

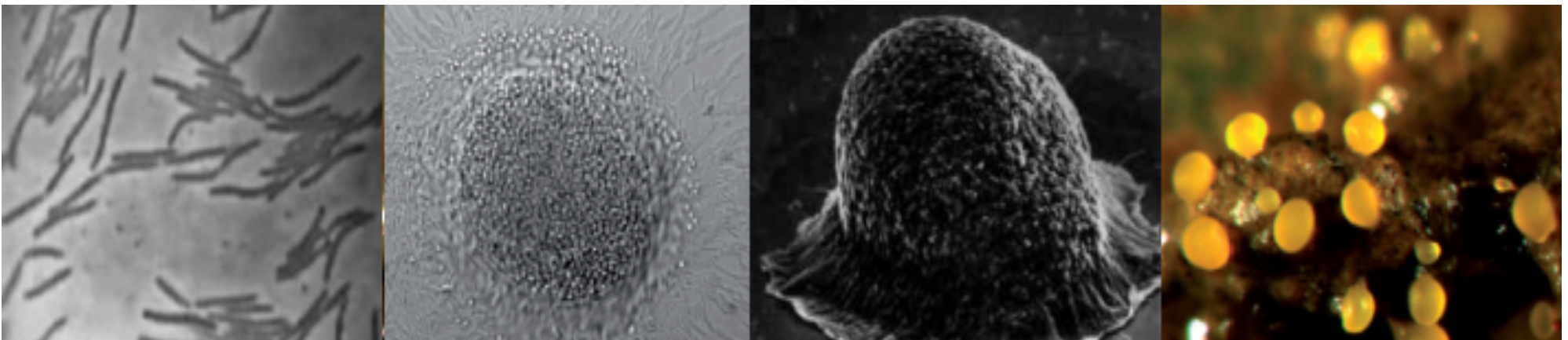
From bacteria to collective motion in heterogeneous media.

Fernando Peruani

In collaboration with:

M. Bär, O. Chepizhko, A. Deutsch, V. Jakovlievic, L. Søgaard Andersen, and J. Starruß

Journées de la physique nicoise - Nice – Dec. 2012



-- first part --

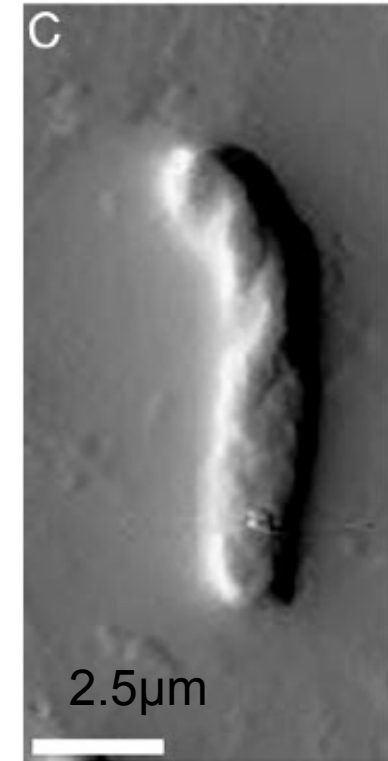
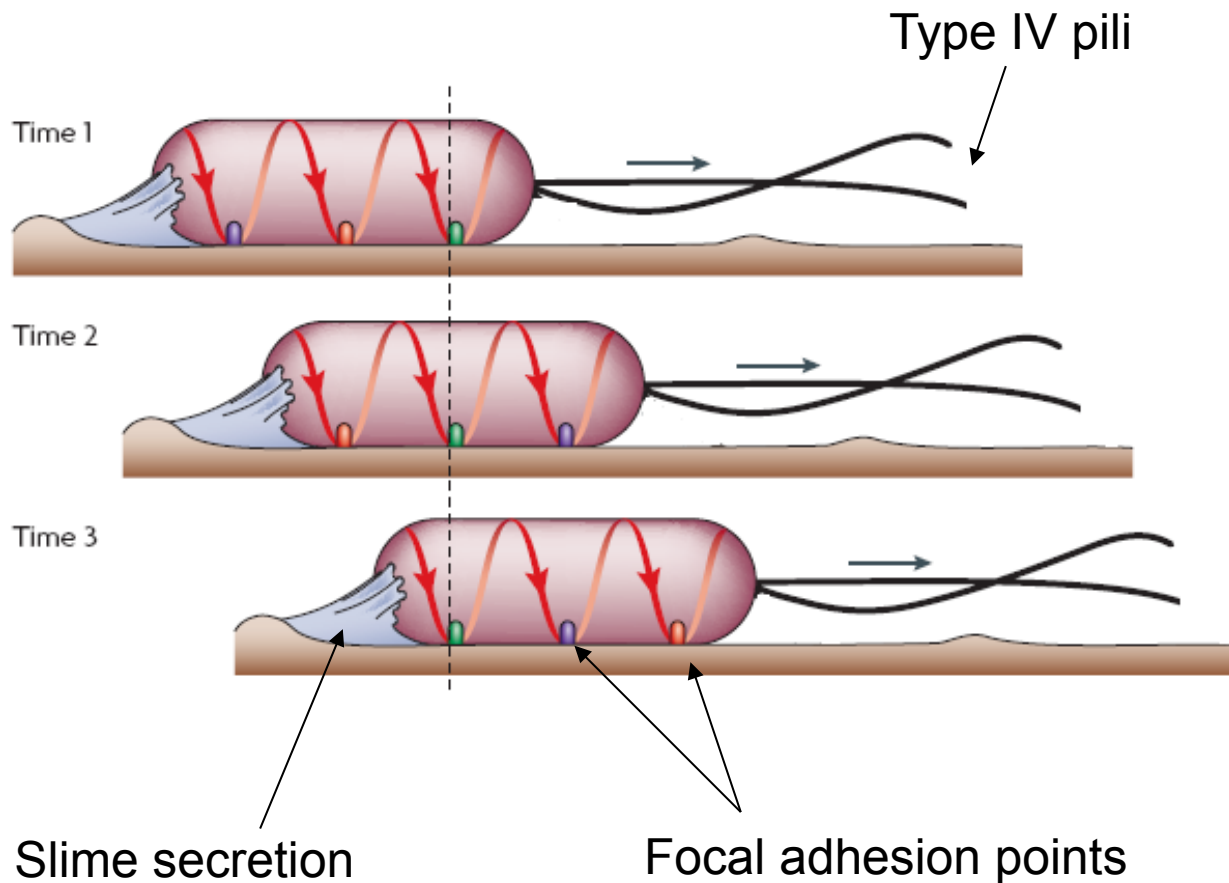
Motivation: collective macroscopic behavior in myxobacteria

