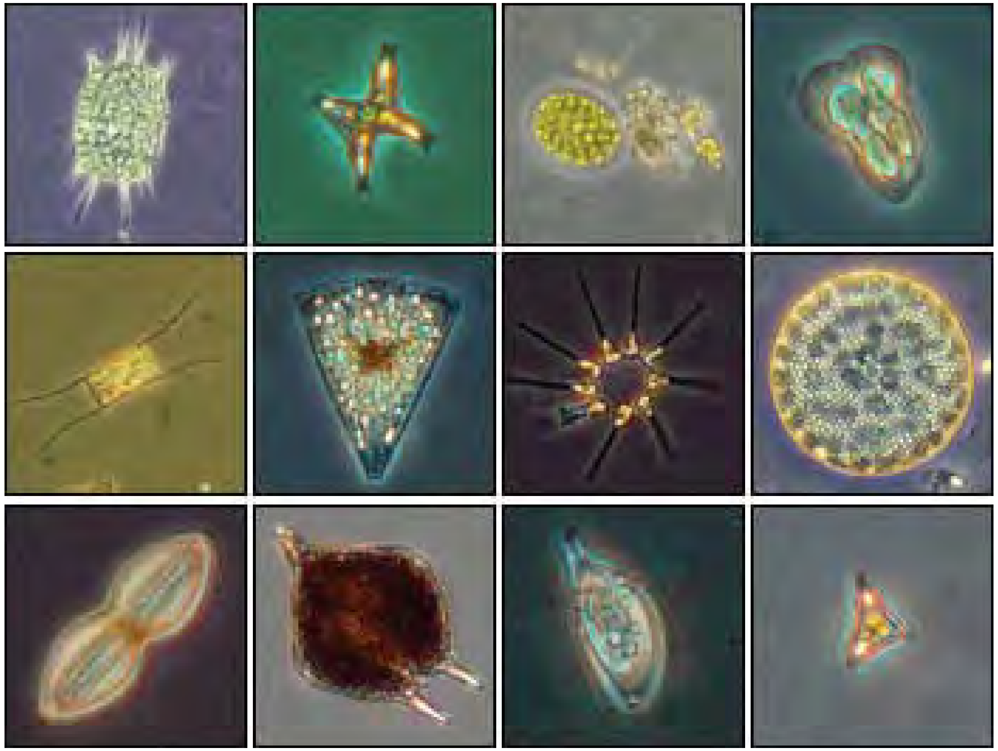




Scales of aquatic microbes



Case study: Gyrotactic Phytoplankton

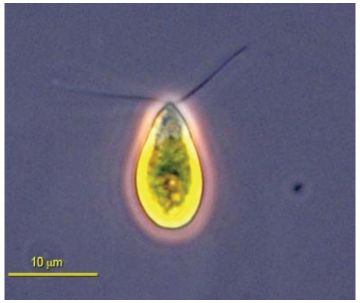


- large diversity of forms
- **primary producers in oceans**
- ≃50% photosynthetic activity on Earth
- **up to 10^4 per milliliter of water**
- at the bottom of marine food web
- **can form Harmful (toxic) Algal Bloom**
- patchiness at different scales
- **many species are able to swim, e.g. 90% toxic algae are able to swim**

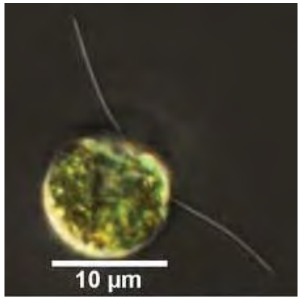
gyrotactic microalgae

Heterosigma akashiwo

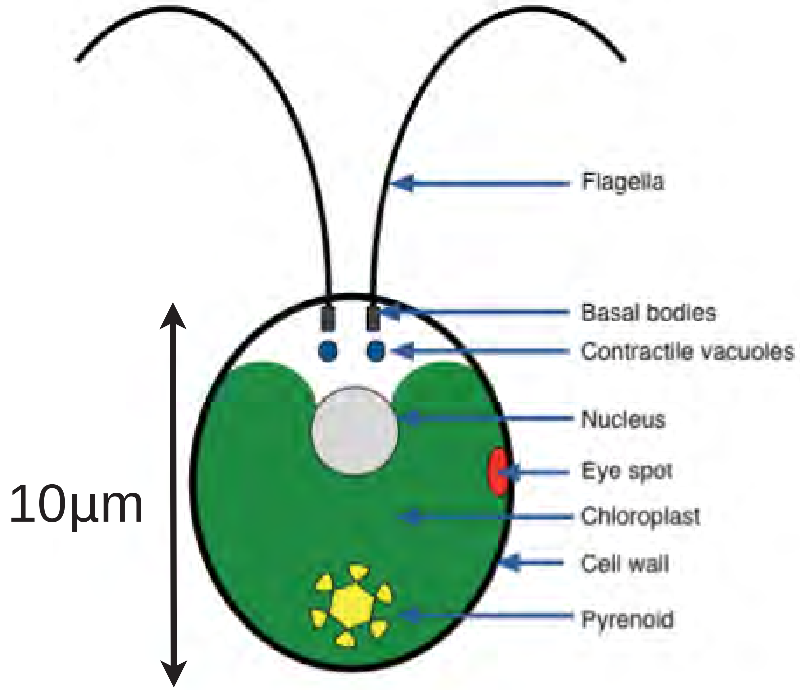
Dunaliella tertiolecta



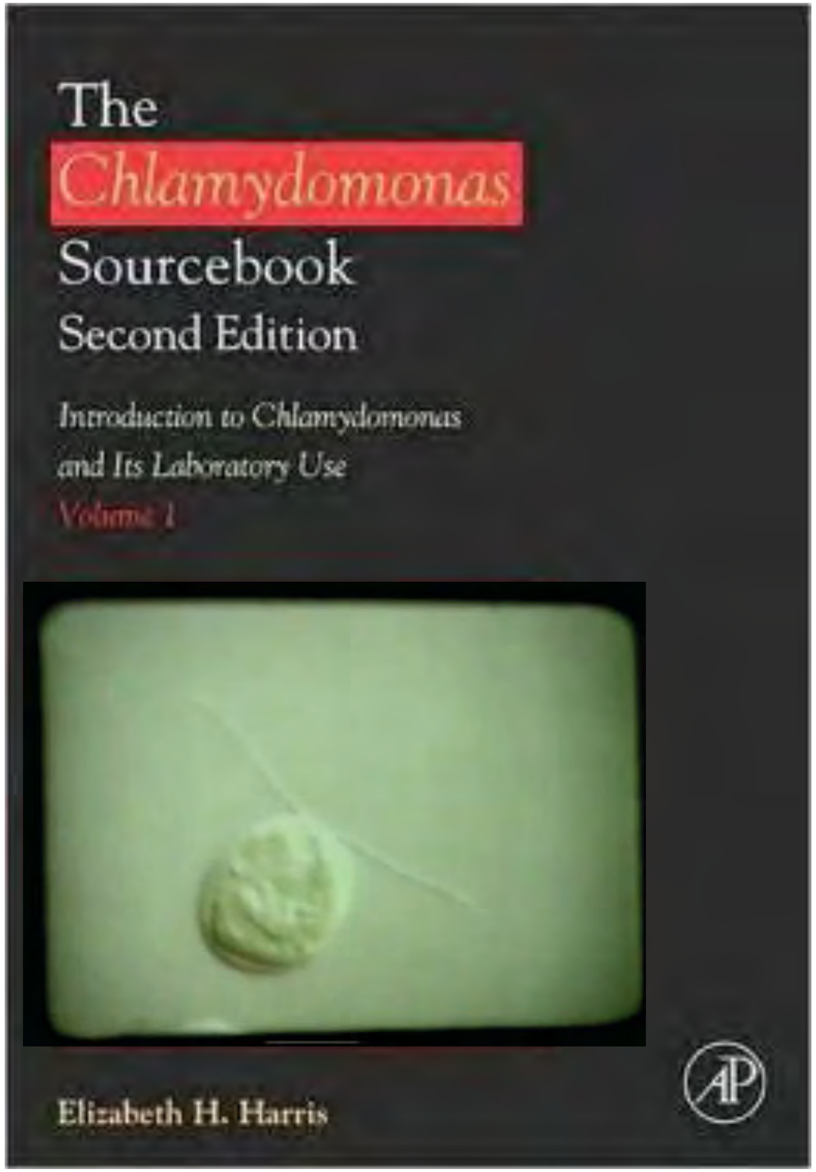
Chlamydomonas reinhardtii



Chlamydomonas



Unicellular biflagellate model
for molecular biology



both sexual and asexual reproduction

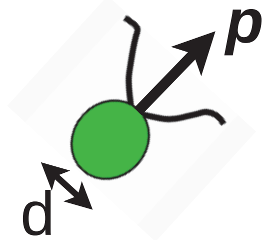
eyespot: for positive/negative phototaxis at low/high intensity

good swimmers v_S ~100µm/s (10 body lengths/sec)

slightly heavier than water ~ neutrally buoyant
sedimentation speed ~3 µm/s << v_S

swimming style
bottom heavy center of mass below center of symmetry (due to chloroplast-mass distribution) naturally swimming upwards against gravity (*negative gravitaxis*)

Model for gyrotaxis



position dynamics ➜ self-propelled tracers

-neutrally buoyant spherical cells
-very small d<<η (no inertia $Re_d \to 0$)
-very dilute (no hydrodynamic effects & “collisions”)
-swimming at constant speed v_s in the direction **p**

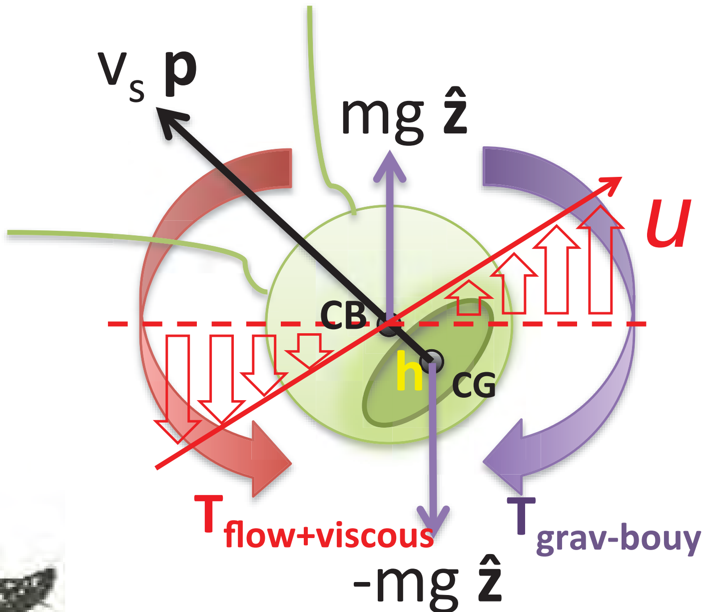
$$\dot{\boldsymbol{X}} = \boldsymbol{u}(\boldsymbol{X}, t) + v_s \boldsymbol{p}$$

swimming direction dynamics

the swimming direction changes due to gravity-buoyancy+ viscous torque and rotation by fluid vorticity

$$\dot{\boldsymbol{p}} = \frac{1}{2B}[\hat{\mathbf{z}} - (\hat{\mathbf{z}} \cdot \boldsymbol{p})\boldsymbol{p}] + \frac{1}{2}\boldsymbol{\omega} \times \boldsymbol{p}$$

$$B = \frac{3\nu}{gh}$$ orientation time-scale



asphericity typically very small
stochastic effects due e.g. to waving or asynchrony in flagella movement

here neglected

Kessler (1985),
Pedley & Kessler (1987),(1992)

Gyrotaxis in laminar flows

$$\dot{\boldsymbol{X}} = \boldsymbol{u}(\boldsymbol{X}, t) + v_s \boldsymbol{p}$$

tends to rotate ***p*** due to local vorticity making cells to tumble

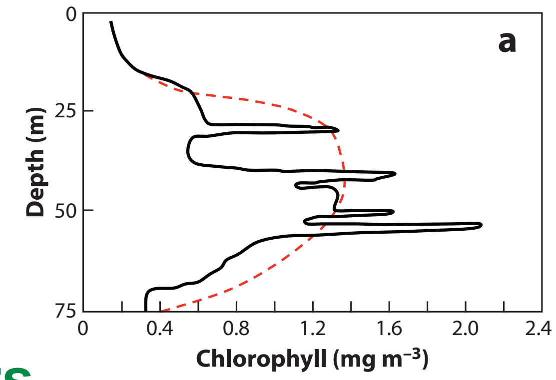
$$\dot{\boldsymbol{p}} = \frac{1}{2B}[\hat{\mathbf{z}} - (\hat{\mathbf{z}} \cdot \boldsymbol{p})\boldsymbol{p}] + \frac{1}{2}\boldsymbol{\omega} \times \boldsymbol{p}$$

