

# Gyrotactic microswimmers in turbulence

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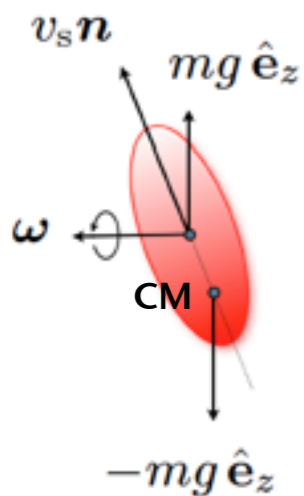
# Active particles

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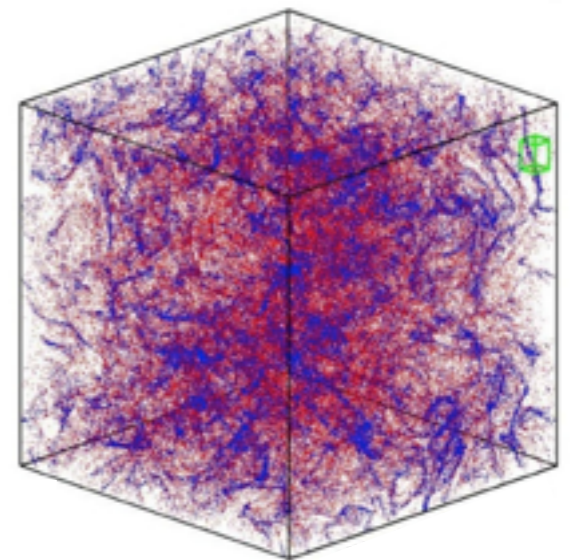
Small-scale patchiness of motile plankton in the unsteady ocean.

Mechanisms: density stratification, predator-prey cycles, chemotaxis, phototaxis, gravitaxis.

DNS of gyrotactic, neutrally buoyant, spherical plankton in turbulence show small-scale patchiness. Theory: strongly gyrotactic plankton gather in downwelling regions of the turbulence.



- $-g \hat{\mathbf{e}}_z$  gravity
- $v_s \mathbf{n}$  swimming velocity (active particle)
- $\omega$  rotation by turbulent flow

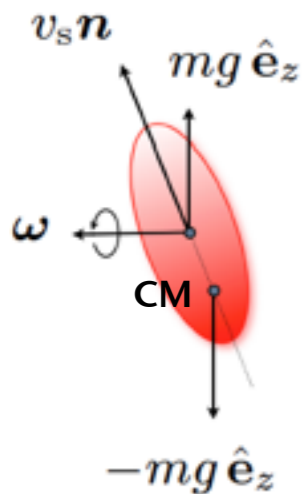


# Active particles

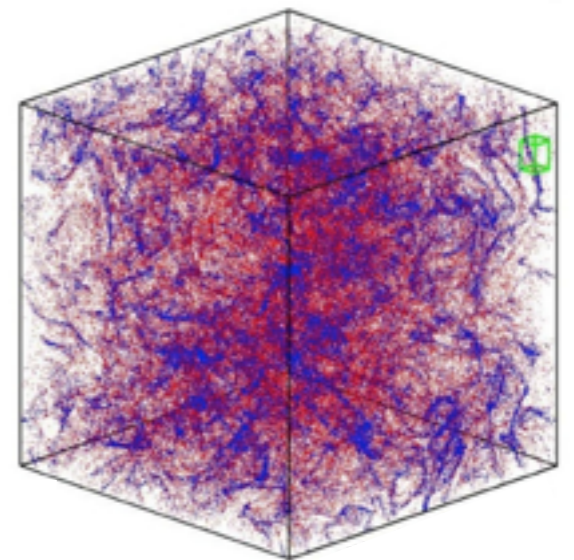
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Assumptions:

- particles neutrally buoyant
- particles move independently of each other
- inertial effects negligible
- particles detach from flow by swimming straight ahead, speed  $v_s \mathbf{n}$
- particles rotated by turbulent flow  
and by gravitational torque (gyrotaxis) since c.o.m. not at centre



- $-g \hat{e}_z$  gravity
- $v_s \mathbf{n}$  swimming velocity  
(active particle)
- $\omega$  rotation by turbulent flow



# Questions

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Formulate and solve statistical model that accounts for the symmetries of the problem. Can be analysed using asymptotic methods and perturbation theory.

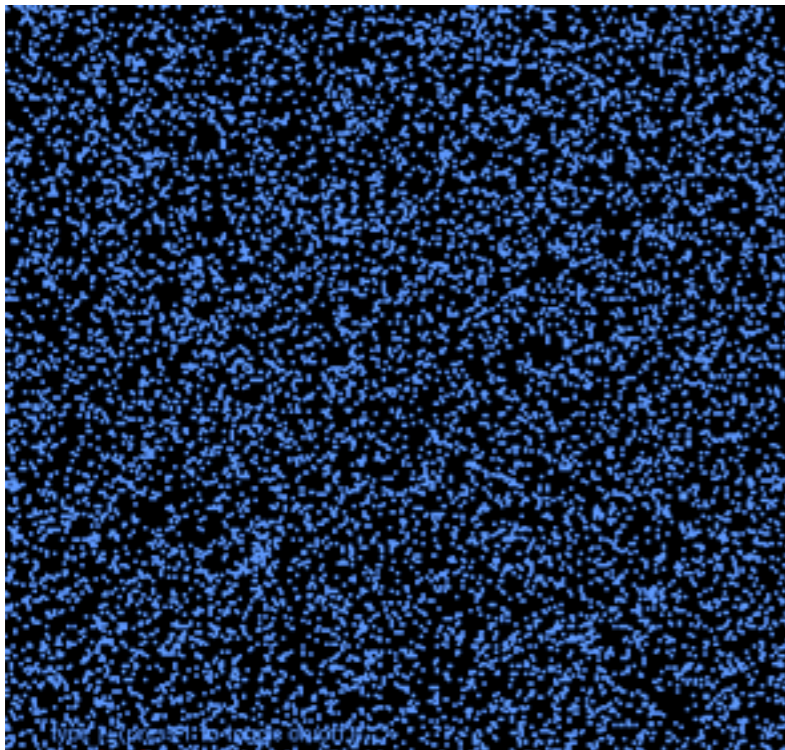
Questions.

- Where do the organisms go in turbulence? [Durham \*et al.\*, Nature Communications 4, 2148 \(2013\)](#)
- How does shape affect the observed spatial patterns?  
Preferential sampling stronger or weaker for non-spherical particles?  
[Zhan \*et al.\*, J. Fluid Mech. 793 \(2014\) 22](#)
- Relation between preferential sampling and small-scale clustering?  
Effect on encounter rates?
- Dependence on dimensionless parameters? Theory for large gravitaxis:  
[Durham \*et al.\*, Nature Communications 4, 2148 \(2013\)](#)
- Caustics

# Analogy with heavy particles in turbulence

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Computer simulation of  $10^4$  particles (blue) in two-dimensional smooth random flow

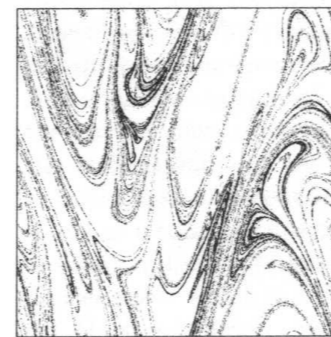


Duncan, Mehlig, Östlund & Wilkinson, Phys. Rev. Lett. **95** (2005) 240602

Direct numerical simulations (DNS) of particles in turbulence

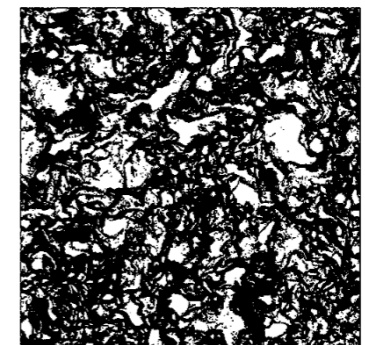


Wang & Maxey, J. Fluid. Mech. **256** (1993) 27



Bec, Phys. Fluids 15 (2003) L81

Coleman & Vassilicos, Phys. Fluids **21** (2009) 113301



Equation of motion:  $\dot{\mathbf{r}} = \mathbf{v}$  and  $\dot{\mathbf{v}} = \mathbf{g} + \gamma(\mathbf{u}(\mathbf{r}, t) - \mathbf{v})$ .