Myxobacteria as self-propelled rods

Spatial self-organization of myxobacteria

Motivation: collective macroscopic behavior in myxobacteria

- Motility engines in *M. xanthus*:



Pelling 05

Myxobacteria (speed = 0.025 to 0.1 $\mu\text{m/s}$)

Cyanobacteria (speed = 10 $\mu\text{m/s}$)

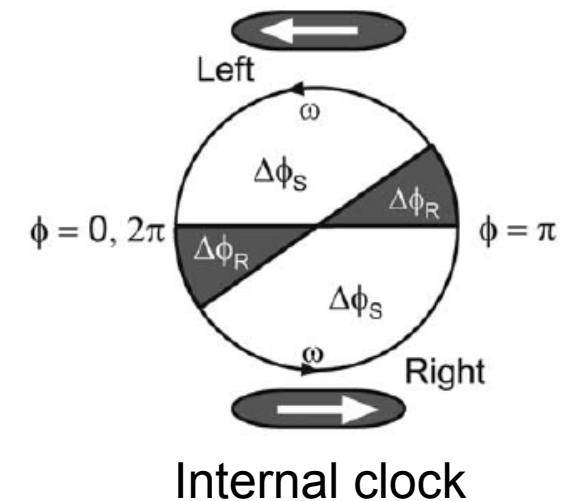
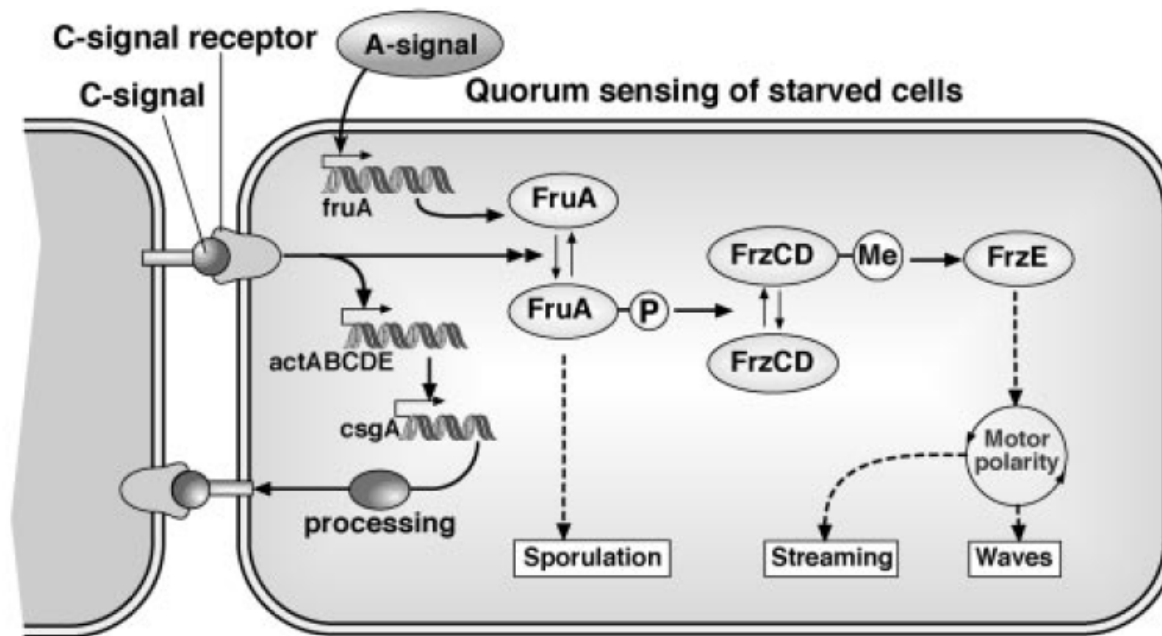
Cytophaga-Flavobacterium (speed = 2 to 4 $\mu\text{m/s}$)

Motivation: collective macroscopic behavior in myxobacteria

• How do *M. xanthus* cells communicate?