tends to align upwards $\boldsymbol{p} \to \hat{\mathbf{z}}$
on a time scale B

Example $\boldsymbol{u} = (u(z), 0, 0)$ $u(z) \approx \omega z$

z θ_{eq}

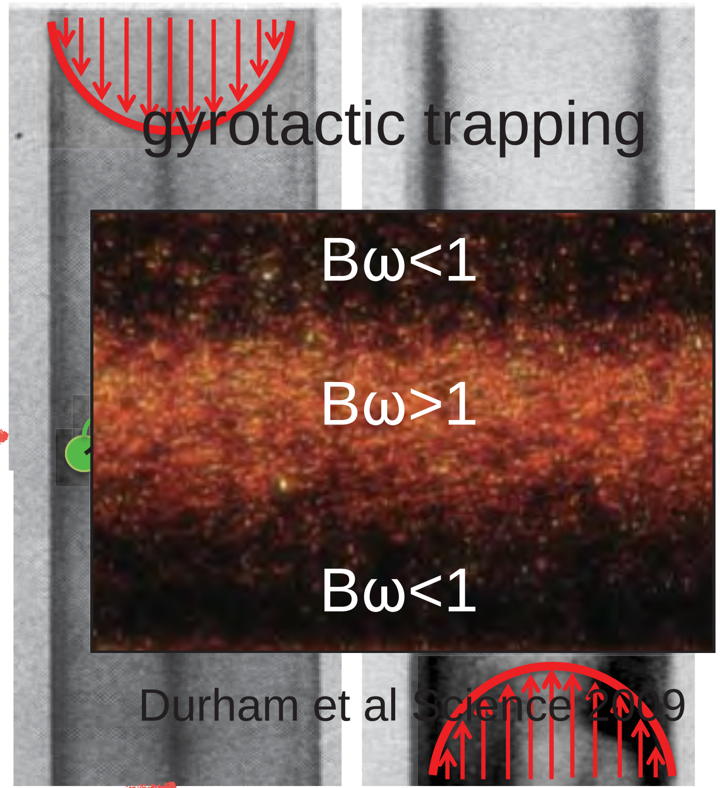
possible explanation for



thin phytoplankton layers

spectacular aggregations of phytoplankton in layers cm-to-m thick

gyrotactic focusing

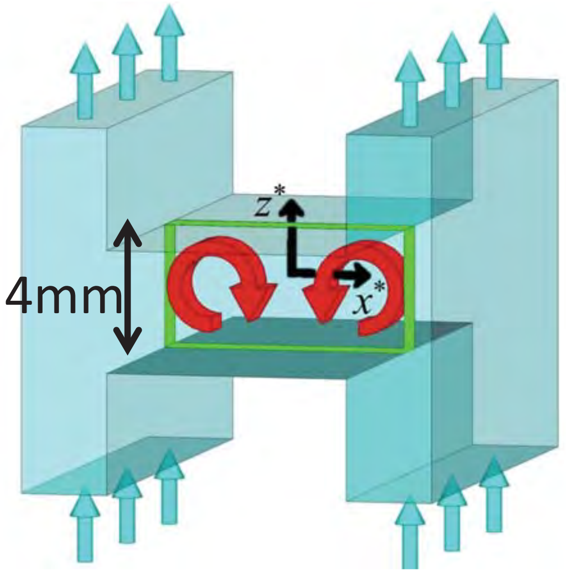


J.O. Kessler Nature (1985)

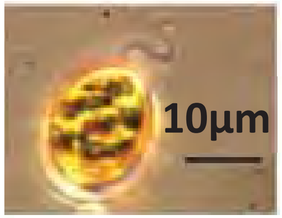
What does happen in more complex flows?

Experiment in a vortical flow

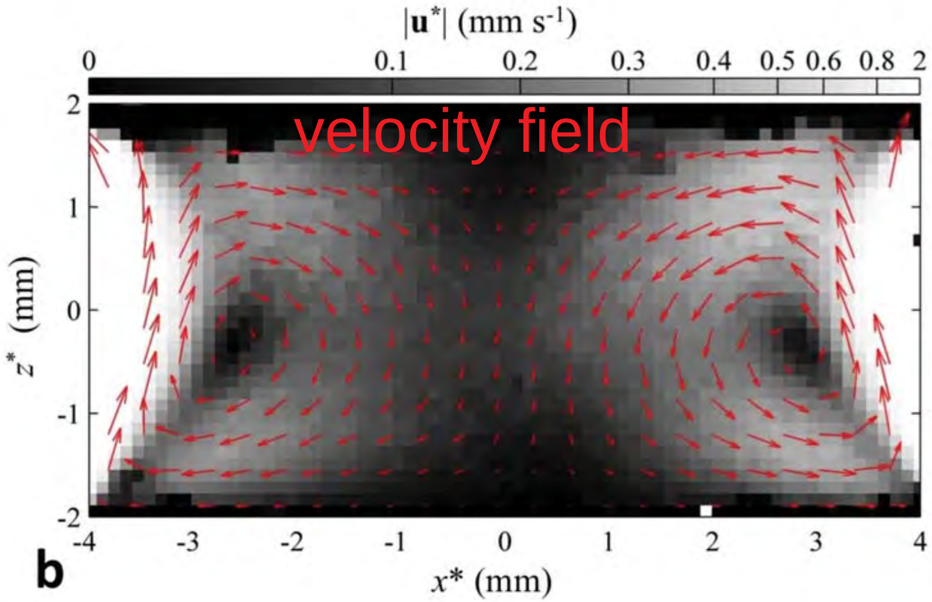
mimicking small-scale turbulent vortices
via microfluidic devices



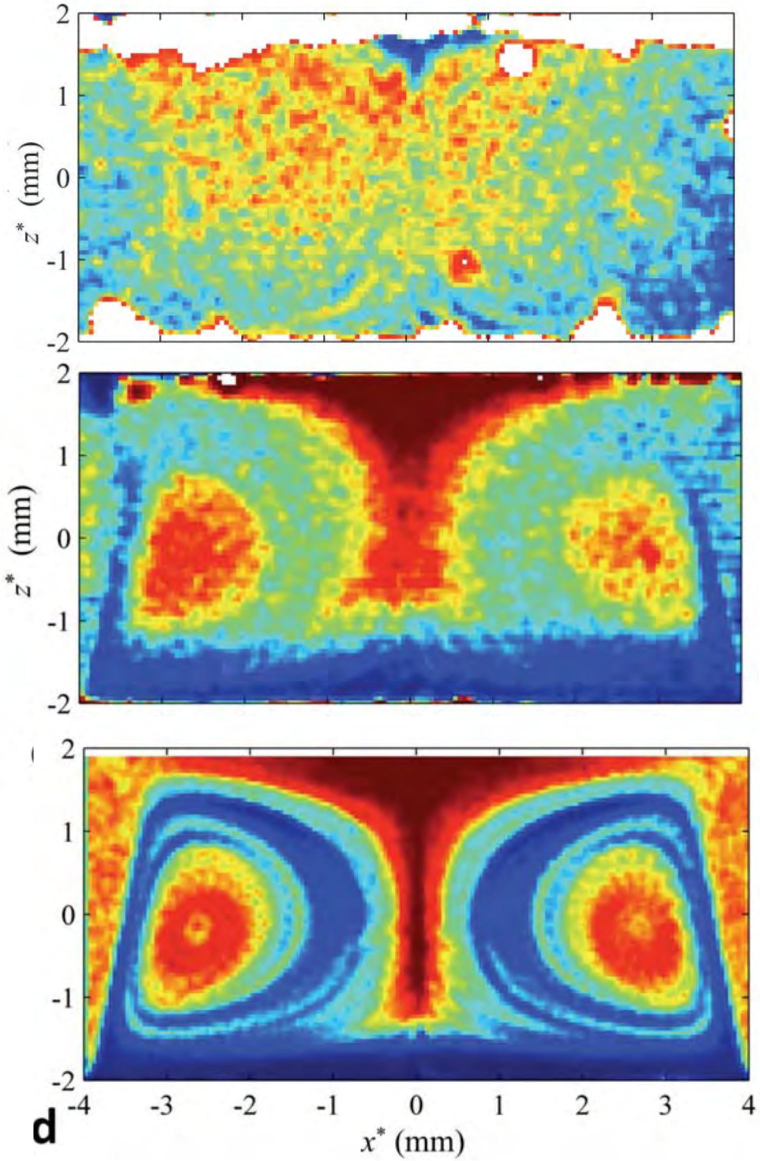
heterosigma akashiwo



a toxic algae



cell's concentration



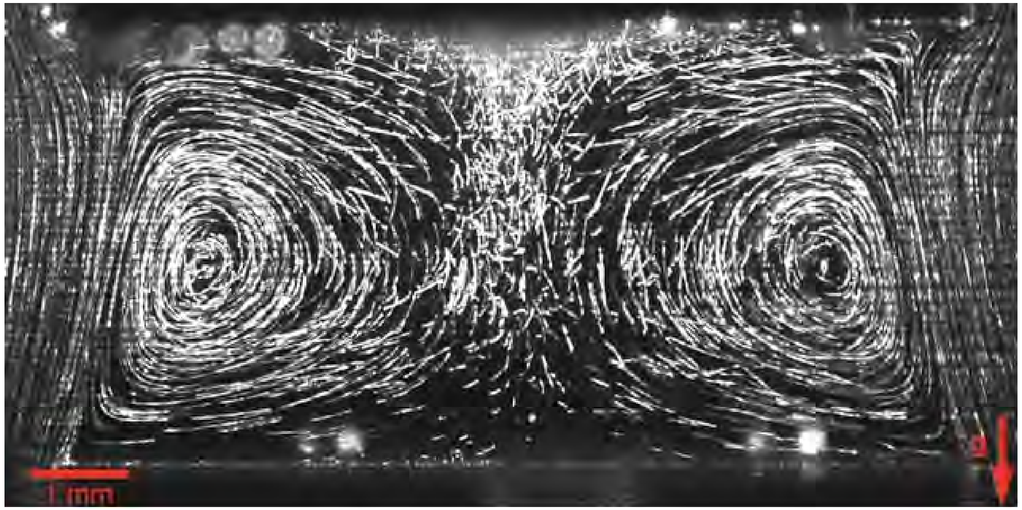
experiment
dead cells

experiment
alive cells

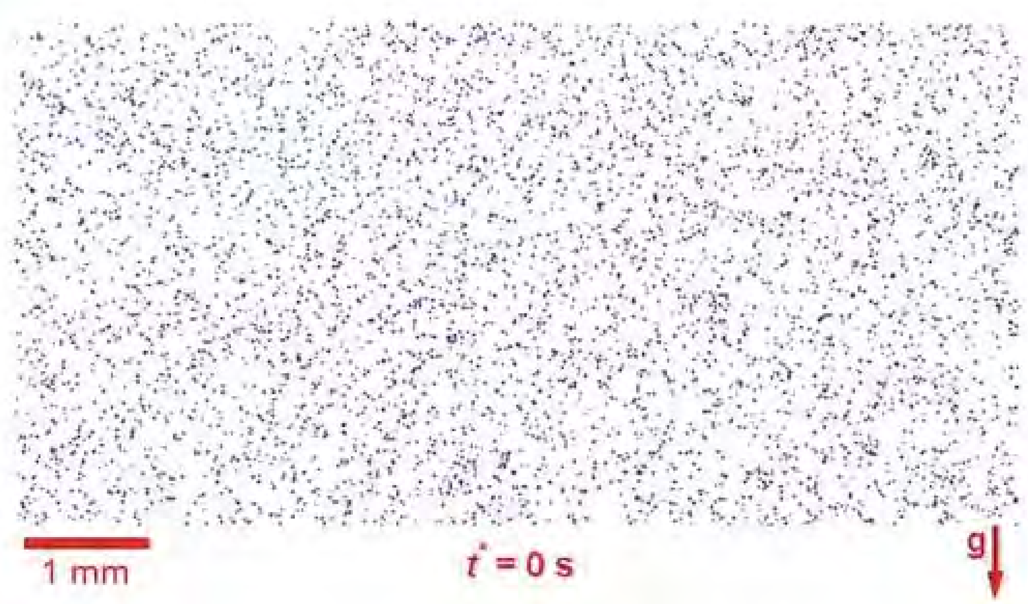
simulation
COMSOL

Experiment in vortical flows

experiment



simulation



observations:
Cells accumulate in the downwelling region between vortices and slightly in the vortex cores

model validation:
Good agreement between experiment and simulation of model equations with B, v_s measured independently

questions:
What does happen in realistic turbulent flows which are unsteady and characterized by a multitude of flow structures?

Gyrotactic swimmers in turbulence

swimmers dynamics

$$\dot{\boldsymbol{X}} = \boldsymbol{u}(\boldsymbol{X}, t) + v_s \boldsymbol{p}$$

$$\dot{\boldsymbol{p}} = \frac{1}{2B}[\hat{\mathbf{z}} - (\hat{\mathbf{z}} \cdot \boldsymbol{p})\boldsymbol{p}] + \frac{1}{2}\boldsymbol{\omega}(\boldsymbol{X}, t) \times \boldsymbol{p}$$

typical numbers

$d \approx 10\mu m$ size

$B \approx 1 - 10s$ orientation time

$v_s = 50 - 500\mu m/s$ swimming velocity

nondimensional cells' parameters

swimming number $\quad \boldsymbol{\Phi} = \dfrac{v_s}{u_\eta}$

stability number $\quad \boldsymbol{\Psi} = B\omega_\eta = \dfrac{B}{\tau_\eta}$

$\boldsymbol{\Psi} << 1$ **stable cells:** directional bias is effective

$\boldsymbol{\Psi} >> 1$ **unstable cells:** tumbling

fluid dynamics

$$\partial_t \boldsymbol{u} + \boldsymbol{u} \cdot \boldsymbol{\nabla} \boldsymbol{u} = \nu \Delta \boldsymbol{u} - \boldsymbol{\nabla} p + \boldsymbol{F}$$