Gravity  $\mathbf{g}$ , fluid-velocity field  $\mathbf{u}(\mathbf{r}, t)$ , Stokes damping constant  $\gamma$ .

# Preferential sampling

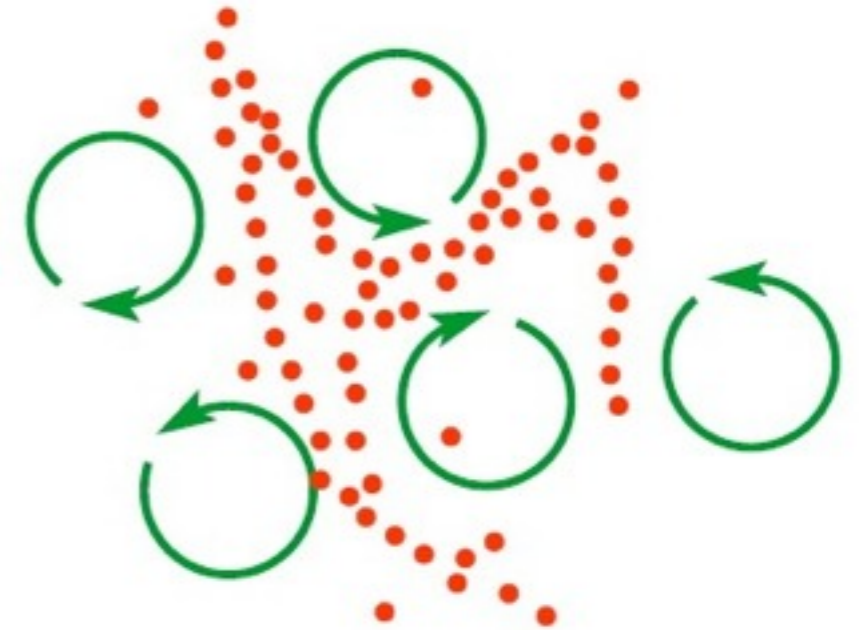
Maxey, J. Fluid Mech. **174** (1987) 441

Preferential sampling, inertial effect. Assume  $St > 0$  but small, and neglect settling due to gravity.

At small  $St$  heavy particles follow effective velocity field  $\mathbf{v}_{\text{eff}}$

$$\dot{\mathbf{r}} = \mathbf{v}_{\text{eff}}, \quad \mathbf{v}_{\text{eff}} \approx \mathbf{u} - \frac{1}{\gamma} \left[ \frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla) \mathbf{u} \right]$$

particle velocity
fluid velocity



Spatial clustering in sinks of  $\mathbf{v}_{\text{eff}}$  where  $\nabla \cdot \mathbf{v}_{\text{eff}} < 0$ :

$$\nabla \cdot \mathbf{v}_{\text{eff}} = -\frac{1}{\gamma} \text{Tr}(\mathbf{A}^2) = -\frac{1}{\gamma} \left[ \underbrace{\text{Tr}(\mathbf{S}^T \mathbf{S})}_{> 0} - \underbrace{\text{Tr}(\mathbf{O}^T \mathbf{O})}_{> 0} \right]$$

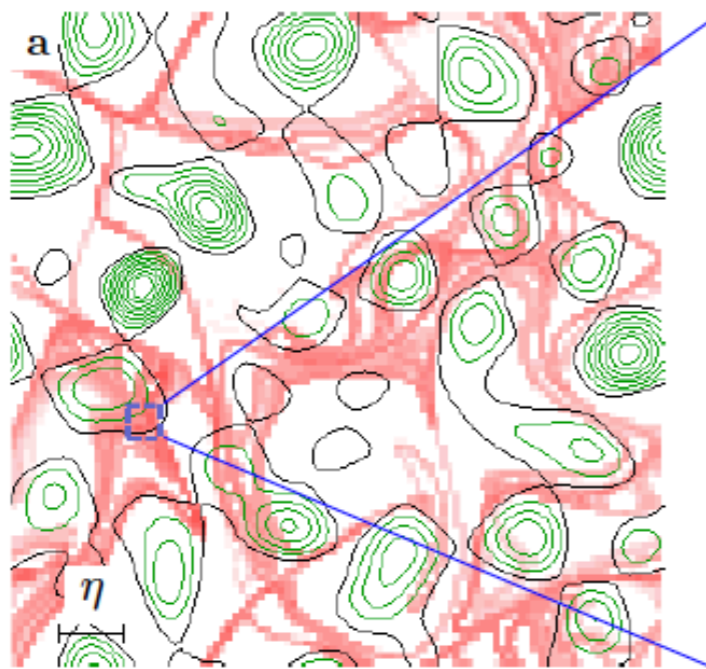
Here  $\mathbf{S} = (\mathbf{A} + \mathbf{A}^T)/2$  is the symmetric (strain) part of the matrix of particle-velocity gradients  $A_{ij} = \partial u_i / \partial r_j$ , and  $\mathbf{O} = (\mathbf{A} - \mathbf{A}^T)/2$  is the antisymmetric part.

‘Maxey’s centrifuge’: particles avoid vortices. Effect of particle inertial. Valid for very small  $St$ .

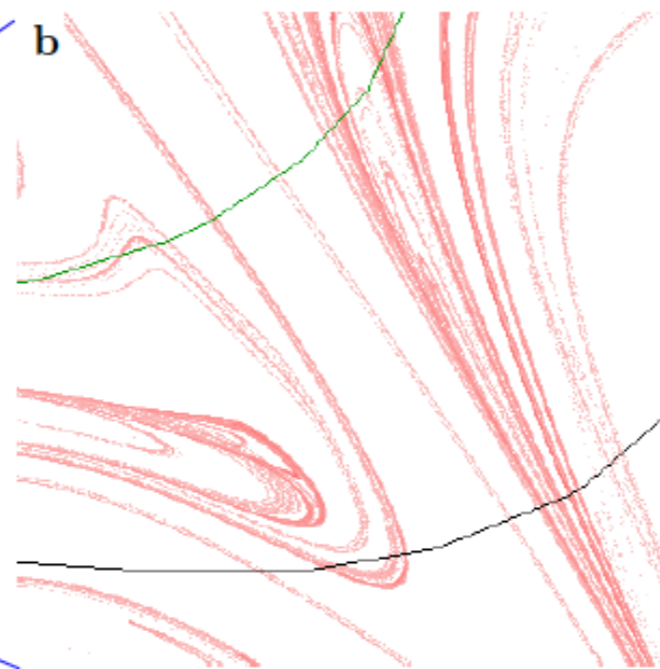
Air bubbles in water ( $\rho_p \ll \rho_f$ )?