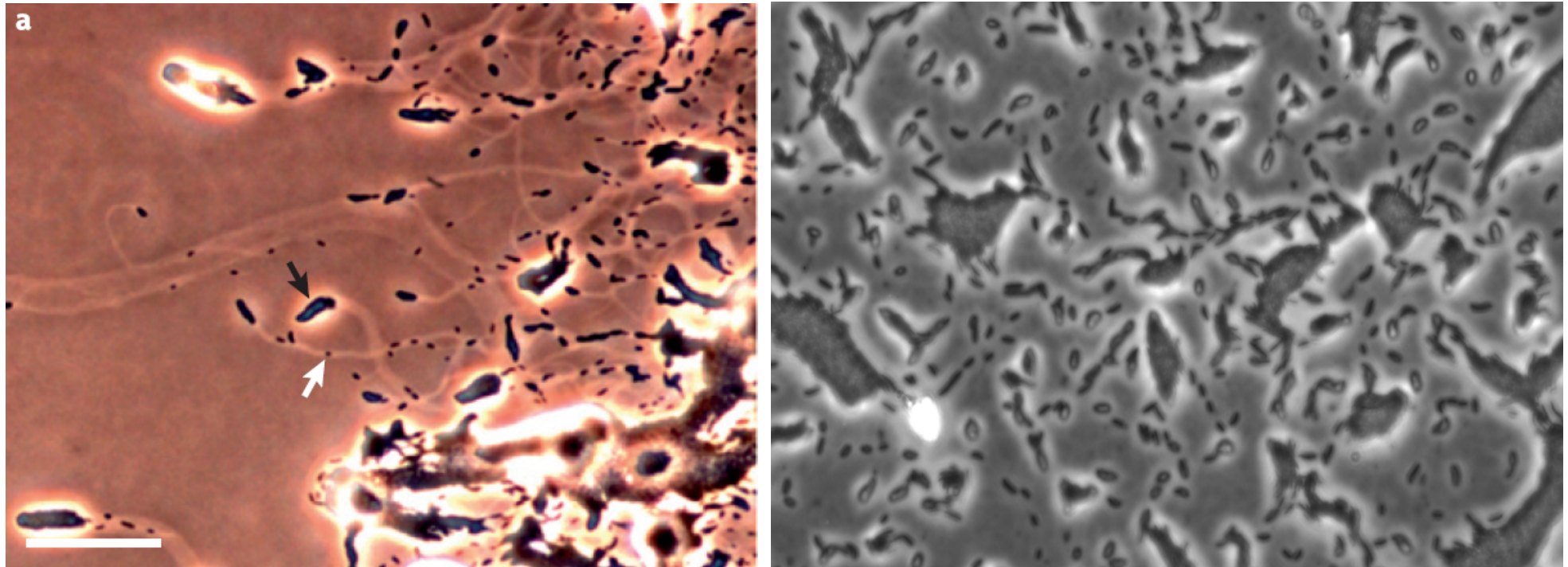
- A quorum sensing diffusive mechanism to trigger the life cycle.
- **There is no evidence of a guiding chemotactic signals involved in collective motion.**
- Cells exchange C-signal which controls cell reversal (it requires cell-cell contact).

• Cell reversal and C-signal:



Motivation: collective macroscopic behavior in myxobacteria

Which mechanism is used by the cells to coordinate their motion?



(Collective motion and clustering in the wild type during the vegetative growth)

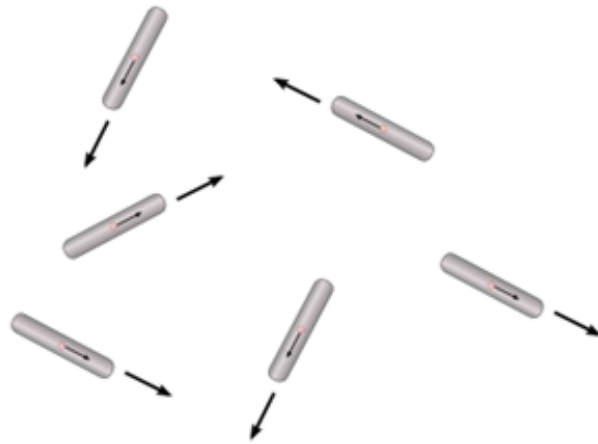
- Is there a hidden guiding chemotactic signal?
- Can slime trail following cause these effects?
- Is there a cell-density sensing mechanism that controls cell speed causing of these effects?
- What is the minimal mechanism that can produce these effects?