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

typical turbulent scales

$\eta = (\nu^3/\epsilon)^{1/4}$ length

$\tau_\eta = (\nu/\epsilon)^{1/2}$ time

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

$\omega_\eta = 1/\tau_\eta$ vorticity

control parameter

$$Re_\lambda = \frac{u_{rms}\lambda}{\nu} \approx \sqrt{Re}$$

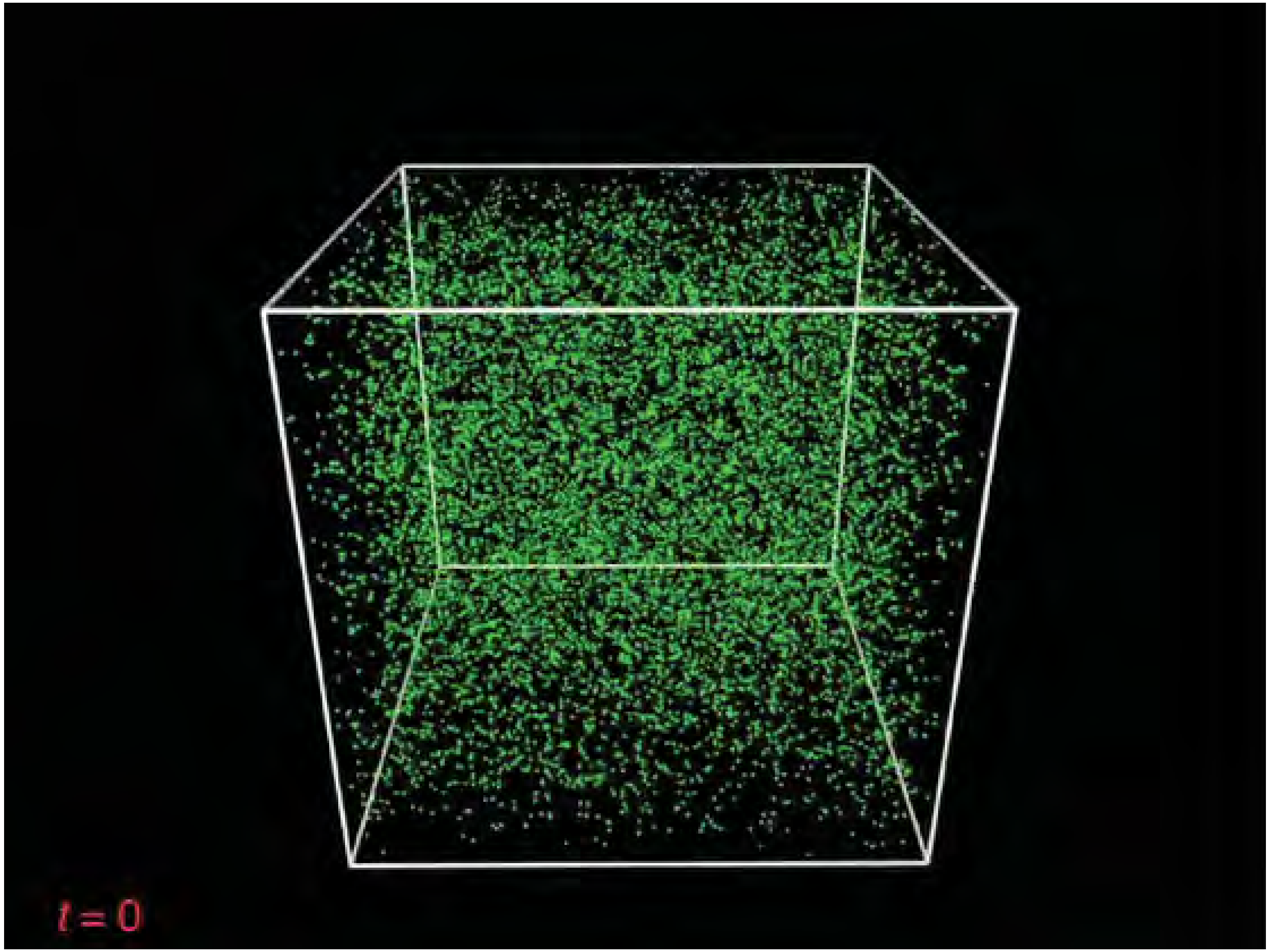
typical values in oceans

ϵ (m^2/s^3)	τ_η (s)	η (mm)	u_η ($\mu m/s$)
10^{-8}	10	3,16	316
10^{-6}	1	1	1.000

Gallager et al Mar. Ecol. Prog. Ser (2004)

in natural conditions values $\boldsymbol{\Psi}$,$\boldsymbol{\Phi} \sim O(1)$ are easily achieved

Gyrotactic phytoplankton in turbulence



Why cells cluster?
Where do they cluster?
How clustering depends on parameters?

Why? Dissipative dynamics

$$\dot{\boldsymbol{X}} = \boldsymbol{v} = \boldsymbol{u} + \Phi \boldsymbol{p}$$
$$\dot{\boldsymbol{p}} = \frac{1}{2\Psi}[\hat{\mathbf{z}} - (\hat{\mathbf{z}} \cdot \boldsymbol{p})\boldsymbol{p}] + \frac{1}{2}\boldsymbol{\omega} \times \boldsymbol{p}$$

$$\partial_t \boldsymbol{u} + \boldsymbol{u} \cdot \boldsymbol{\nabla} \boldsymbol{u} = \nu \Delta \boldsymbol{u} - \boldsymbol{\nabla} p + \boldsymbol{F}$$
$$\boldsymbol{\nabla} \cdot \boldsymbol{u} = 0$$

u "stochastic" & smooth at small scales r<η

smooth dissipative dynamical system in phase space (**X,p**) of dimension 2d-1 with phase-space volume contraction rate

$$\Gamma \tau_\eta = \tau_\eta \sum_{i=1}^{d} \frac{\partial \dot{X}_i}{\partial X_i} + \frac{\partial \dot{p}_i}{\partial p_i} = -\frac{d-1}{2\Psi} p_z$$

from general considerations on dissipative dynamical systems

(multi-)fractal dynamical attractor with $D_2 < 2d-1$

if $D_2 < d$ clustering is observed in position space

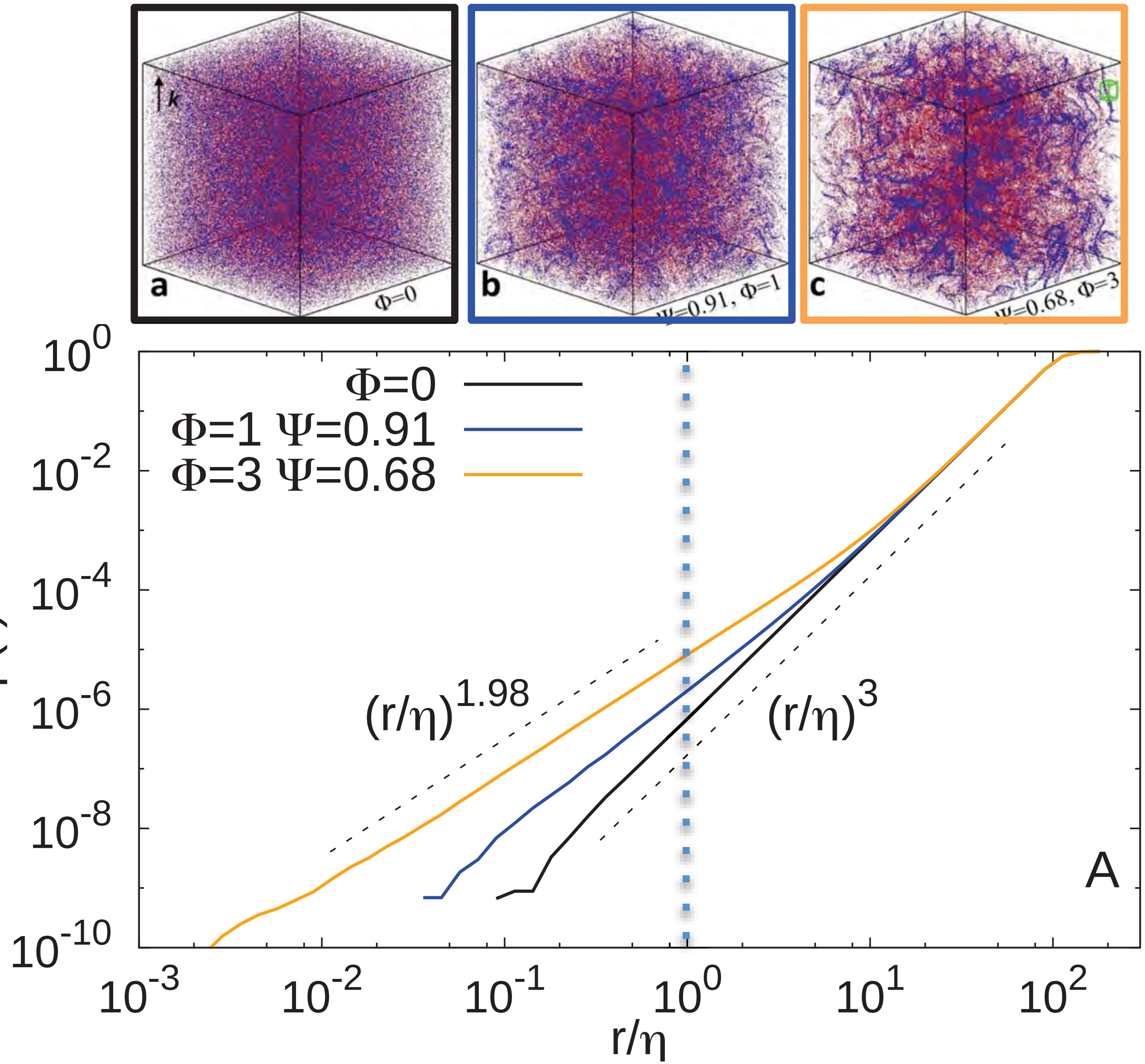
Fractal clustering

correlation dimension

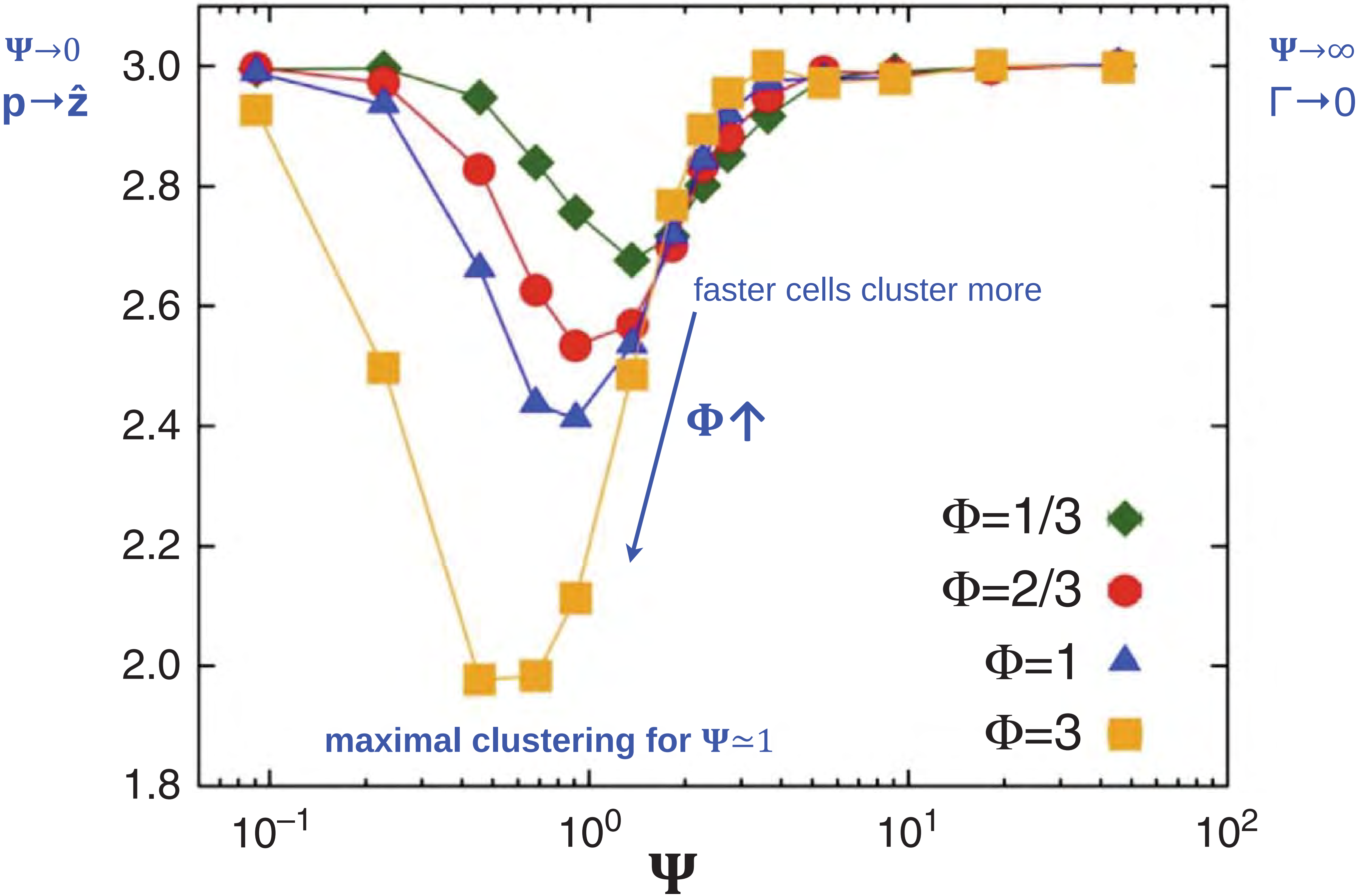
$$p(r) = Prob\{|\boldsymbol{X}_i - \boldsymbol{X}_j| \leq r\}$$

$$\boxed{p(r) \sim r^{D_2}}$$

$D_2<3$ fractal clustering



Fractal clustering



Limit of stable cells Ψ<<1

$$\dot{\boldsymbol{X}} = \boldsymbol{v} = \boldsymbol{u} + \Phi \boldsymbol{p}$$

$$\dot{\boldsymbol{p}} = \frac{1}{2\Psi}[\hat{\mathbf{z}} - (\hat{\mathbf{z}} \cdot \boldsymbol{p})\boldsymbol{p}] + \frac{1}{2}\boldsymbol{\omega} \times \boldsymbol{p}$$

$$\partial_t \boldsymbol{u} + \boldsymbol{u} \cdot \boldsymbol{\nabla} \boldsymbol{u} = \nu \Delta \boldsymbol{u} - \boldsymbol{\nabla} p + \boldsymbol{F}$$