# Preferential sampling - small-scale clustering

Preferential sampling affects but does not explain small-scale clustering. Which mechanism brings particles in a straining region closer together?



preferential sampling



small-scale clustering

red: number density of particles

green: vortical regions

flow-correlation length  $\eta$

# Small-scale clustering

Sommerer & Ott, Science **259** (1993) 351

Exponents  $\lambda_1 > \lambda_2 > \lambda_3$  describe rate of contraction or expansion of small length element  $\delta r_t$ , area element  $\delta \mathcal{A}_t$ , and volume element  $\delta \mathcal{V}_t$  of particles

$$\lambda_1 = \lim_{t \rightarrow \infty} t^{-1} \log_e(\delta r_t)$$

$$\lambda_1 + \lambda_2 = \lim_{t \rightarrow \infty} t^{-1} \log_e(\delta \mathcal{A}_t)$$

$$\lambda_1 + \lambda_2 + \lambda_3 = \lim_{t \rightarrow \infty} t^{-1} \log_e(\delta \mathcal{V}_t) .$$

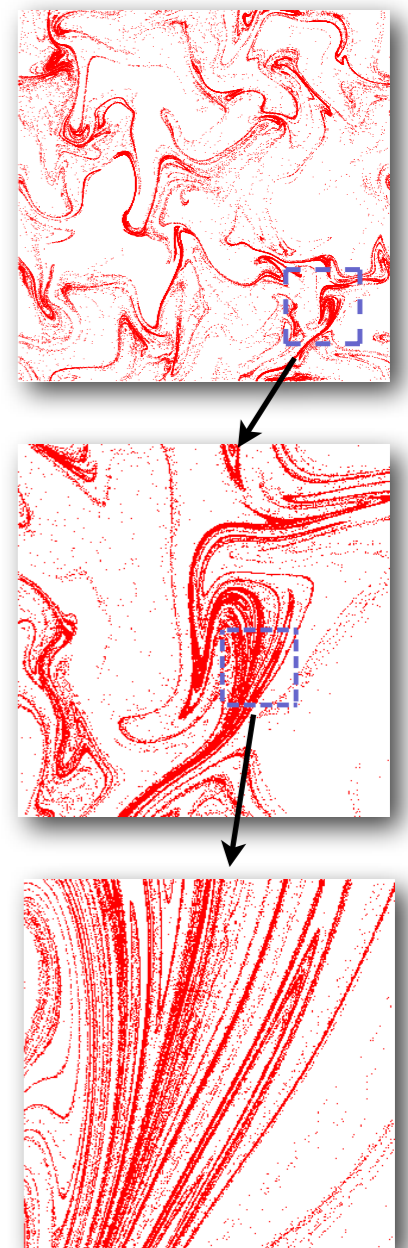
Lyapunov fractal dimension

$$d_L = \kappa + \frac{\sum_{\mu=1}^{\kappa} \lambda_{\mu}}{|\lambda_{\kappa+1}|} = d - \Delta_L$$

where  $\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_d$  and  $\kappa$  is largest integer for which  $\lambda_{\kappa} > 0$ .

Dimension deficit  $\Delta_L = d - d_L$ .

Compute exponents from  $\mathbf{Z}(\mathbf{r}_t, t)$ . For example  $\lambda_1 + \lambda_2 + \lambda_3 = \langle \text{Tr} \mathbf{Z} \rangle$ .





# Equation of motion

Kessler, Nature 313 (1985) 218

Kessler's model for centre-of-mass and orientational dynamics

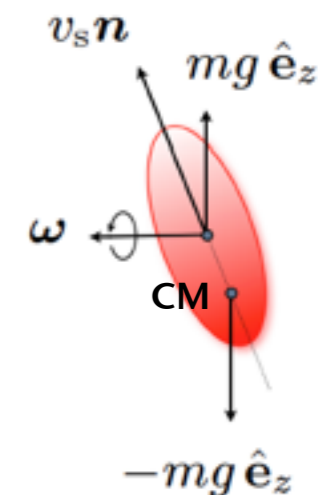
$$\dot{\mathbf{r}} \equiv \mathbf{v} = \mathbf{u}(\mathbf{r}, t) + \underbrace{v_s \mathbf{n}}_{\text{swimming}}, \quad \dot{\mathbf{n}} = \boldsymbol{\omega}(\mathbf{r}, t) \wedge \mathbf{n}.$$

Particle position  $\mathbf{r}$ , particle orientation  $\mathbf{n}$ , time  $t$ , fluid velocity  $\mathbf{u}(\mathbf{r}, t)$ , swimming speed  $v_s$ , swimming direction  $\mathbf{n}$ .

Particle angular velocity

$$\boldsymbol{\omega}(\mathbf{r}, t) = \underbrace{-(\mathbf{n} \wedge \hat{\mathbf{g}})/(2B)}_{\text{gravitaxis}} + \underbrace{\boldsymbol{\Omega}(\mathbf{r}, t) + \Lambda \mathbf{n} \wedge [\mathbb{S}(\mathbf{r}, t)\mathbf{n}]}_{\text{effect of turbulent velocity gradients}}.$$

Jeffery, Proc. Roy. Soc. London Ser. A 102 (1922) 161



Orientation parameter  $B$ , and  $\hat{\mathbf{g}} = -\hat{\mathbf{e}}_z$ .

Fluid-velocity gradient matrix  $\mathbb{A}$ ,  $\mathbb{S} = (\mathbb{A} + \mathbb{A}^T)/2$ ,  $\mathbb{O} = (\mathbb{A} - \mathbb{A}^T)/2$ , and  $\mathbb{O}\mathbf{n} = \boldsymbol{\Omega} \wedge \mathbf{n}$ .

Shape factor:  $\Lambda = 1$  rod,  $\Lambda = 0$  sphere.

# Gravitational vs. hydrodynamic torque

P. R. Jonsson, Mar. Ecol. Prog. Ser. 52 (1989) 39

Gyrotactic torque is due to inhomogeneity in particle-mass density.

Shape asymmetry gives rise to hydrodynamic torque for homogeneous particles.

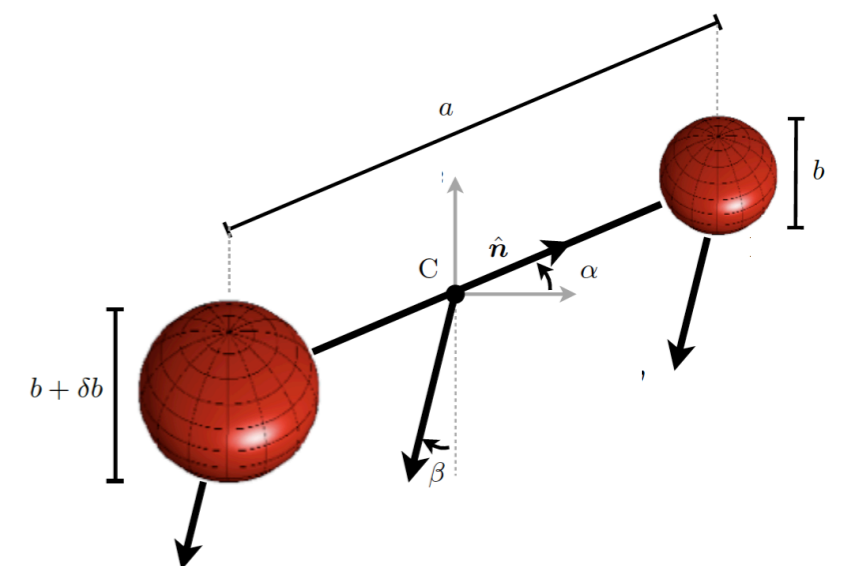
Consider small needle or dumbbell settling with velocity  $v_g$  so that  $Re_p = av_g/\nu \approx 0$ .  
A symmetric needle or dumbbell (fore-aft symmetry) continues to settle at initial orientation.  
Particle size  $a$ , kinematic viscosity  $\nu$ . Happel & Brenner, *Low Reynolds Hydrodynamics* (1983)

Inertial torque (first order in  $Re_p$ ) turns symmetric needle (dumbbell) to horizontal orientation.  
Cayat & Cox, *J. Fluid Mech.* 209 (1989) 435

*Asymmetric* dumbbell at  $Re_p \approx 0$  turns so that larger sphere settles first (spheres have same mass density).