Motivation: collective macroscopic behavior in myxobacteria

**Self-propulsion of bacteria + elongated shape
= collective behavior ?**



**What macroscopic effects emerge
in a system of self-propelled rods ?**



Myxobacteria as self-propelled rods

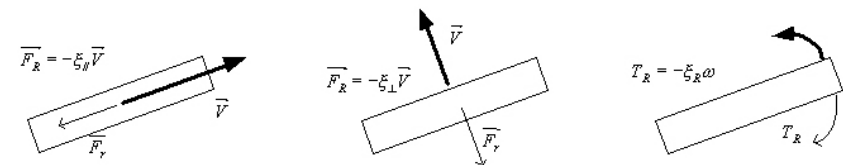
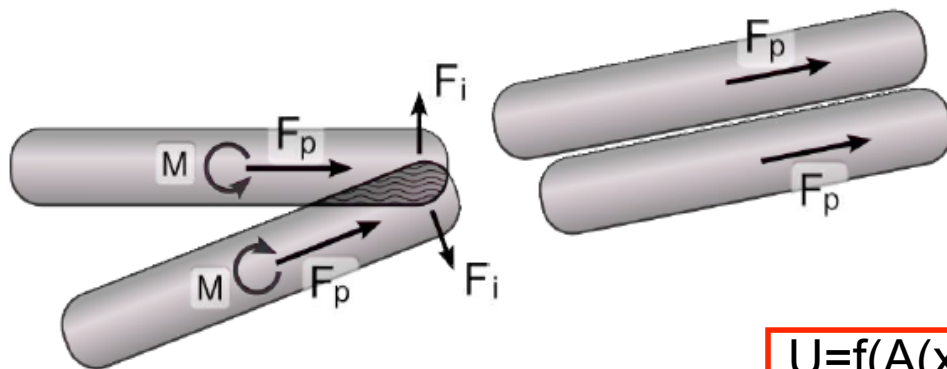
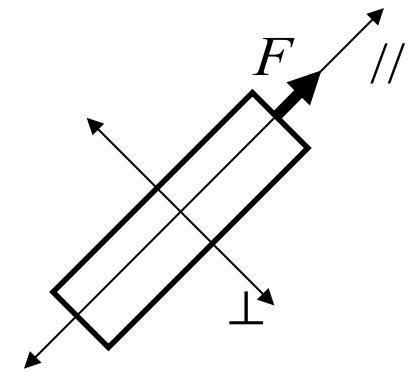
• A simple model for self-propelled rods

We consider the over-damped situation in which we have:

Self-Propelling force

$$\left\{ \begin{aligned} (v_{\parallel}^{(i)}, v_{\perp}^{(i)}) &= \left(\frac{1}{\zeta_{\parallel}} (R_{\parallel}^{(i)} + F - \frac{\partial U^{(i)}}{\partial x_{\parallel}}), \frac{1}{\zeta_{\perp}} \left(R_{\perp}^{(i)} - \frac{\partial U^{(i)}}{\partial x_{\perp}} \right) \right) \\ \dot{\theta}^{(i)} &= \frac{1}{\zeta_{\theta}} \left(R_{\theta}^{(i)} - \frac{\partial U^{(i)}}{\partial \theta} \right) \end{aligned} \right.$$

$R_{\parallel}, R_{\perp}, \tilde{R}$ are white noises!