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

if $\boldsymbol{\Psi}$<<1 assuming equilibrium $\dot{\mathbf{p}} \approx 0$

to leading order $\mathbf{p}_{eq} \approx (\Psi\omega_y, -\Psi\omega_x, 1)$.

cell velocity field

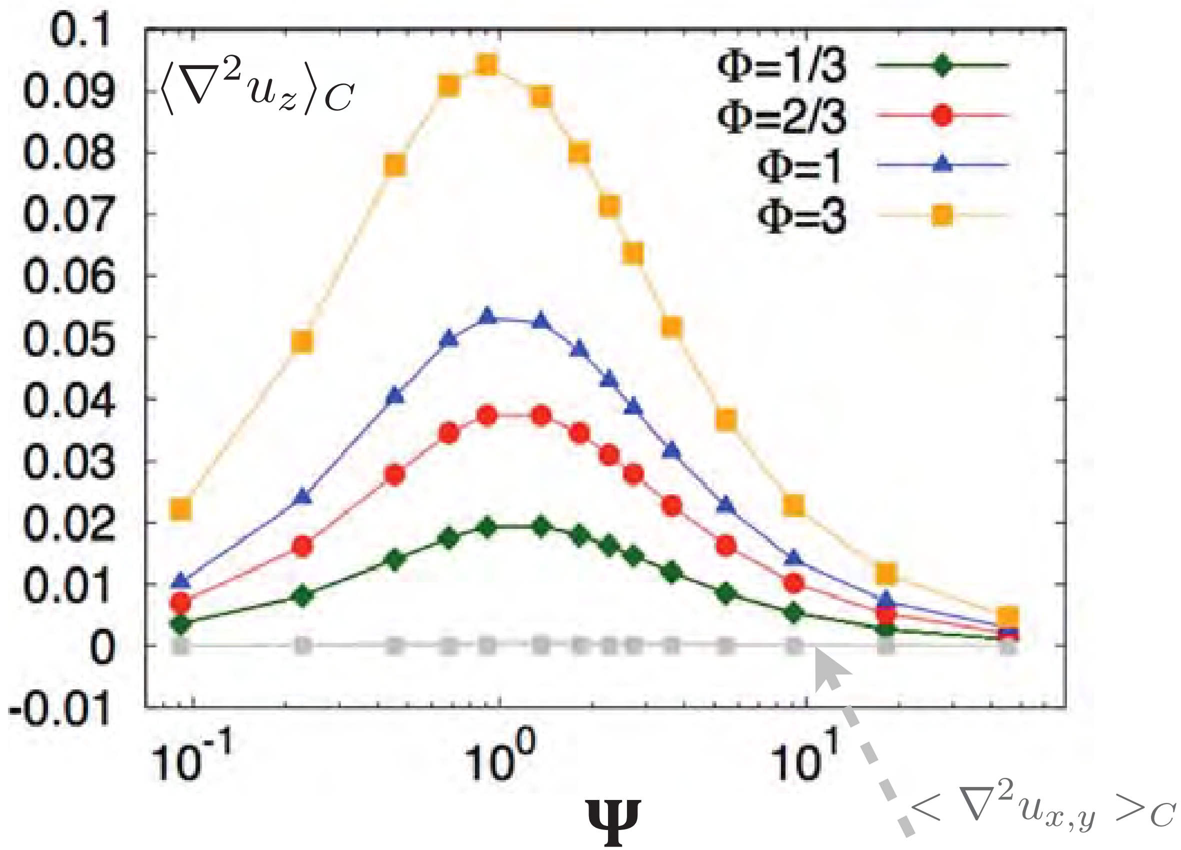
$$\boldsymbol{v} = \boldsymbol{u} + \Phi \boldsymbol{p}_{eq}$$

is compressible

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

accumulation in compressing regions

$$\boldsymbol{\nabla} \cdot \boldsymbol{v} < 0 \Longrightarrow \nabla^2 u_z > 0$$



Prediction on fractal dimension

tracers in weakly compressible flows

$$\dot{\boldsymbol{X}} = \boldsymbol{v} = \boldsymbol{u} + \boldsymbol{u}'$$

ε<<1 d-D2 ∝ ε²

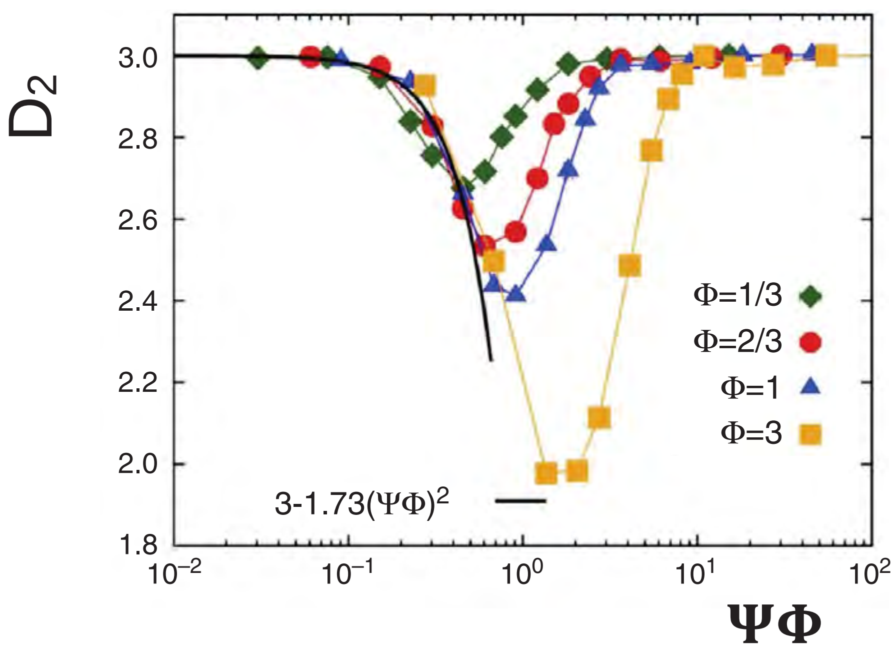
$$\boldsymbol{\nabla} \cdot \boldsymbol{v} = \boldsymbol{\nabla} \cdot \boldsymbol{u}' = O(\epsilon)$$

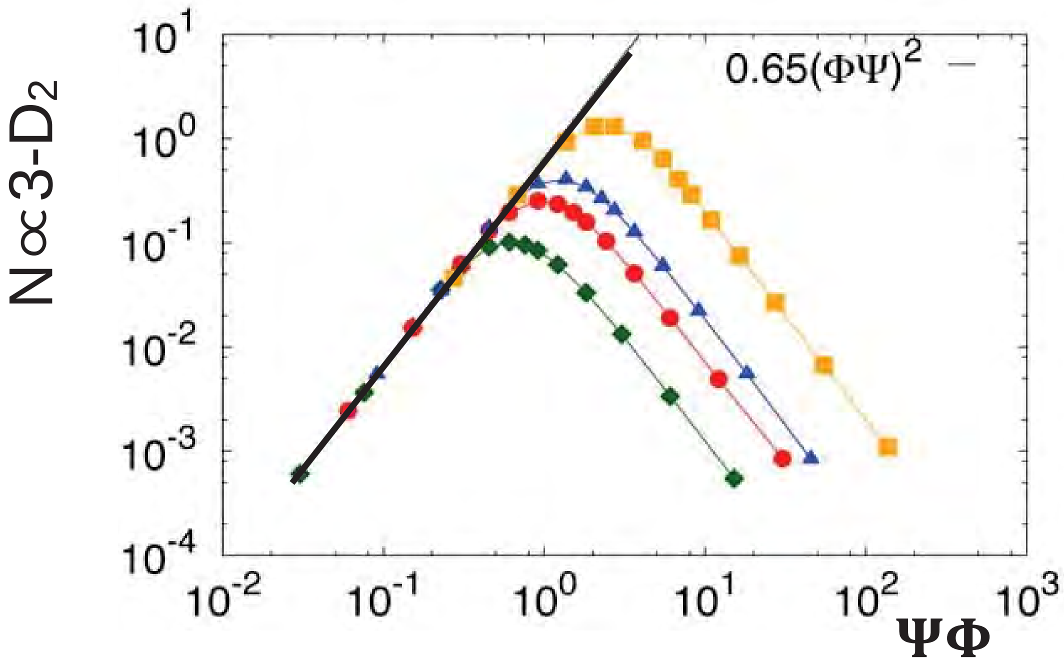
Falkovich et al Nature (2002), Fouxon PRL (2011)

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

for $\boldsymbol{\Psi}$<<1 $\boldsymbol{\nabla} \cdot \boldsymbol{v} = -\Psi\Phi\nabla^2 u_z$

$$d - D_2 \propto (\Psi\Phi)^2$$





n- number of particles in a box of size Λ≈O(η)

$$\sigma^2 = \langle n^2 \rangle - \langle n \rangle^2 \qquad \sigma_P^2 = \langle n \rangle$$

$N = (\sigma - \sigma_P)/\langle n \rangle \propto$ 3-D2

Dubrulle and Lachiéze-Rey A&A (1994)

Where do cells go?

compressible cell velocity field

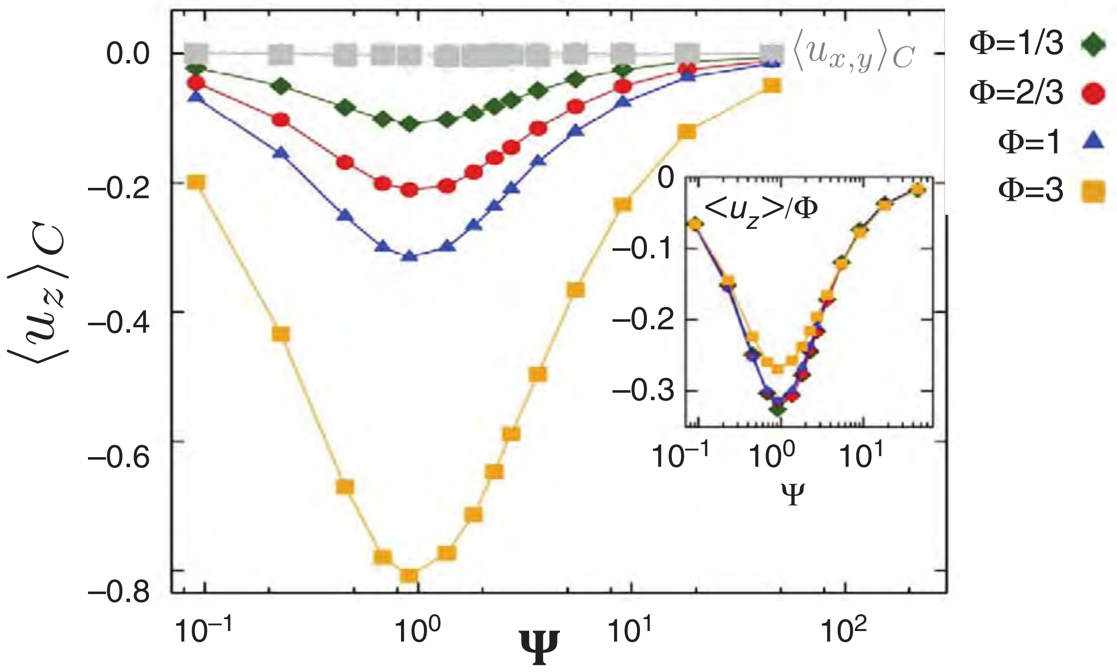
$$\nabla \cdot \boldsymbol{v} = -\Psi\Phi\nabla^2 u_z < 0 \Longrightarrow \nabla^2 u_z > 0$$

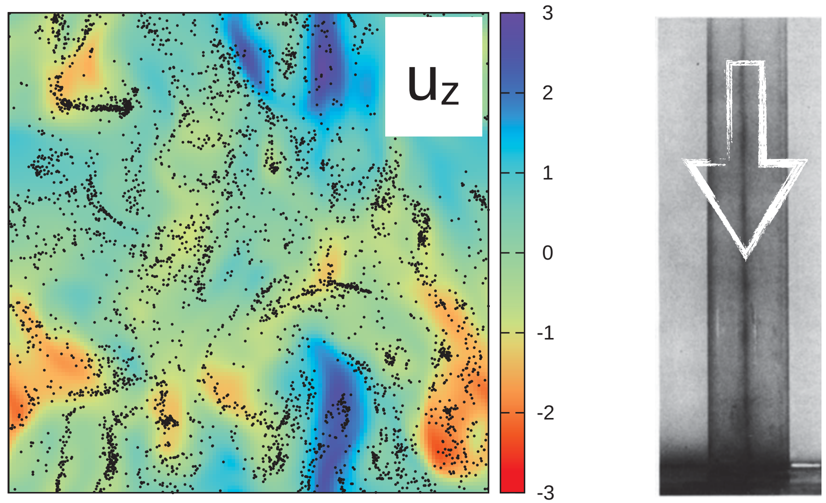
Energy dissipation in isotropic turbulence

$$0 < \epsilon = \nu\langle(\nabla\mathbf{u})^2\rangle = -3\nu\langle u_z \nabla^2 u_z\rangle$$