*Asymmetric* dumbbell to first order in  $Re_p$ : hydrodynamic and inertial torques balance at certain angle  $\alpha$  that depends on asymmetry and  $Re_p$ .

Candelier & Mehlig, *J. Fluid Mech.* (2016)



# Model for turbulent velocity field

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Statistical model for turbulent aerosols

$$\dot{\mathbf{r}} = \mathbf{v} \text{ and } \dot{\mathbf{v}} = \mathbf{g} + \gamma(\mathbf{u}(\mathbf{r}, t) - \mathbf{v}).$$

Incompressible, homogeneous, isotropic  
Gaussian random function  $\mathbf{u}(\mathbf{r}, t)$ .

Correlation time  $\tau$ .

Correlation length  $\eta$ .

Typical speed  $u_0$ .

No inertial range.

Method: approximate analytical solution  
using 'trajectory expansions' (Ku-expansion).  
Gustavsson & Mehlig, Adv. Phys. (2016)

## REVIEW ARTICLE

### Statistical models for spatial patterns of heavy particles in turbulence

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The dynamics of heavy particles suspended in turbulent flows is of fundamental importance for a wide range of questions in astrophysics, atmospheric physics, oceanography, and technology. Laboratory experiments and numerical simulations have demonstrated that heavy particles respond in intricate ways to turbulent fluctuations of the carrying fluid: non-interacting particles may cluster together and form spatial patterns even though the fluid is incompressible, and the relative speeds of nearby particles can fluctuate strongly. Both phenomena depend sensitively on the parameters of the system. This parameter dependence is difficult to model from first principles since turbulence plays an essential role. Laboratory experiments are also very difficult, precisely since they must refer to a turbulent environment. But in recent years it has become clear that important aspects of the dynamics of heavy particles in turbulence can be understood in terms of statistical models where the turbulent fluctuations are approximated by Gaussian random functions with appropriate correlation functions. In this review we summarise how such statistical-model calculations have led to a detailed understanding of the factors that determine heavy-particle dynamics in turbulence. We concentrate on spatial clustering of heavy particles in turbulence. This is an important question because spatial clustering affects the collision rate between the particles and thus the long-term fate of the system.

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# Dimensionless parameters

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Measure of how rapidly  $\mathbf{u}(\mathbf{r}, t)$  fluctuates: Kubo number  $\text{Ku} = \frac{u_0 \tau}{\eta}$ .

Duncan, Mehlig, Östlund & Wilkinson, Phys. Rev. Lett. 95 (2005) 165503

Shape factor  $\Lambda$ .

Swimming speed:  $\Phi = v_S / u_0$ .

Gyrotactic relaxation time  $\Psi = B / \tau$  ( $\Psi \rightarrow \infty$  : vanishing effect).

Dimensionless parameters in DNS of turbulence:

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

$$\Phi_{\text{DNS}} = v_S / u_K \quad \text{and} \quad \Psi_{\text{DNS}} = B / \tau_K$$

Kolmogorov scales, Kolmogorov time  $\tau_K \equiv 1 / \sqrt{\text{tr}\langle \mathbb{A}\mathbb{A} \rangle} \sim \eta / u_0$ .

Correspondence:  $\Phi_{\text{DNS}} = \Phi / \text{Ku}$  and  $\Psi_{\text{DNS}} = \Psi \text{Ku}$ .

# Preferential sampling - large $\Phi$

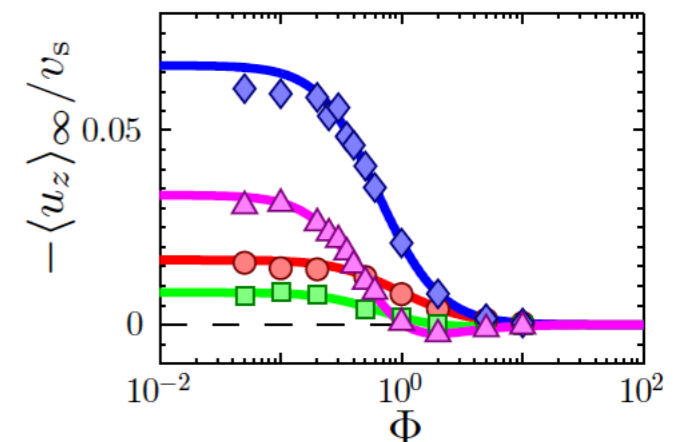
Preferential sampling of  $u_z$  and its  $z$ -gradient  $A_{zz}$  (evaluated at the particle position).  
Small swimming speed  $\Phi = v_S/u_0$ :

$$\langle A_{zz} \rangle_\infty \frac{\eta}{u_0} \sim \text{Ku} \Phi^2 \frac{d(1-\Lambda) + 2(\Lambda+2)}{d} \frac{\Psi(4\Psi + 1)}{(2\Psi + 1)^2}$$

$$\frac{\langle u_z \rangle_\infty}{u_0} \sim -\text{Ku} \Phi \frac{d(1-\Lambda) + 2}{d} \frac{\Psi}{2\Psi + 1}$$

## Conclusions

- particles preferentially sample sinks of transversal velocity field,  $\text{tr}_\perp \mathbb{A} = -A_{zz} < 0$
- particles preferentially sample downwelling regions,  $u_z < 0$ .
- $\langle u_z \rangle_\infty / v_S$  independent of  $\Phi$  for small  $\Phi$ .



# Preferential sampling - large $\Phi$

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Preferential sampling of  $u_z$  and its  $z$ -gradient  $A_{zz}$  (evaluated at the particle position).  
Large swimming speed  $\Phi = v_S/u_0$  :

$$\langle A_{zz} \rangle_\infty \frac{\eta}{u_0} \sim \frac{Ku}{\Phi} \frac{d+1}{2d} (1 - \Lambda) \sqrt{\frac{\pi}{2}}$$

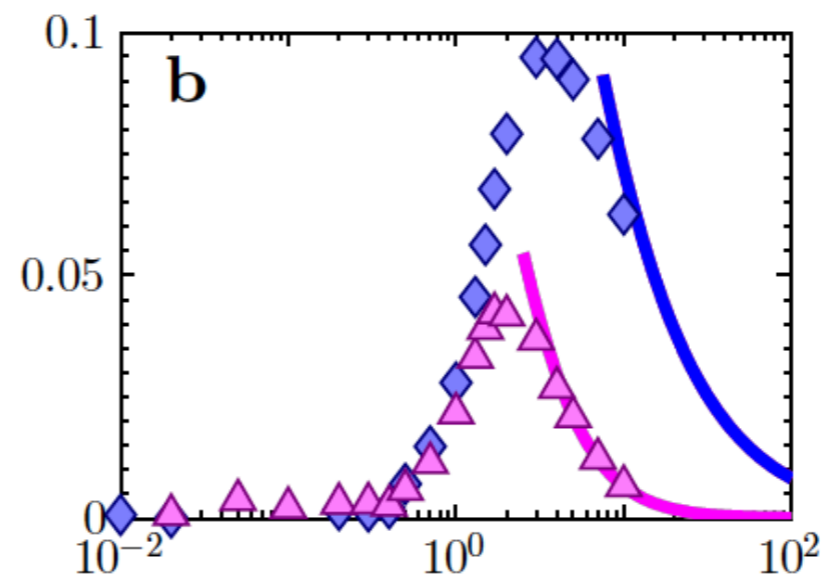
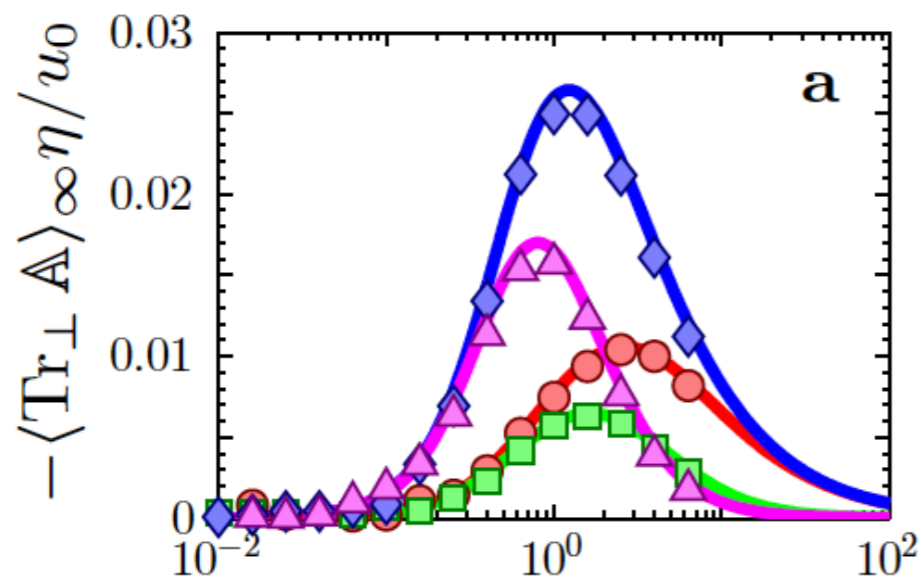
$$\frac{\langle u_z \rangle_\infty}{u_0} \sim \frac{Ku}{\Phi} \frac{(d(\Lambda - 1) + 2\Lambda)}{2d}$$