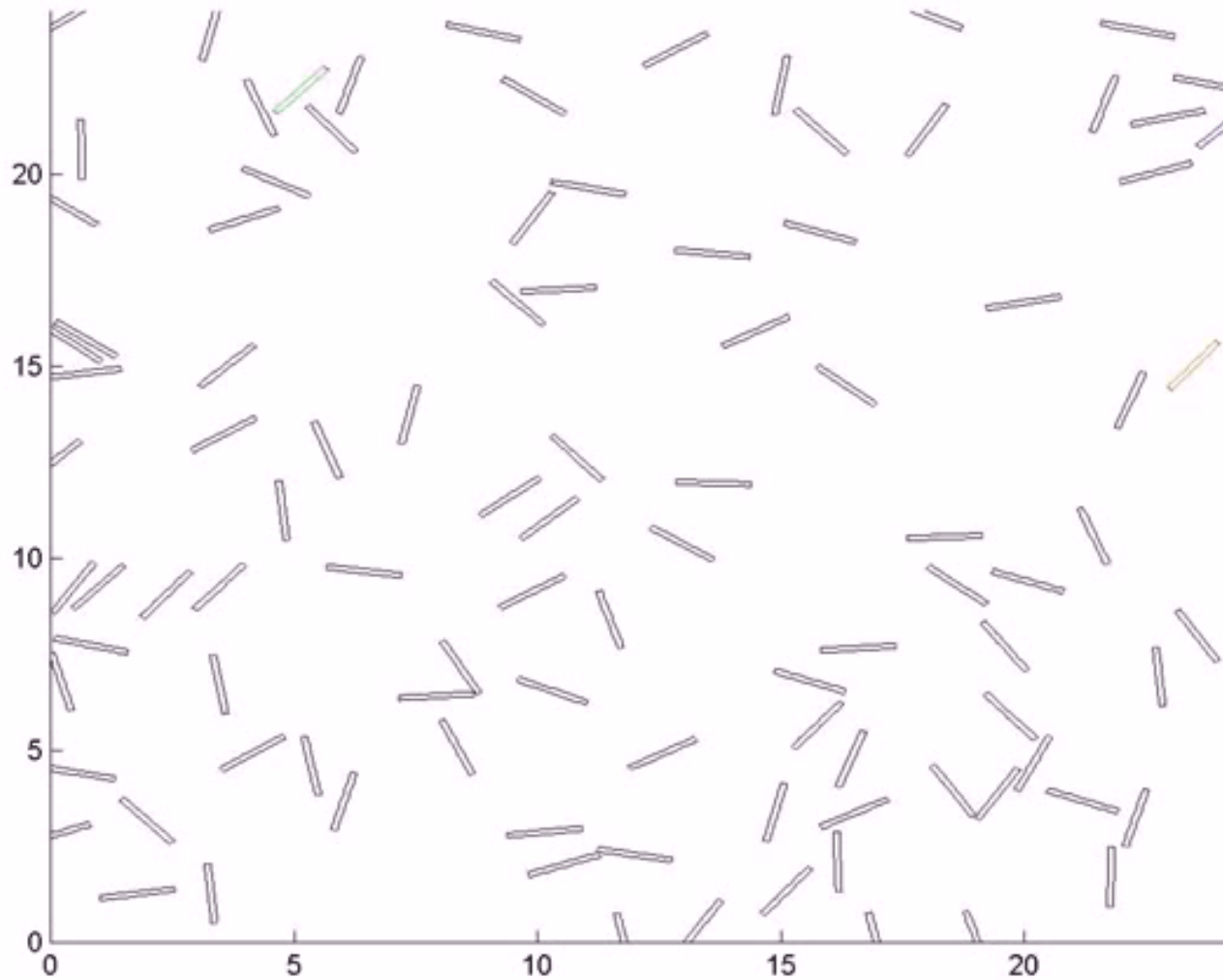


Interactions are due to overlapping of particles :

$U=f(A(x_i, \theta_i, x_j, \theta_j))$ where A is the overlapping area between particle i and j .

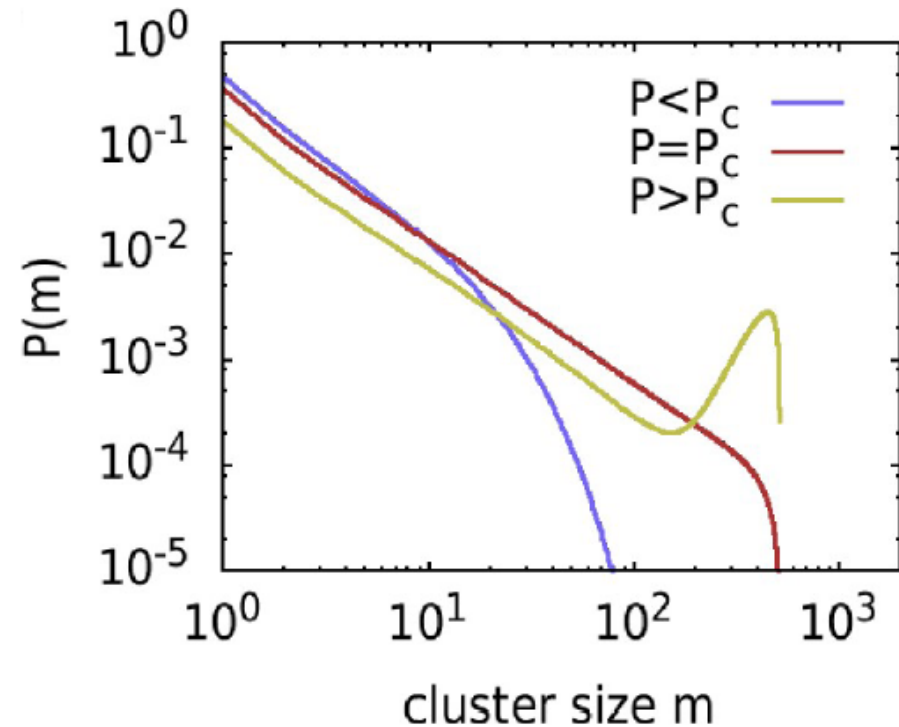
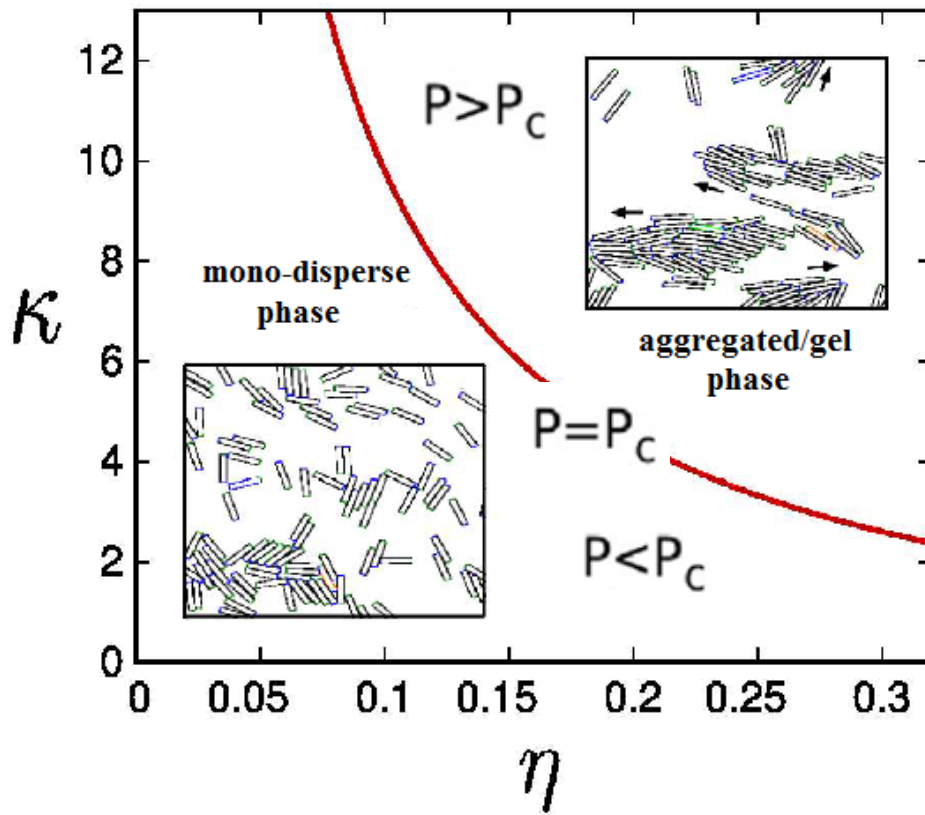
Myxobacteria as self-propelled rods