$$\nabla^2 u_z > 0 \Longrightarrow u_z < 0$$

preferential accumulation in downwelling flow regions



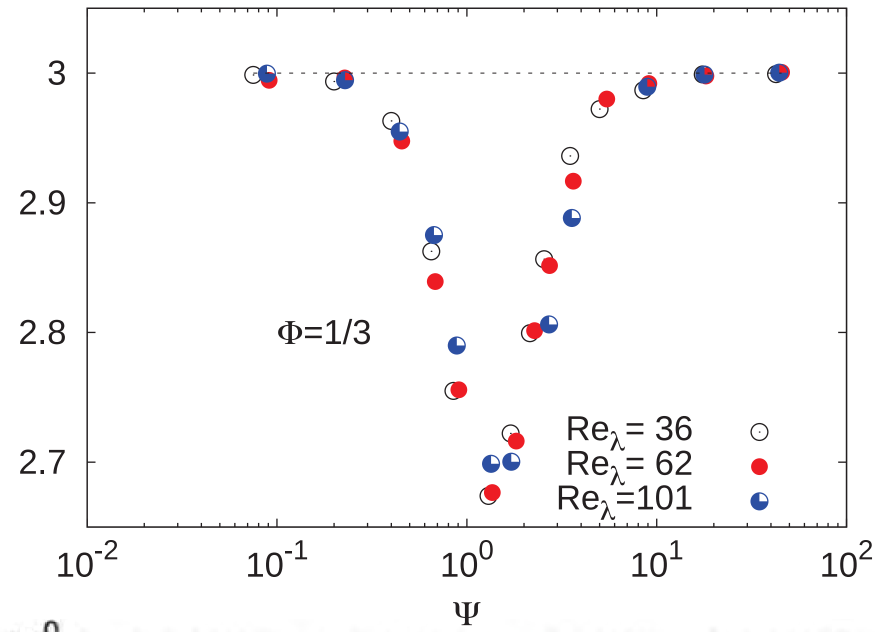


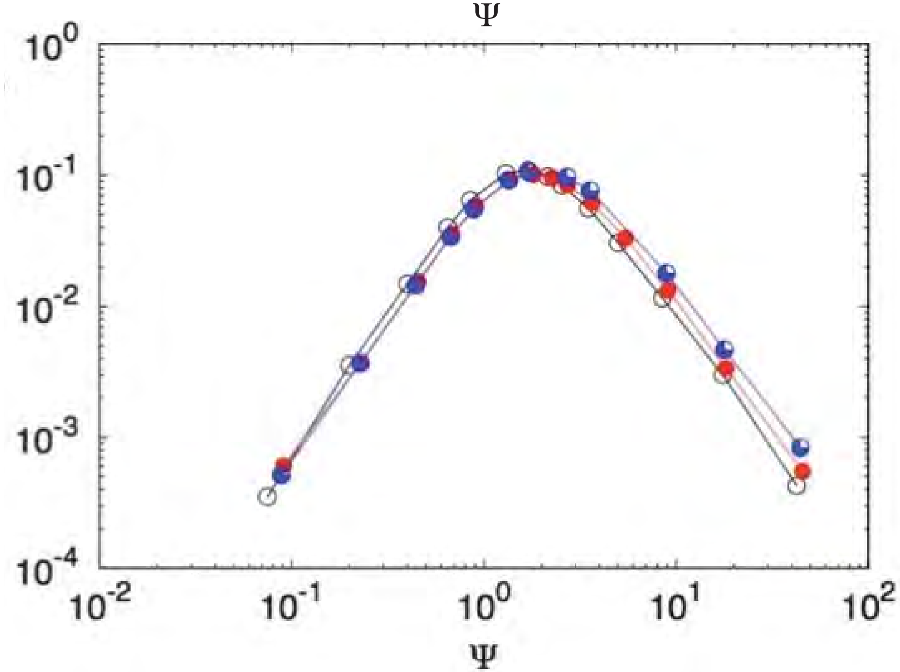
this mechanism generalizes to turbulent flows
Kessler observation in pipe laminar flows

The mechanism of preferential accumulation may be more general
(Gustavsson et al PRL (2016))

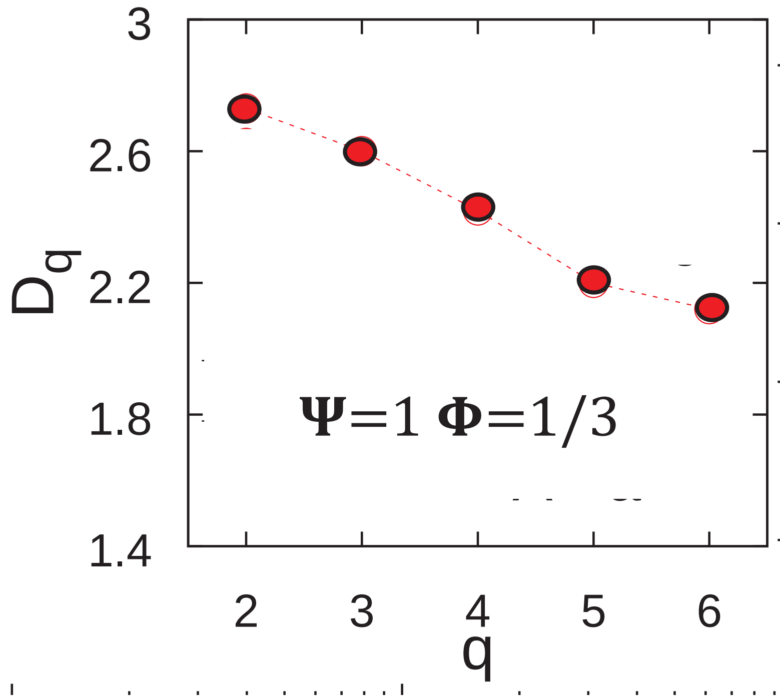
Reynolds dependence & multifractality

weak (if any) Re dependence





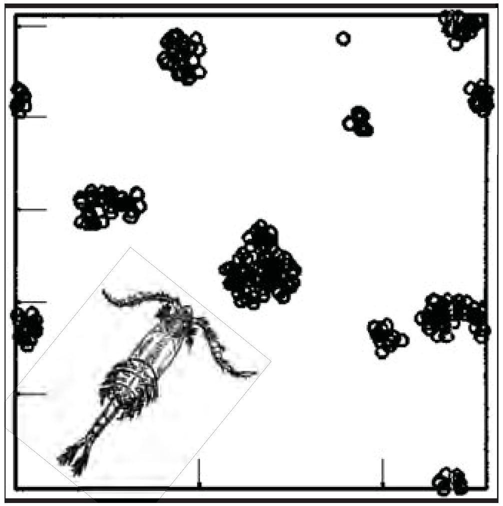
multifractal distribution



the generalized dimensions display a non-trivial dependence on the order q demonstrating the presence of multifractality as expected

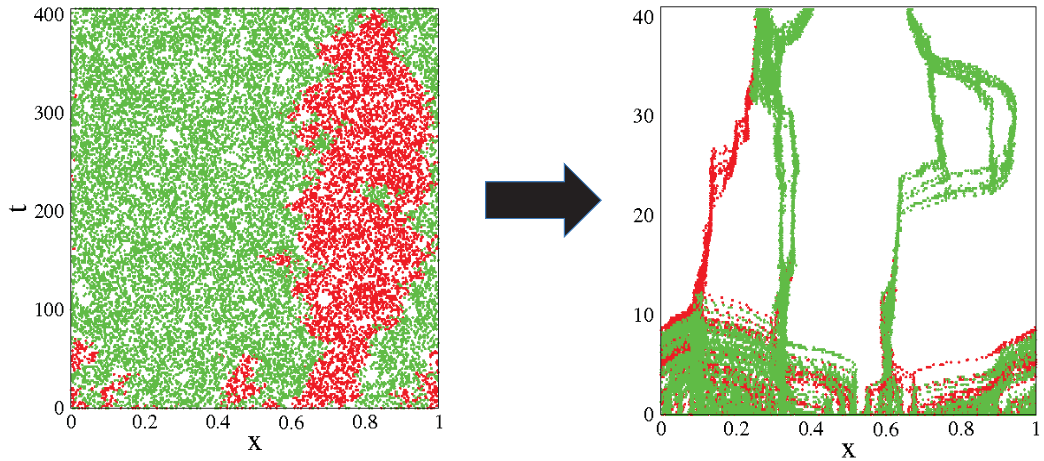
Why small scale clustering may be important?

Predations



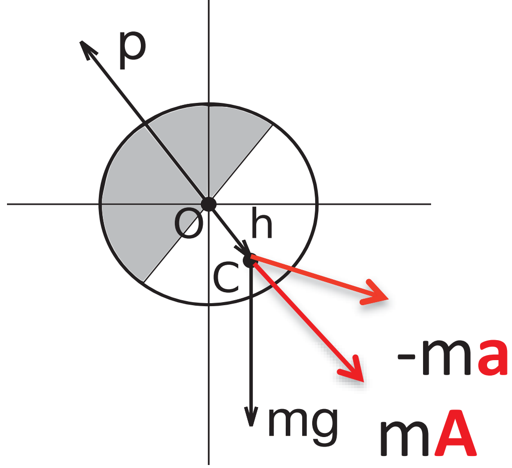
Reproduction

Population dynamics
in compressible flows



Benzi, Jensen, Pigolotti, Nelson (2012)

Model refinement



Bottom heaviness makes the cell an accelerometer so cell acceleration due to the fluid should also matter summing up to gravitational acceleration

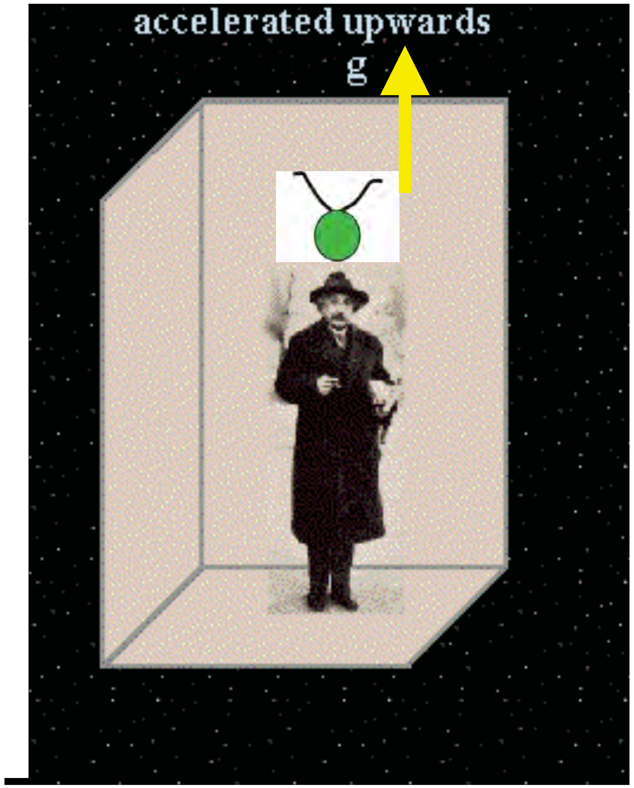
$V_0 = \frac{3\nu}{h}$ re-orientation speed spherical cells

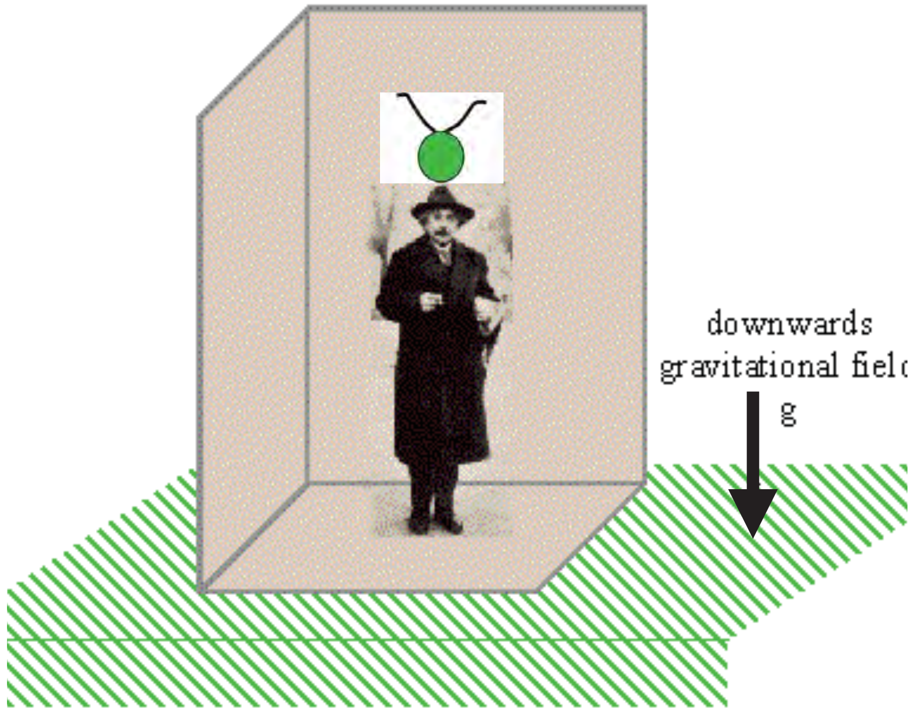
$B = \frac{V_0}{g}$ re-orientation time

$$\dot{\boldsymbol{p}} = -\frac{1}{2V_O}[\boldsymbol{A} - (\boldsymbol{A}\cdot\boldsymbol{p})\boldsymbol{p}] + \frac{1}{2}\boldsymbol{\omega}\times\boldsymbol{p}$$