## Conclusions

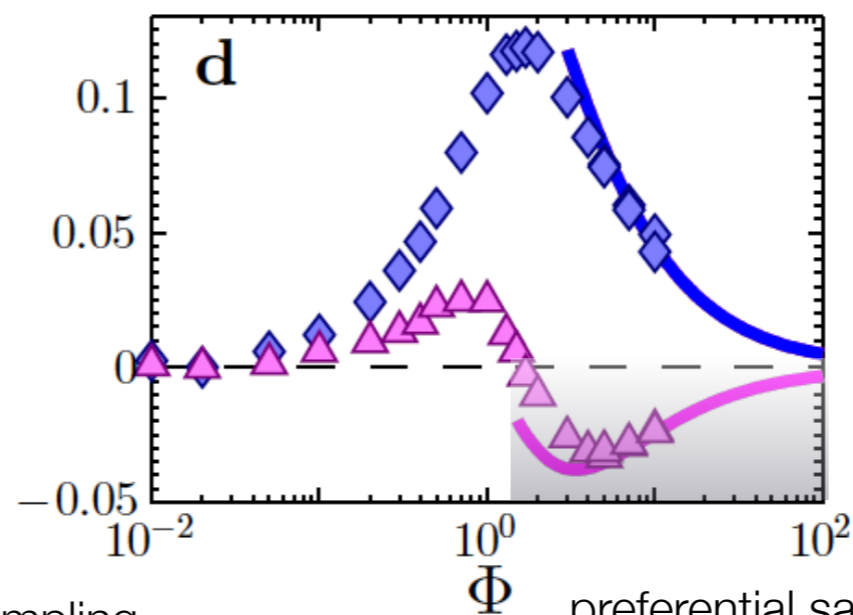
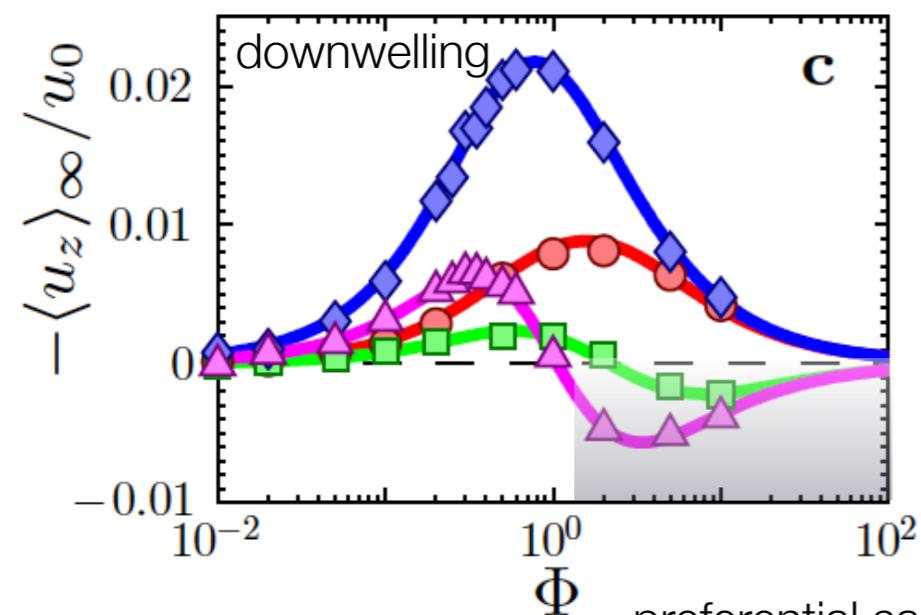
- particles preferentially sample sinks of transversal velocity field,  $\text{tr}_\perp \mathbb{A} = -A_{zz} < 0$
- spherical particles preferentially sample downwelling regions,  $u_z < 0$ , rods upwelling regions,  $u_z > 0$
- phase transition at  $\Lambda = d/(d + 2)$

# Comparison with statistical-model simulations

Left:  $d = 2$  and  $Ku = 0.1$ . Right  $d = 3$  and  $Ku = 1$ .



- $\Psi = 0.1 \quad \Lambda = 0$
- ◆  $\Psi = 1 \quad \Lambda = 0$
- $\Psi = 0.1 \quad \Lambda = 1$
- ▲  $\Psi = 1 \quad \Lambda = 1$



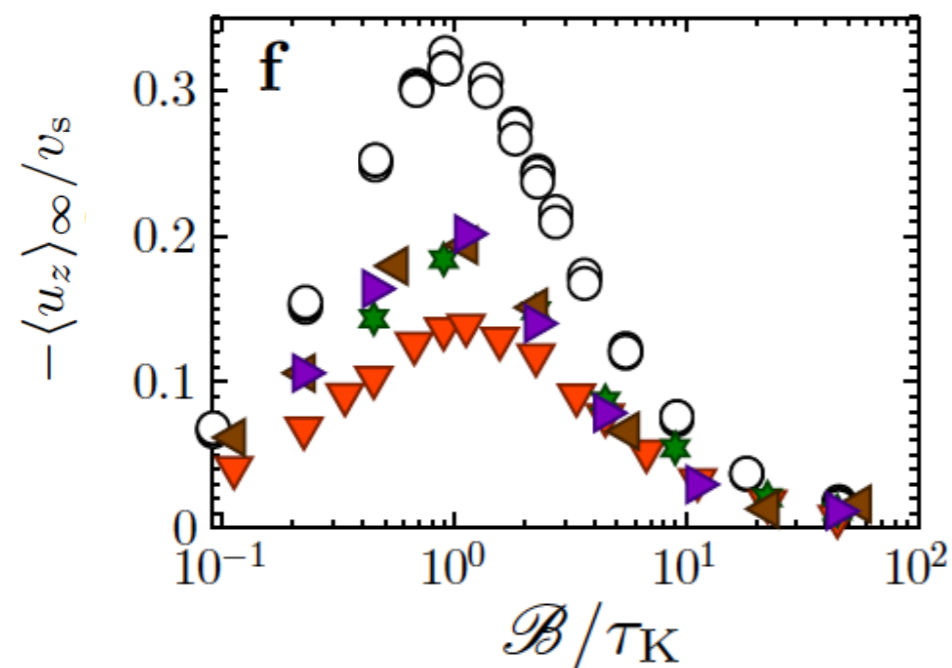
large- $\Phi$  limit  
universal,  $Ku$ -independent

preferential sampling  
of upwelling regions

preferential sampling  
of upwelling regions

# Comparison with DNS

Comparison of statistical-model simulations with DNS



Open symbols: DNS (Durham *et al.*, Nature Communications 4, 2148 (2013))

Filled symbols: statistical-model simulations for  $Ku = 1, 2, 5, 10$ .