- How is the behavior in the bulk? - Simulate with periodic boundary conditions



Myxobacteria as self-propelled rods

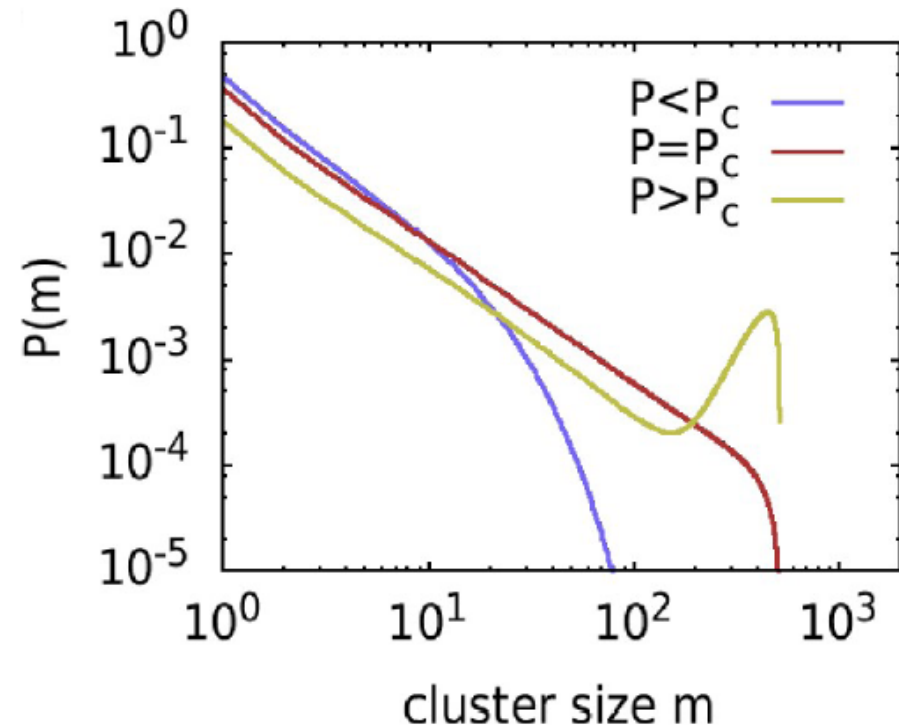
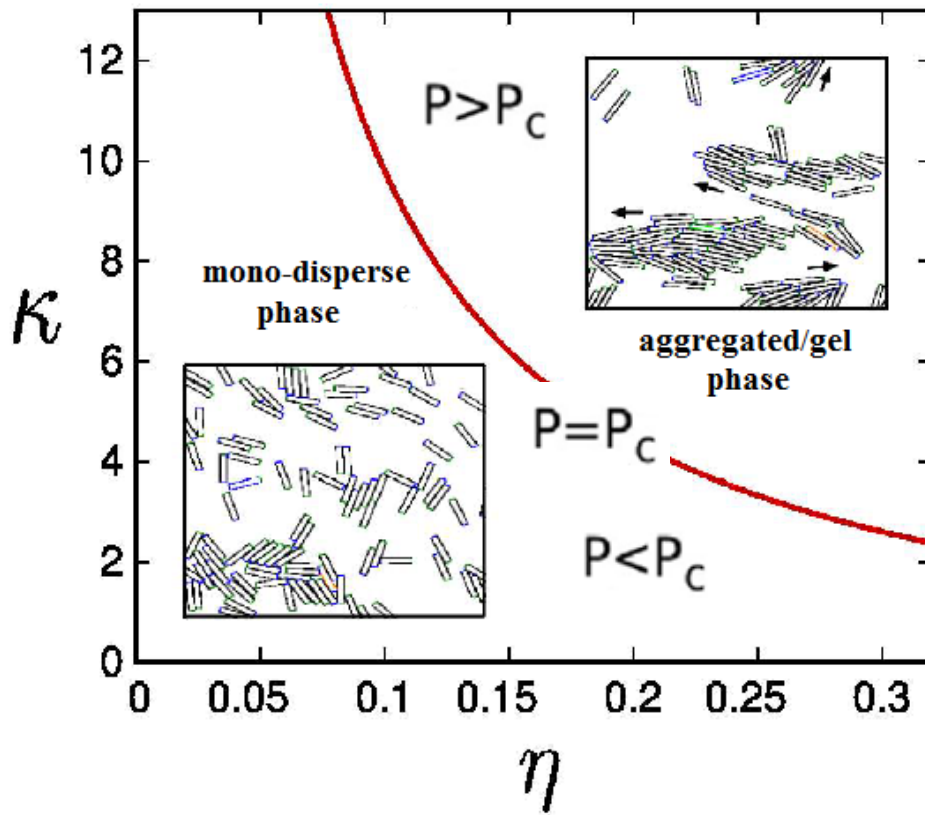
Clustering properties of a system of SP rods