a fluid acc. at cell position

A=g-a total acc. felt by the cell



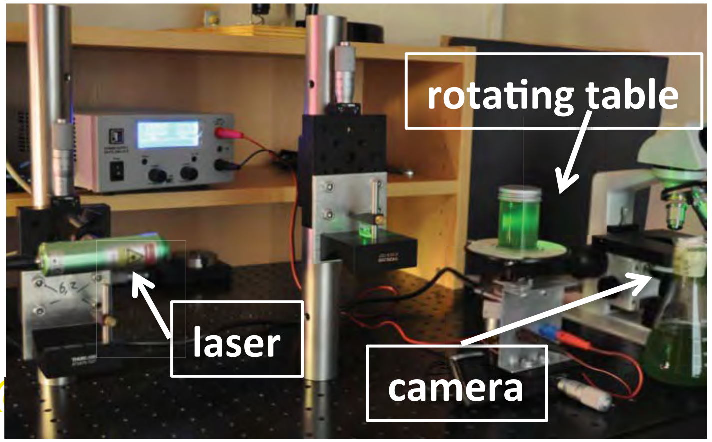


Gyrotaxis in uniform vorticity

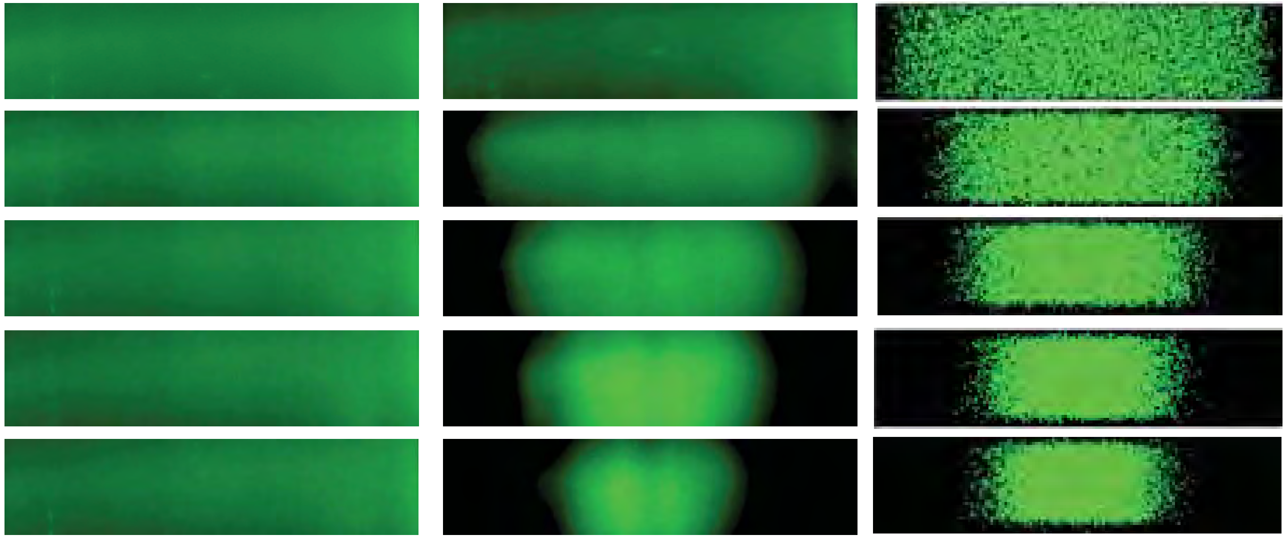
model with gravitational bias only ➔ NO FOCUSING
refined model with fluid acceleration ➔FOCUSING

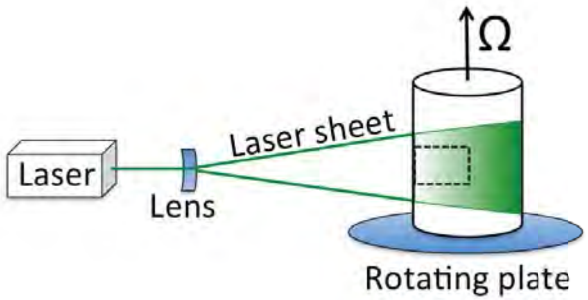
due to fluid acc swimming direction is centripetal

rotational diffusion stabilizes cells' distribution
in its absence model predicts cells' collapse on rotation axis



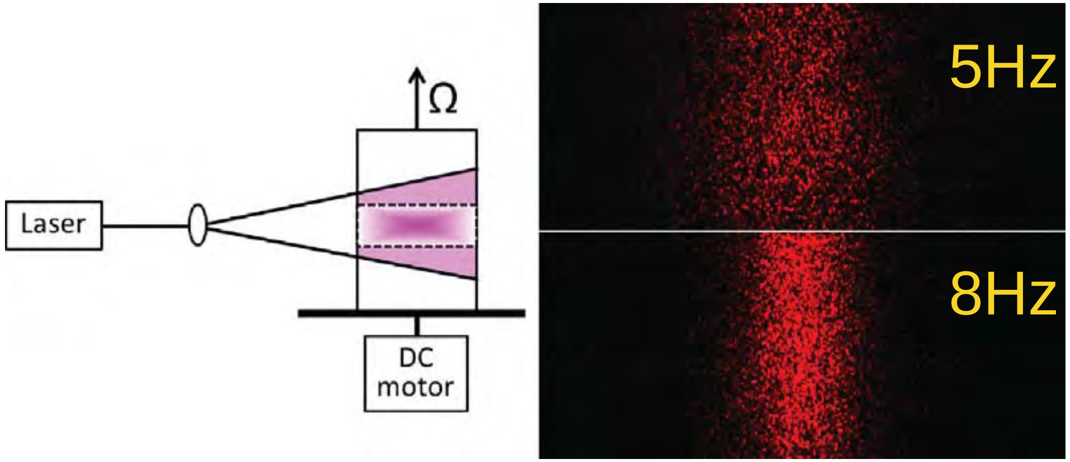
laboratory setup





the "standard" model without fluid acceleration would not reproduce the experiment

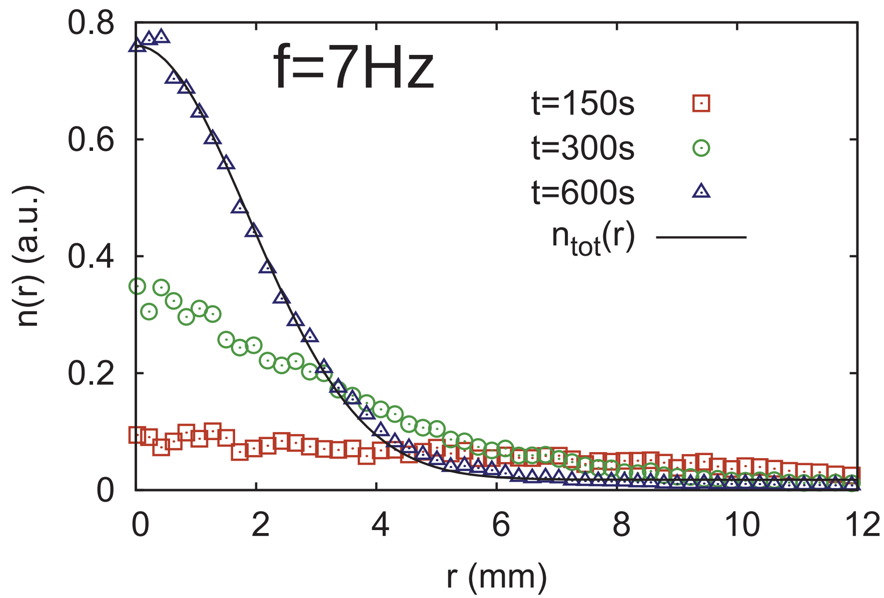
Gyrotaxis in uniform vorticity



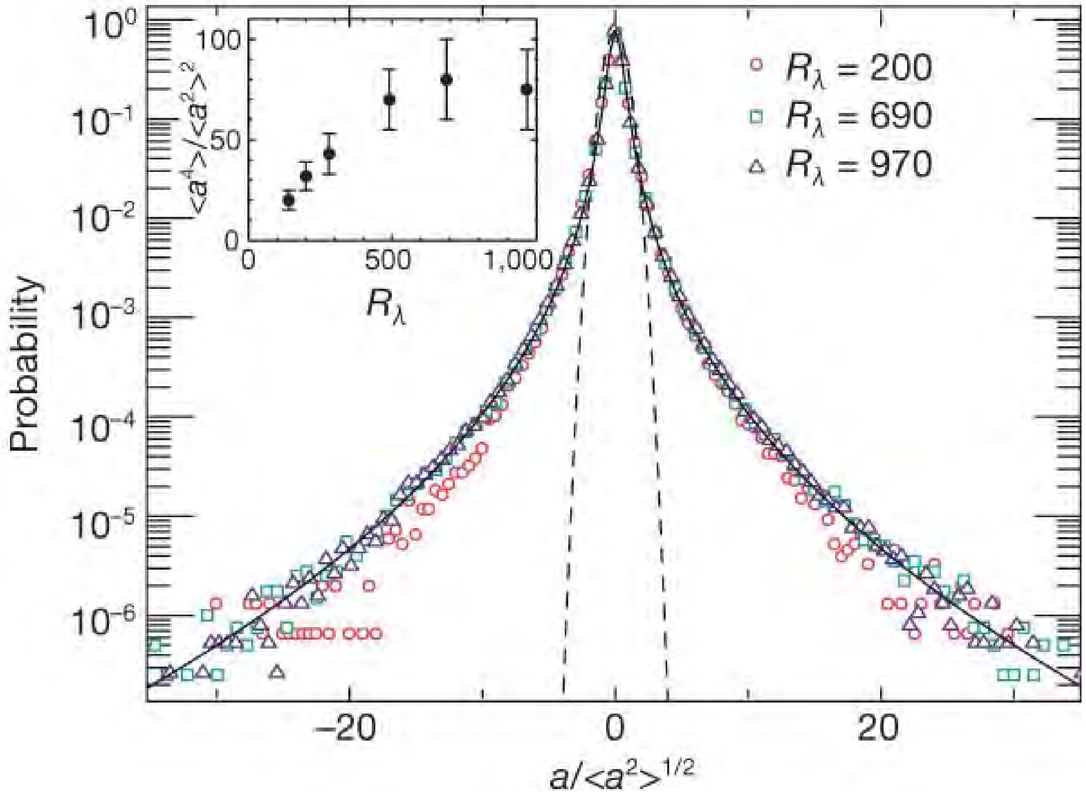
Input: laser 655nm (blue)
output: cell fluorescence 450nm (red)

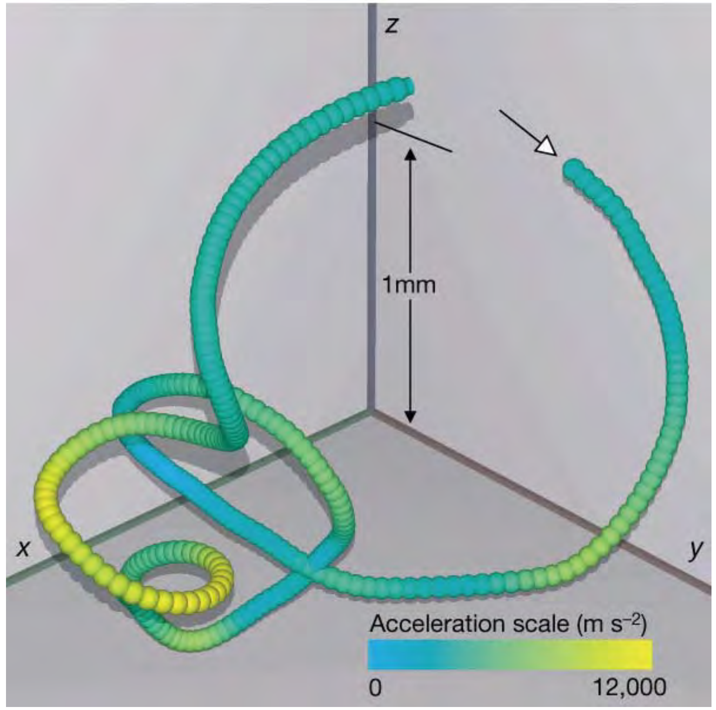
Chlamydomonas augustae
low concentration 1-5 10^4cells/ml

Radial distribution **n(r,t)** as a function of time

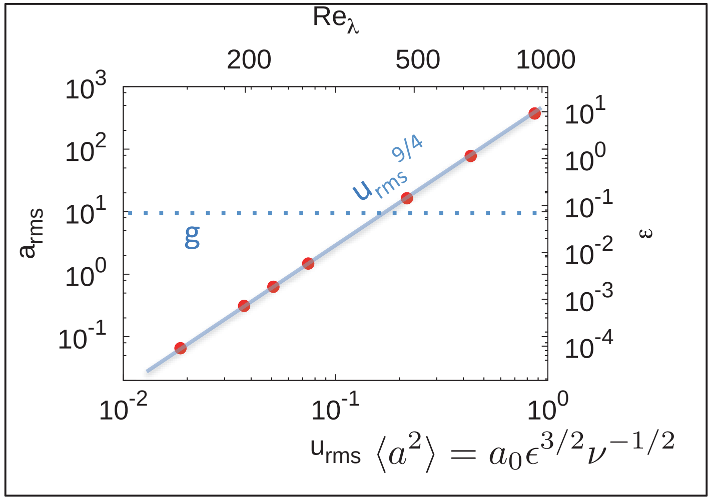


Why acceleration may be important?