Statistical-model results independent of  $Ku$  for large  $Ku$ .

Qualitative agreement with DNS. Factor due to difference between universal small-scale fluctuations of turbulence and statistical model

Schumacher *et al.*, PNAS 11 (2014) 10961



# Small-scale clustering

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Small-scale clustering determined by the particle-velocity gradients  $\mathbb{Z}$  - follow separations between a cloud of particles that are initially infinitesimally close together.

At zero swimming speed,  $\Phi = 0$ , the particle centre-of-mass follows the flow. In this case  $\mathbb{Z} = \mathbb{A}$ . In general not.

$\text{tr}\mathbb{Z}$  determines small-scale clustering. Time evolution of volume  $\mathcal{V}_t$  of particle cloud:

$$\frac{d}{dt} \mathcal{V}_t = \text{tr}\mathbb{Z} \mathcal{V}_t \quad .$$

Steady-state average

$$\langle \text{tr}\mathbb{Z} \rangle_{\infty} \equiv \langle \nabla \cdot \mathbf{v} \rangle_{\infty} = \lambda_1 + \dots + \lambda_d \quad .$$

# Small-scale clustering - $\langle \text{tr} \mathbb{Z} \rangle_\infty \equiv \langle \nabla \cdot \mathbf{v} \rangle_\infty$

---

Expand equations of motion for small  $\Phi$  :

$$\nabla \cdot \mathbf{v} \sim v_s B \left[ -(1+\Lambda) \partial_z^2 u_z + (1-\Lambda) (\partial_z^2 u_z - \Delta u_z) \right]$$

Derived earlier for  $\Lambda = 0$ . Durham *et al.*, Nature Communications 4, 2148 (2013)  
Fouxon & Leshansky, Phys. Rev. E 92 (2015) 013017

Average in statistical model

$$\langle \nabla \cdot \mathbf{v} \rangle_\infty \eta / u_0 \sim -\text{Ku} (\Phi \Psi)^2 B_d(\Lambda) \quad \text{for} \quad \Phi \ll 1$$

with shape factor  $B_d(\Lambda) \equiv [(d+2)(d+4) - 2d(d+4)\Lambda + (4+2d+d^2)\Lambda^2] / d$  , and

$$\langle \nabla \cdot \mathbf{v} \rangle_\infty \eta / u_0 \sim -\text{Ku} \Phi \Psi^2 E_d(\Lambda) \quad \text{for} \quad \Phi \gg 1$$

with  $E_d(\Lambda) \equiv \sqrt{\pi/2} (d+1)(d+3)(\Lambda-1)^2 / d$  .

Conclusions: rods cluster less than spheres.

# Fractal dimension

Lyapunov fractal dimension  $d_L = 2 - (\lambda_1 + \lambda_2)/\lambda_2$  (for  $d = 2$ )

Lyapunov exponents  $\lambda_1$  and  $\lambda_2$ .

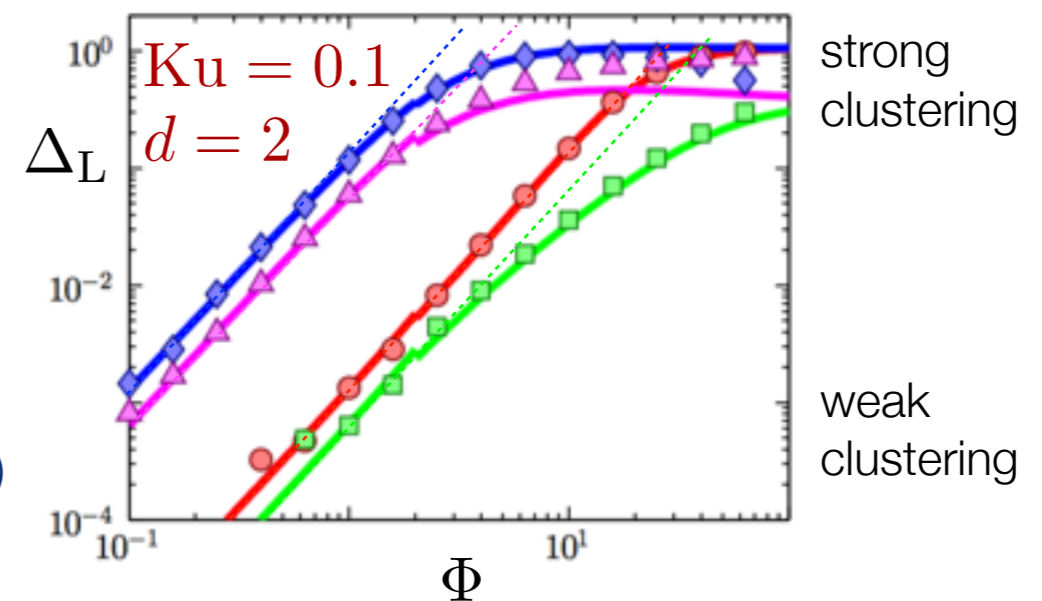
Small-scale clustering if  $\Delta_L = d - d_L > 0$ .

Theory (solid lines). Simulations (symbols).

Dashed lines:  $\Delta_L \sim \Phi^2 \Psi^2$

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

Fouxon & Leshansky, Phys. Rev. E 92 (2015) 013017



strong gravitaxis	● $\Psi = 0.1$	$\Lambda = 0$	■ $\Psi = 0.1$	$\Lambda = 1$
intermediate gravitaxis	◆ $\Psi = 1$	$\Lambda = 0$	▲ $\Psi = 1$	$\Lambda = 1$
	spherical		rod-shaped	