**There is a dramatic change in the clustering properties of the system!
The cluster size distribution $p(m)$ encodes this information.**

Myxobacteria as self-propelled rods

Clustering properties of a system of SP rods

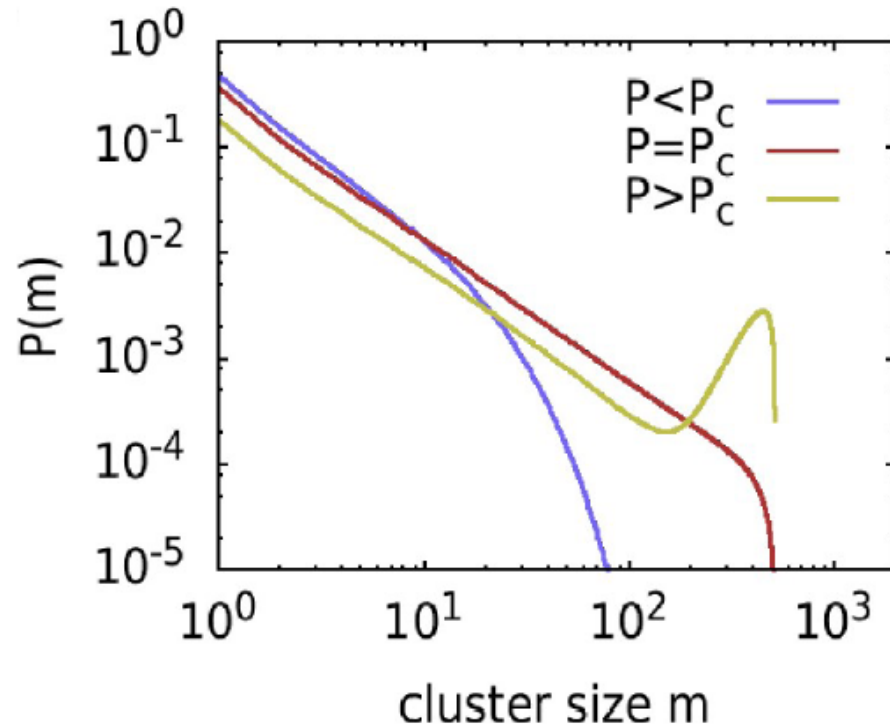


**There is a dramatic change in the clustering properties of the system!
The cluster size distribution $p(m)$ encodes this information.**

Myxobacteria as self-propelled rods

Clustering properties of a system of SP rods

Summary:



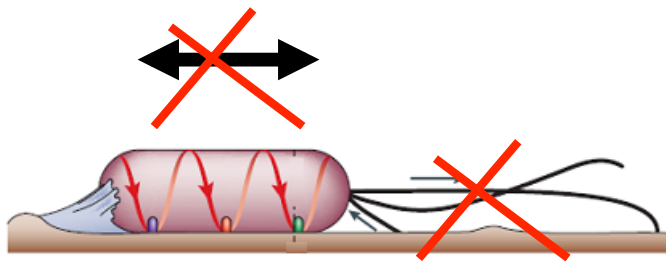
- low density – exponential (*mono-dispersed phase*)
- at critical density – power-law
- large density – peak at large m (*collect. mot. phase*)

Spatial self-organization of myxobacteria

What kind of clustering properties exhibit real myxobacteria ?

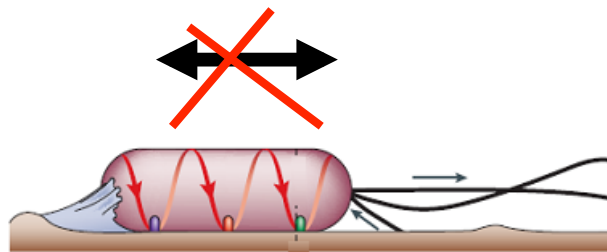
• Experiments with:

***A+S-Frz-* mutants**



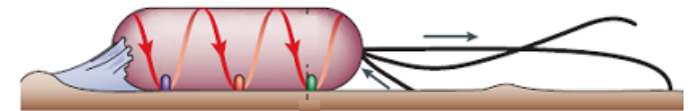
- * Cells do not reverse
- * Social motility engine – off
- * Advent. motility engine - on