La Porta et al Nature (2001)



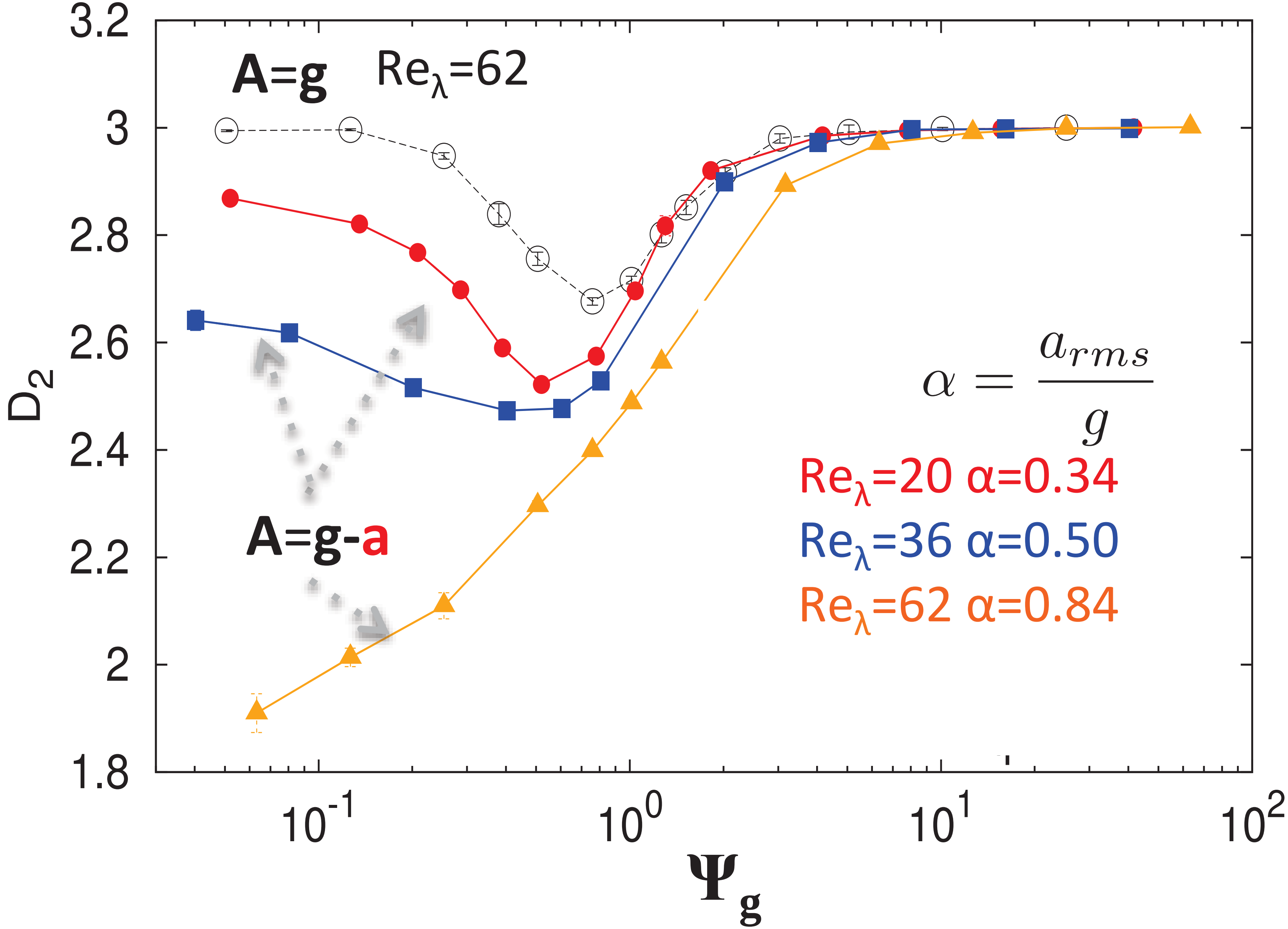
from Voth *et al*, JFM (2002)

fluid acceleration is important at high Re
even when a_{rms}<g locally a(**x**,t)>g

high acceleration associated to small scale vortices

previous results hold when g >> a_{rms}
what does happen when a_{rms} >> g?

Effect of turbulent acceleration



turbulent acceleration enhances small scale clustering

Clustering in high vorticity regions

g=0 $\dot{\boldsymbol{X}} = \boldsymbol{v} = \boldsymbol{u} + \Phi \mathrm{p}$

$$\dot{\mathbf{p}} = \frac{1}{2\Psi_a}[\boldsymbol{a} - (\boldsymbol{a}\cdot\mathbf{p})\mathbf{p}] + \frac{1}{2}\boldsymbol{\omega}\times\mathbf{p}$$

$$\boldsymbol{a} = \partial_t \boldsymbol{u} + \boldsymbol{u}\cdot\boldsymbol{\nabla}\boldsymbol{u} = \nu\Delta\boldsymbol{u} - \boldsymbol{\nabla}p + \boldsymbol{F}$$

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

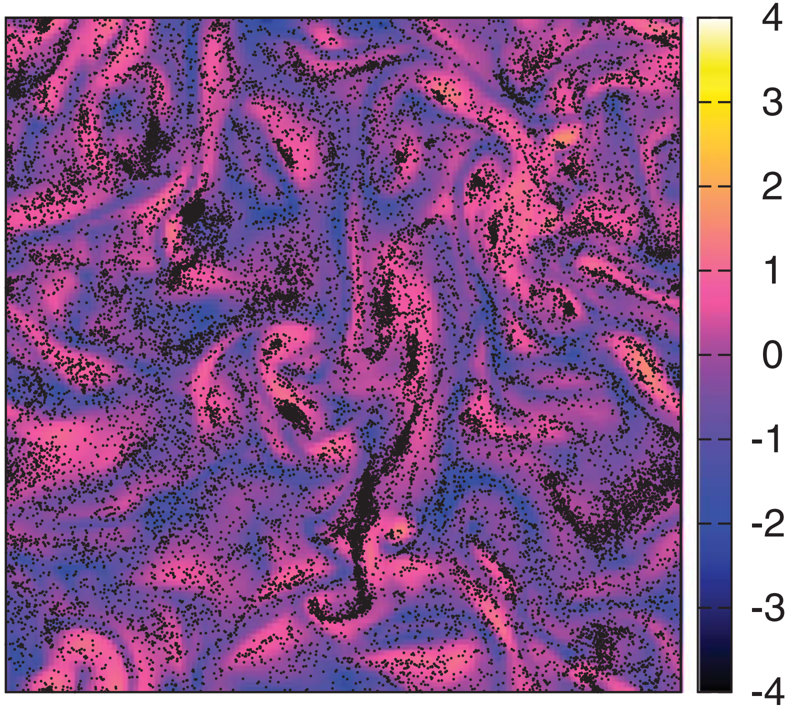
$$\Psi_a = \frac{v_O \omega_{rms}}{a_{rms}}$$

if $\Psi_a \to 0$ to leading order $\mathbf{p} \to \hat{\boldsymbol{a}}$

$$\boldsymbol{v} = \boldsymbol{u} + \Phi\hat{\boldsymbol{a}}$$

compressible effective flow

$$\boldsymbol{\nabla}\cdot\boldsymbol{v} \approx \Phi\boldsymbol{\nabla}\cdot\hat{\boldsymbol{a}} \sim \Phi\boldsymbol{\nabla}\cdot\boldsymbol{a} = \Phi\left(S^2 - \Omega^2\right)$$ **< 0**



Effects of fluid acceleration

dissipative dynamics -> fractal clustering

weak compressibility $\boldsymbol{\Phi} << 1$

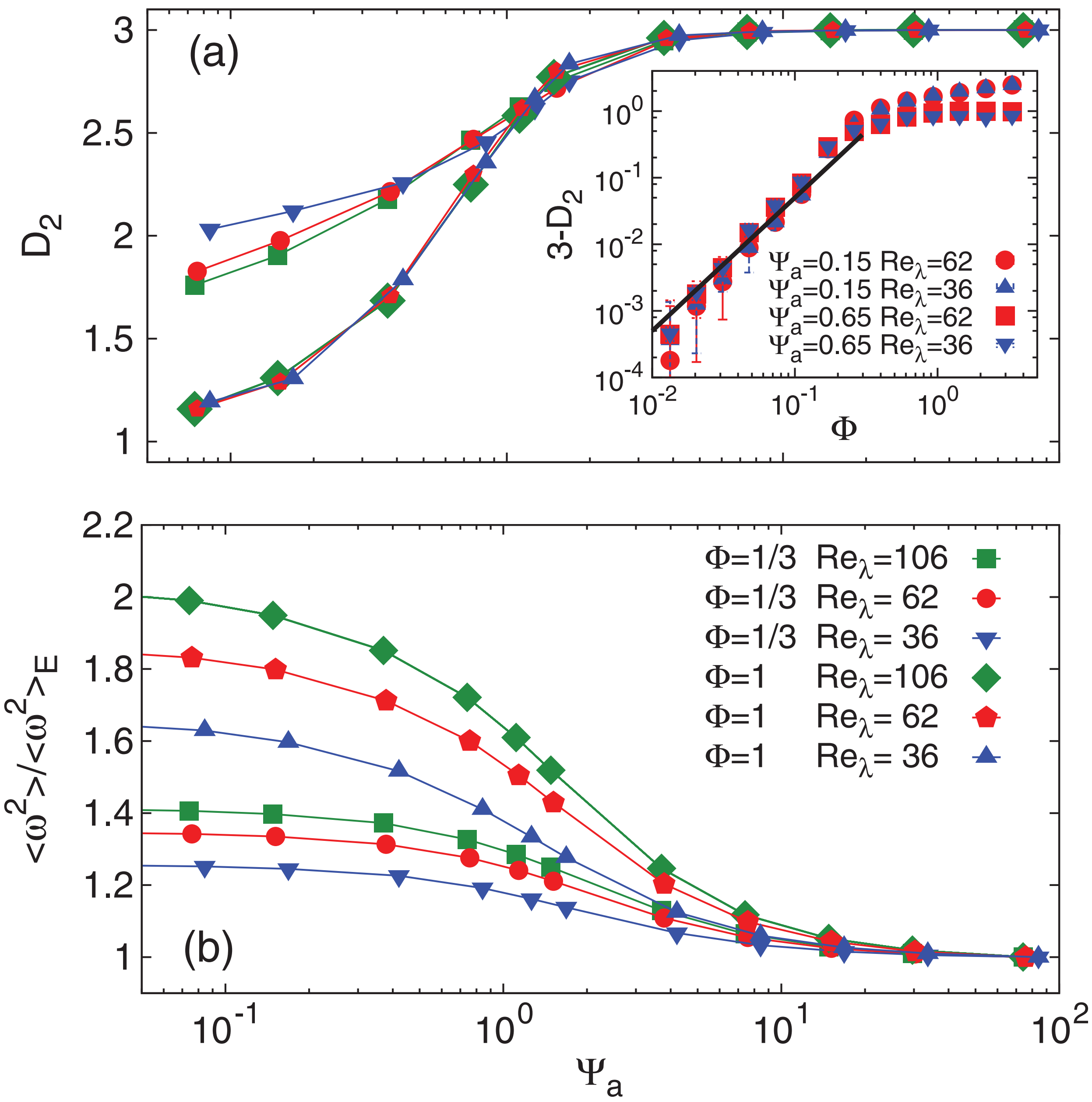
$$3 - D_2 \propto \Phi^2$$

compressible flow

$$\boldsymbol{\nabla} \cdot \boldsymbol{v} \approx \Phi \boldsymbol{\nabla} \cdot \hat{\boldsymbol{a}} \sim \Phi \boldsymbol{\nabla} \cdot \boldsymbol{a}$$

accumulation in high vorticity regions

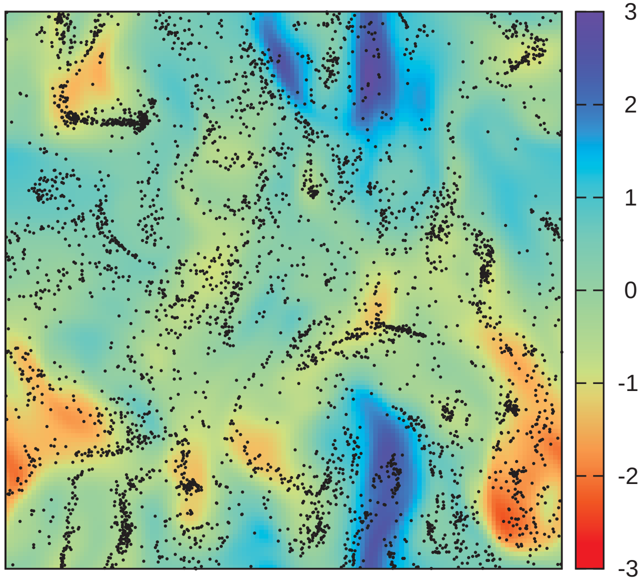
$$\boldsymbol{\nabla} \cdot \boldsymbol{v} < 0 \Longrightarrow (S^2 - \Omega^2) < 0$$



Summary

Combination of swimming and turbulence generates small-scale (fractal) patchiness in gyrotactic phytoplankton distribution: ⟸ dissipative dynamics

Small Reynolds numbers (ocean)

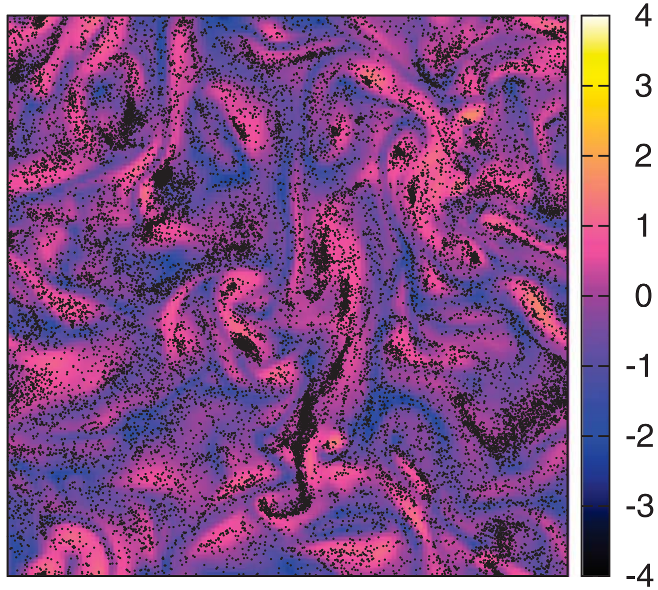


$g \gg a_{rms}$

preferential accumulation in downwelling regions

Large Reynolds numbers (lab)

$g \ll a_{rms}$



preferential accumulation in vorticity regions

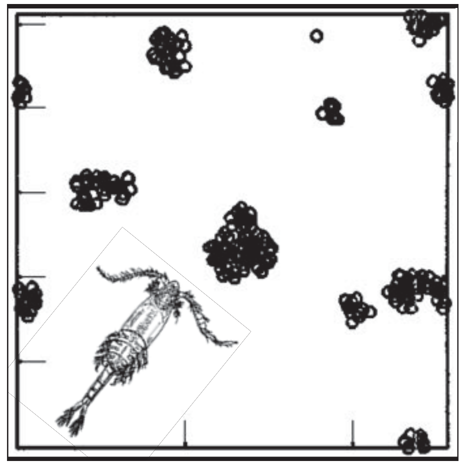
clustering is stronger for faster swimmers
fluid acceleration increases clustering