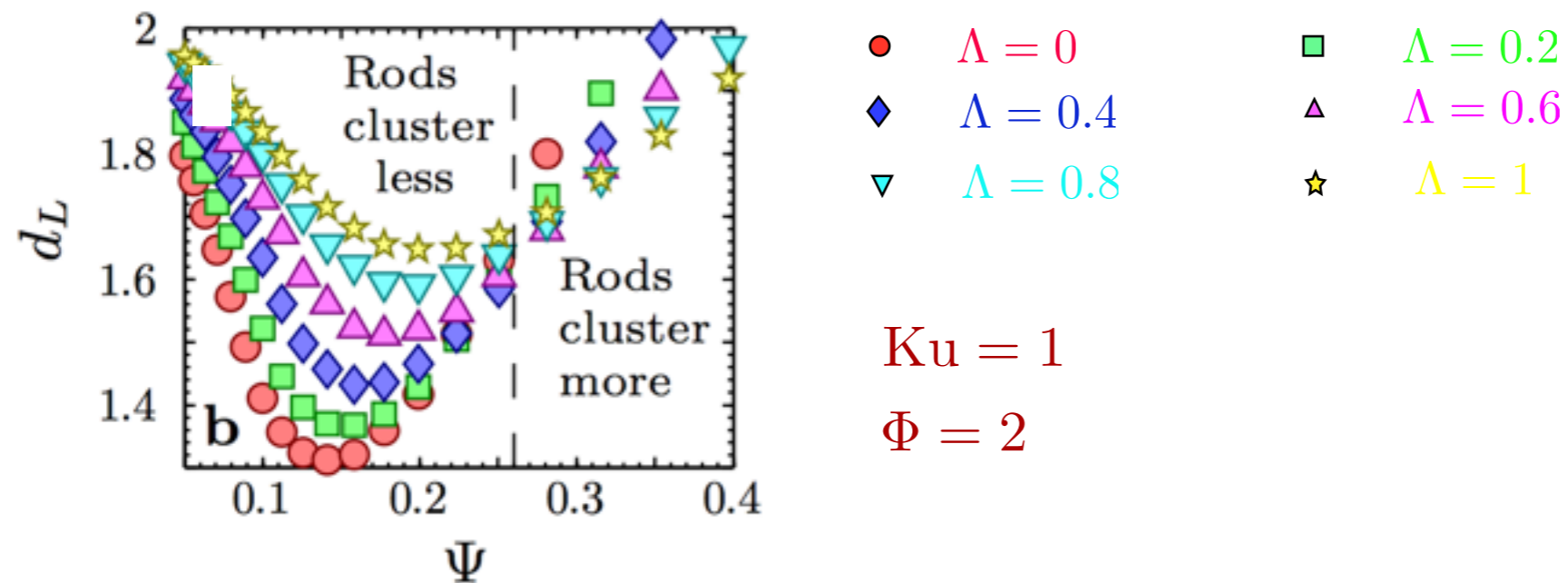
## Conclusions

-rods cluster less than spheres.

-theory fails at large values of  $\Psi$  (caustics).

# Small-scale clustering - weak gyrotaxis

Weak gravitaxis ( $\Psi \gg 1$ ): clustering stronger for rod-shaped particles.



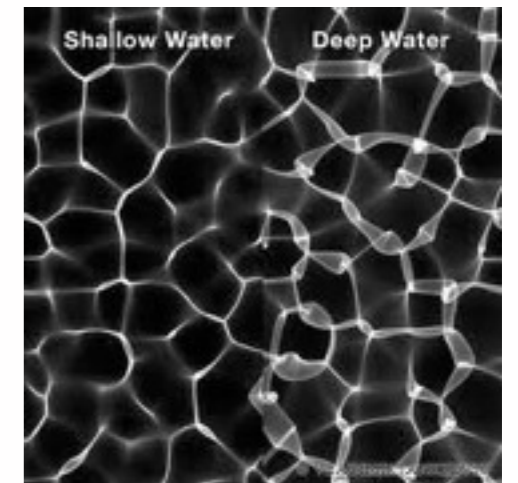
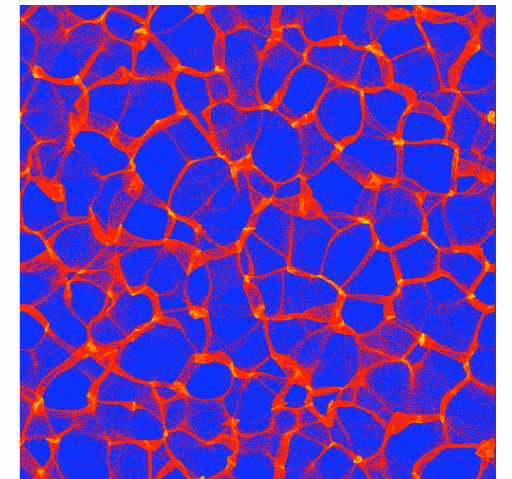
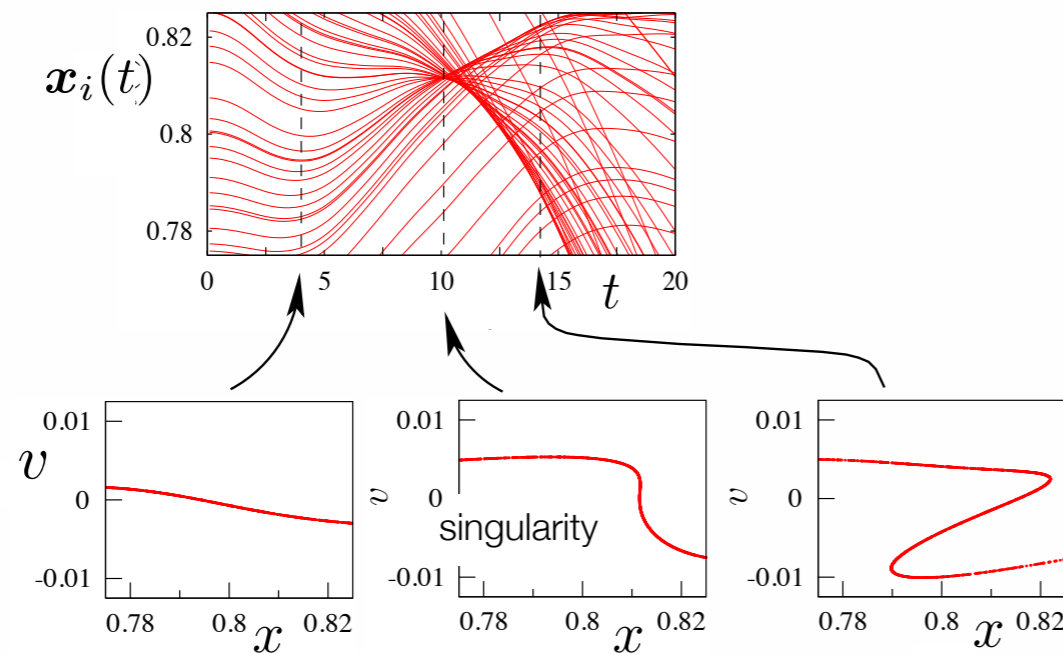
Expected since spheres do not cluster in the limit  $\Psi \rightarrow \infty$ .

Theory fails at large values of  $\Psi$  (caustics)

# Caustics - heavy particles in turbulence

Wilkinson & Mehlig, Europhys. Lett. 71 (2005) 186

One-dimensional model  $\ddot{x} = \gamma(u(x, t) - \dot{x})$ .



V. Jankievic

This singularity (caustic) gives rise to large relative velocities of closeby particles.

Same as 'sling effect'. Falkovich, Fouxon & Stepanov, Nature 419 (2002)151

Caustics give rise to 'random uncorrelated motion' and 'crossing trajectories'. Février, Simonin & Squires, J. Fluid Mech. 533 (2005) 1

# Multi-valued particle velocities

The commonly employed smooth hydrodynamic approach for the particle-number density  $\varrho(\mathbf{r}, t)$

$$\frac{\partial}{\partial t} \varrho(\mathbf{r}, t) + [\nabla \cdot \mathbf{v}(\mathbf{r}, t)] \varrho(\mathbf{r}, t) = 0$$

(and corresponding theory for correlation functions) cannot be used for  $St > 0$  because particle velocity field is multivalued.

Phase-space approach required:

Gustavsson, Mehlig, Wilkinson & Uski, *Phys. Rev. Lett.* **101** (2008) 174503

Gustavsson & Mehlig, *Phys. Rev. E* **87** (2012) 023016

Gustavsson & Mehlig, *J. Turbulence* **15** (2014) 34

Kinetic phase-space approach

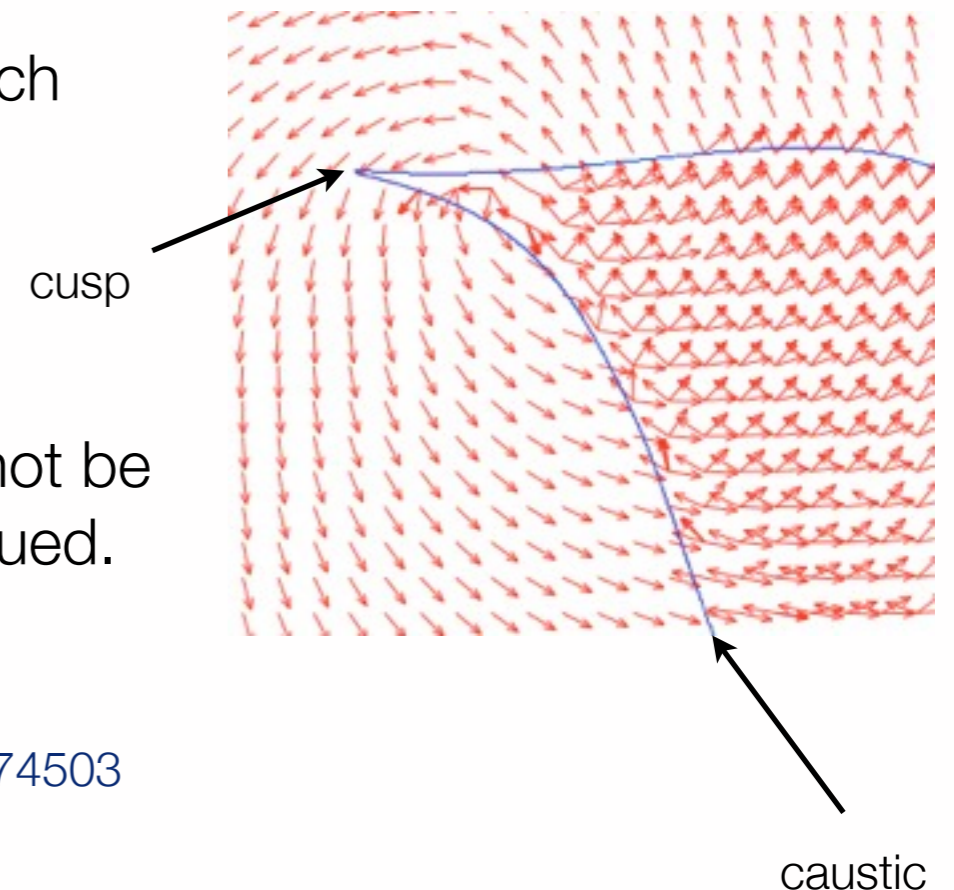
Reeks, *Phys. Fluids A* **3** (1991) 446

Zaichik & Alipchenkov, *Phys. Fluids* **15** (2003) 1776

Random uncorrelated motion

Simonin *et al.*, *Phys. Fluids* **18** (2006) 125197

Février, Simonin & Squires, *J. Fluid Mech.* **533** (2005) 1



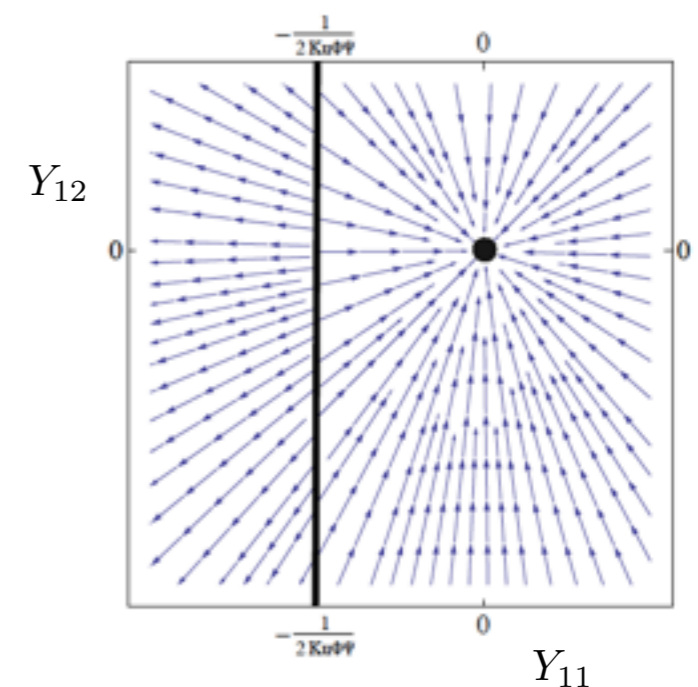
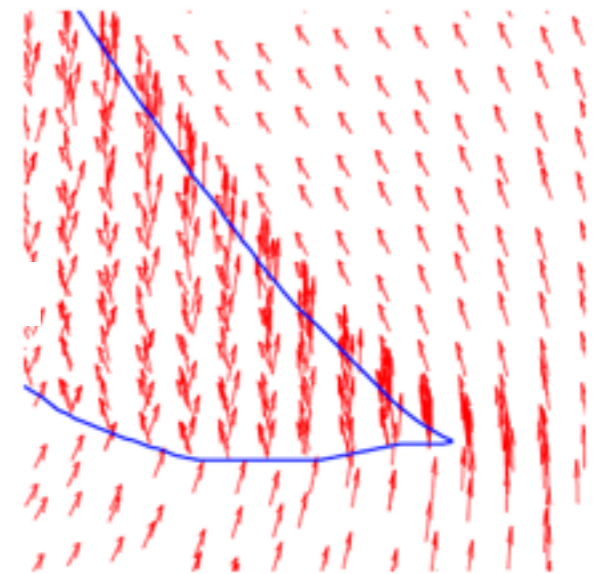
# Caustics - microswimmers

Analogy with inertial-particle problem:  
velocities of active particles multi-valued.  
Cusp catastrophe. Numerical simulation  
of statistical model ( $d = 2$ ).

Cusp ( ——— ), particle velocities ( —→ ).

Caustic formation is a Kramers escape  
process of the matrix  $\mathbb{Y}$ , elements  $Y_{ij} = \partial n_i / \partial r_j$ .

Dynamics in  $Y_{11} - Y_{12}$ -plane. Noise-induced escape  
from stable fixed point  $(0, 0)$  via line of unstable  
fixed points ( $d = 2$ ).



# Conclusions

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Statistical model for the dynamics of active particles.

Admits approximate analytical solution using 'trajectory expansions'

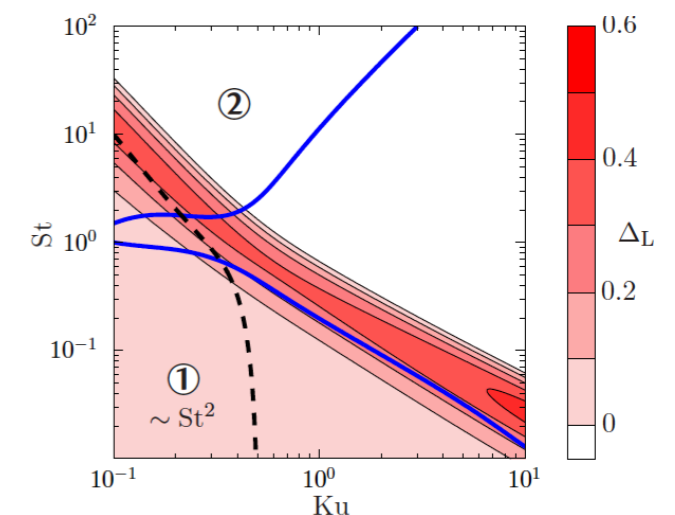
Gustavsson & Mehlig, *Adv. Phys.* (2016)

-Preferential sampling: instantaneous correlations with flow structures.

Whether clustering in down- or upwelling regions depends upon dimensionless parameters. But  $\langle (\nabla \cdot \mathbf{u})_{\perp} \rangle$  always negative. Gyrotaxis breaks symmetry.

-Small-scale clustering: history of flow gradients that the particles experienced in the past matter. Clustering of rod-like particles weaker or stronger than spherical ones. Depends on dimensionless parameters.

-Statistical-model results become independent of  $Ku$  for large  $Ku$  and agree with DNS results of turbulence. Similar in heavy-particle problem.





# Open questions

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- Caustics give rise to multi-valued particle velocities. Mapped to peculiar Kramers escape problem. Compute rate of caustic formation
- Large- $\Psi$  limit (difficult because caustics are frequent)
- Encounter rates