Durham, Climent, Barry, De Lillo, Boffetta, MC, Stocker Nat Comm (2013)
De Lillo, MC, Durham, Barry, Stocker, Climent, Boffetta PRL (2014)
Santamaria, De Lillo, MC, Boffetta Phys. Fluids (2014)
MC, Santamaria, Franchino, Boffetta JTB (2016)

Perspectives

Predations

understanding how model of predators (zooplankton) perform in fractal patches of preys (gyrotactic cells)



Nutrient uptake

understanding the interplay of swimming, turbulence and clustering in setting the rate of nutrient uptake per cell

Acknowledgments

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Eric Climent

Thanks

extra slides

Gyrotaxis in uniform vorticity

$$\dot{\boldsymbol{x}} = \boldsymbol{u} + v_s \boldsymbol{p}$$

$$\dot{\boldsymbol{p}} = -\frac{1}{2V_O}[\boldsymbol{A} - (\boldsymbol{A}\cdot\boldsymbol{p})\boldsymbol{p}] + \frac{1}{2}\boldsymbol{\omega}\times\boldsymbol{p} + \boxed{\boldsymbol{\Gamma}_r}$$

Rotational diffusion to mimic random effects

$$\boldsymbol{u} = (-\Omega y, \Omega x, 0)$$
$$\boldsymbol{\omega} = (0, 0, 2\Omega)$$
$$\boldsymbol{a} = (-\Omega^2 x, -\Omega^2 y, 0)$$
$$\boldsymbol{A} = (\Omega^2 x, \Omega^2 y, -g)$$

with $\boldsymbol{\Gamma}_r=0$ it is easy to solve in cylindrical coordinates $\mathbf{r}=(x,y)$, z

orientation is the fast process
equilibrium swimming direction

$$\dot{\boldsymbol{p}} = 0 \qquad \mathbf{p}^{eq} = \frac{\boldsymbol{a}-\mathbf{g}}{|(\boldsymbol{a}-\mathbf{g})|} = \left(\frac{-\gamma\mathbf{r}}{\sqrt{1+(\gamma r)^2}}, \frac{1}{\sqrt{1+(\gamma r)^2}}\right) \qquad \gamma = \frac{\Omega^2}{g}$$

$$\dot{r} = -\gamma v_s \frac{r}{\sqrt{1+(\gamma r)^2}} \quad \Rightarrow \quad \frac{r}{r_0}\frac{1+\sqrt{1+(\gamma r_0)^2}}{1+\sqrt{1+(\gamma r)^2}} e^{\sqrt{1+(\gamma r)^2}-\sqrt{1+(\gamma r_0)^2}} = e^{-\gamma v_s t}$$

$$\gamma r \ll 1 \qquad r(t) = r(0)e^{-\gamma v_s t}$$ (ok asymptotically)

BUT our experiments is macroscopic R=2cm times order minutes so random effects in swimming direction cannot be neglected

$D_r \approx 1/15\ s^{-1}$

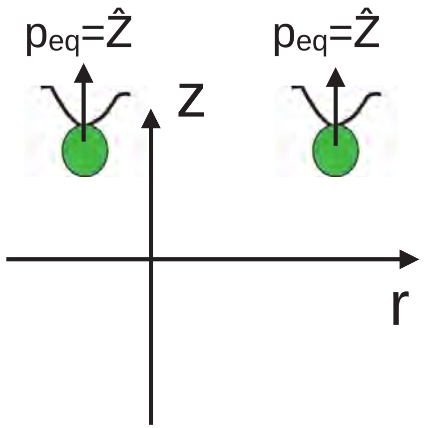
Gyrotaxis in uniform vorticity

Sketch of the idea $P(\boldsymbol{x},\boldsymbol{p},t)$ probability to find a cell in **x** with orientation **p**

$$\partial_t P + \nabla_{\boldsymbol{x}}(\dot{\boldsymbol{x}}P) + \nabla_{\boldsymbol{p}}(\dot{\boldsymbol{p}}P - D_r\nabla_{\boldsymbol{p}}P) = 0$$

$$\partial_t n + \nabla_{\boldsymbol{x}}(\boldsymbol{V}n) - \mathbb{D}\nabla_{\boldsymbol{x}}n) = 0 \quad n(\boldsymbol{x},t) = \int d\boldsymbol{p}P(\boldsymbol{x},\boldsymbol{p},t)$$

This has been solved when **A**=**g** by *R. Bearon, M. Bees & O. Croze (2012)*
assuming orientation is the fast process and using
Generalised Taylor dispersion theory (*I. Frankel H Brenner (1989)*)



A=**g**

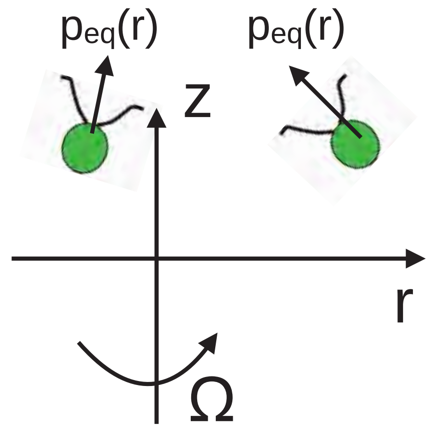
$$\boldsymbol{p}^{\Omega}_{eq} = \mathbb{R}[\Omega, r]\boldsymbol{p}^{0}_{eq}$$

von Mises-Fisher

$$f(\boldsymbol{p}) = \frac{\lambda e^{\lambda \boldsymbol{p}\cdot\hat{\boldsymbol{p}}_{eq}}}{4\pi\sinh\lambda}$$

$$\boldsymbol{V}^{\Omega} = \mathbb{R}\boldsymbol{V}^{0}$$

$$\mathbb{D}^{\Omega} = \mathbb{R}\mathbb{D}^{0}\mathbb{R}^{T}$$



A=**g**-**a**

Gyrotaxis in uniform vorticity

$$\partial_t n + \nabla_{\boldsymbol{x}}(\boldsymbol{V} n) - \mathbb{D}\nabla_{\boldsymbol{x}} n) = 0$$

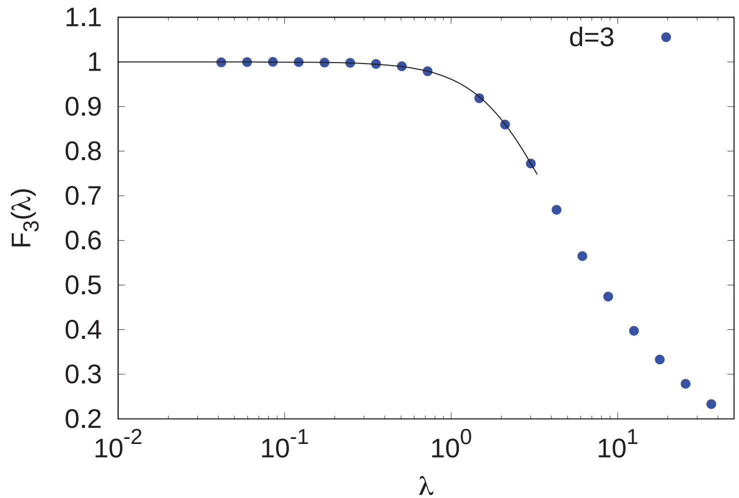
$$V_r(r)n - \mathbb{D}_{rr}(r)dn/dr = 0$$

solving at stationarity in the radial direction

in the limit γr<<1 we have a Gaussian approximation

$$n(r) \propto e^{-G(r)} \qquad G(r) = \frac{1}{2}\frac{\gamma r^2}{v_s B F_3^2(\lambda)}$$

F_3 can be expressed as a series *(Bearon, Bees Croze 2012)*



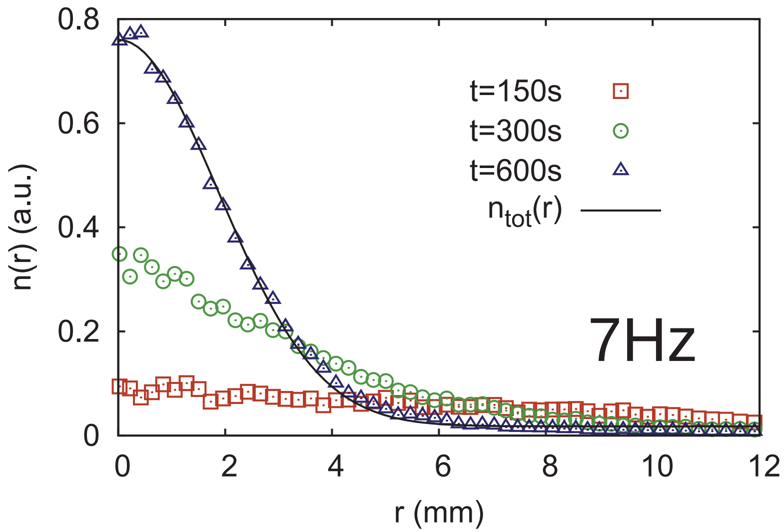
Now the strategy is to fix the parameters from the measurement of stationary distribution and from literature

$$v_s = 100\mu m/s$$
$$D_r = 0.067\, rad/s$$

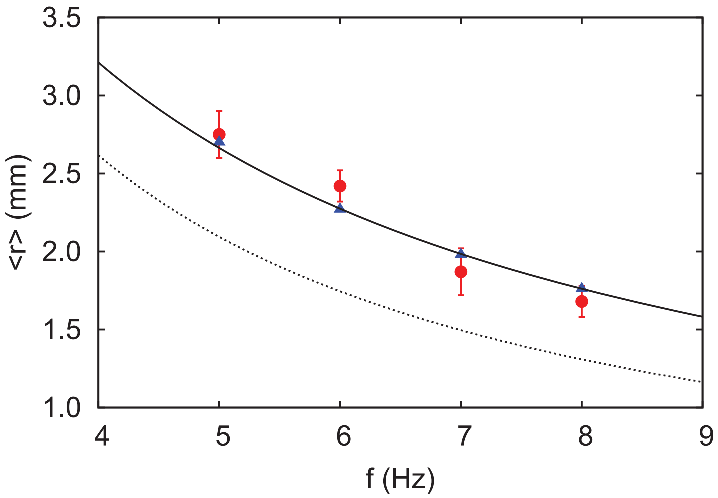
B=7.5s (fitted)

Then we have to take into account the presence of some background we can interpret as non-swimming cells

$$n_t(r,t) = n(r,t) + b$$



Gyrotaxis in uniform vorticity

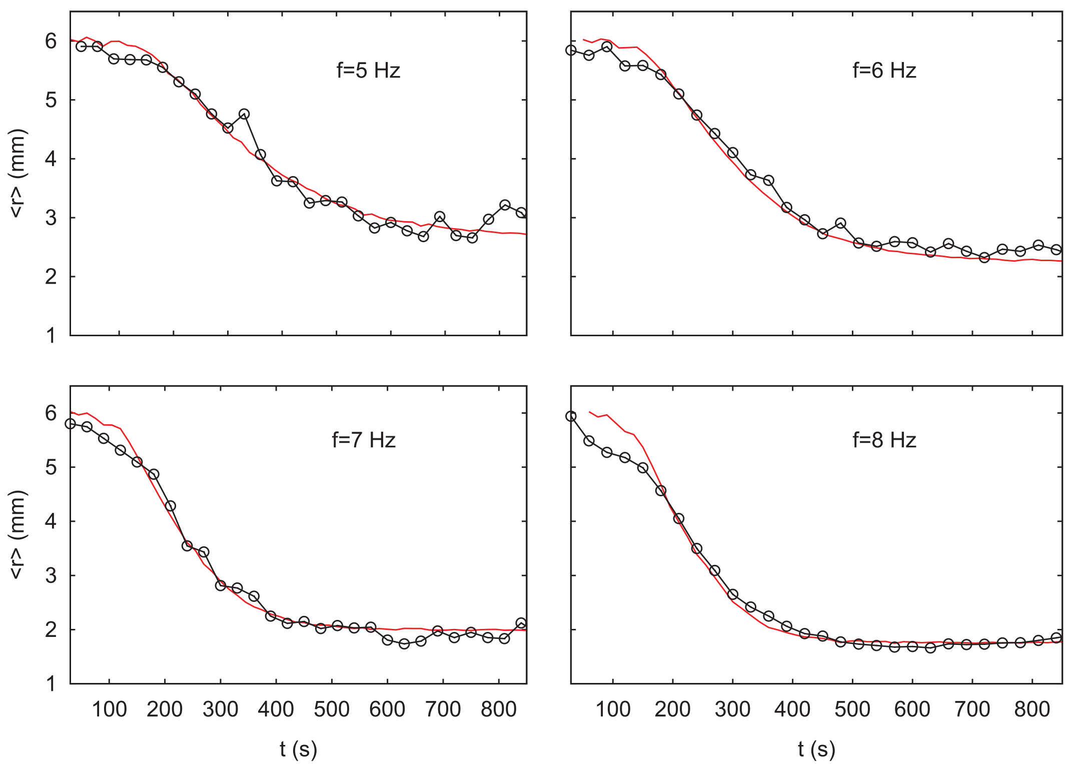


$$\langle r \rangle_s \equiv \frac{\int_0^R r n_s(r)\, dr}{\int_0^R n_s(r)\, dr} = \sqrt{\frac{2}{\pi}} \left(\frac{v_s B}{\gamma} \right)^{1/2} F_3(\lambda).$$

$$\langle r \rangle = \frac{1 + c^2 \beta}{\langle r \rangle_s^{-1} + 2c\beta R^{-1}}$$

taking into account correction due to background
(c relates to geometry)

$$\beta = N_b / N_s$$



evolution of the average radial distance
comparison between experiments (symbols) and stochastic simulations (red) with parameters fixed by measurements done at stationarity