***A+S+Frz-* mutants**



- * Cells do not reverse
- * Social motility engine – on
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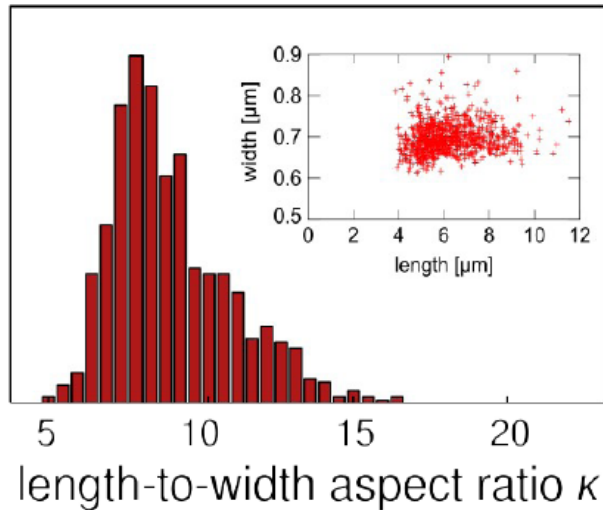
Wild-type



- * Cells do reverse
- * Social motility engine – on
- * Advent. motility engine - on

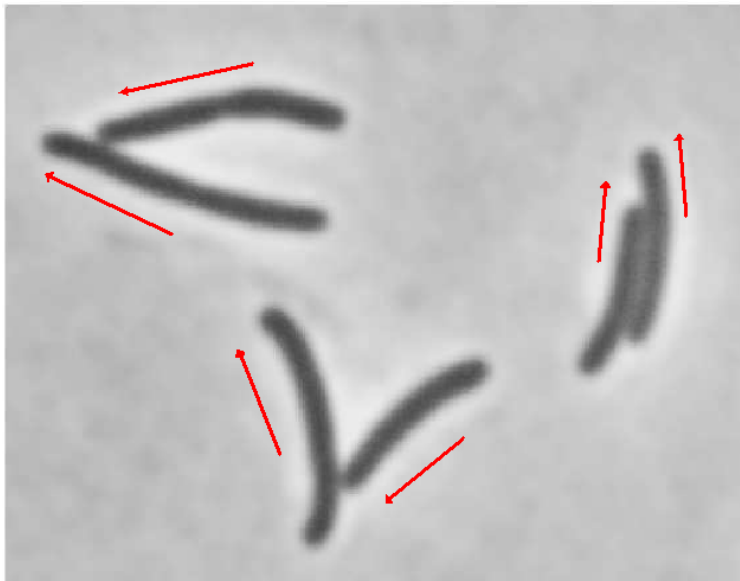
Spatial self-organization of myxobacteria

• Alignment and clustering (A+S-Frz- & A+S+Frz-)

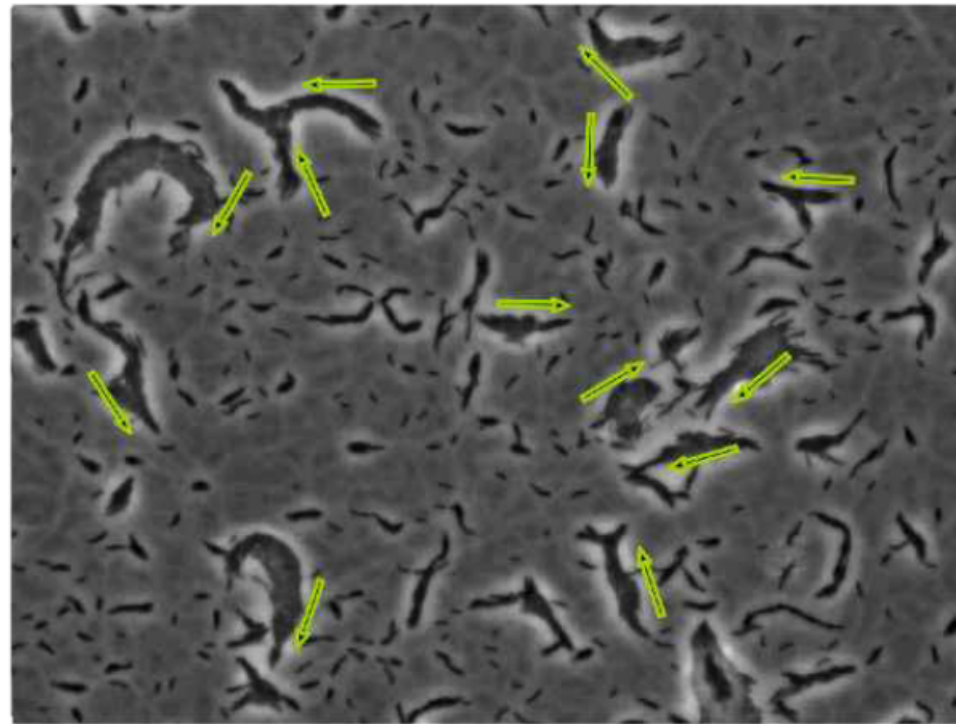


- Gliding speed = $3.10 \pm 0.35 \mu\text{m}/\text{min}$
- $W=0.7 \mu\text{m}$, $L=6.3 \mu\text{m}$, $a=4.4 \mu\text{m}$
- $\kappa=8.9 \pm 1.95$

Cell collision leads to alignment:

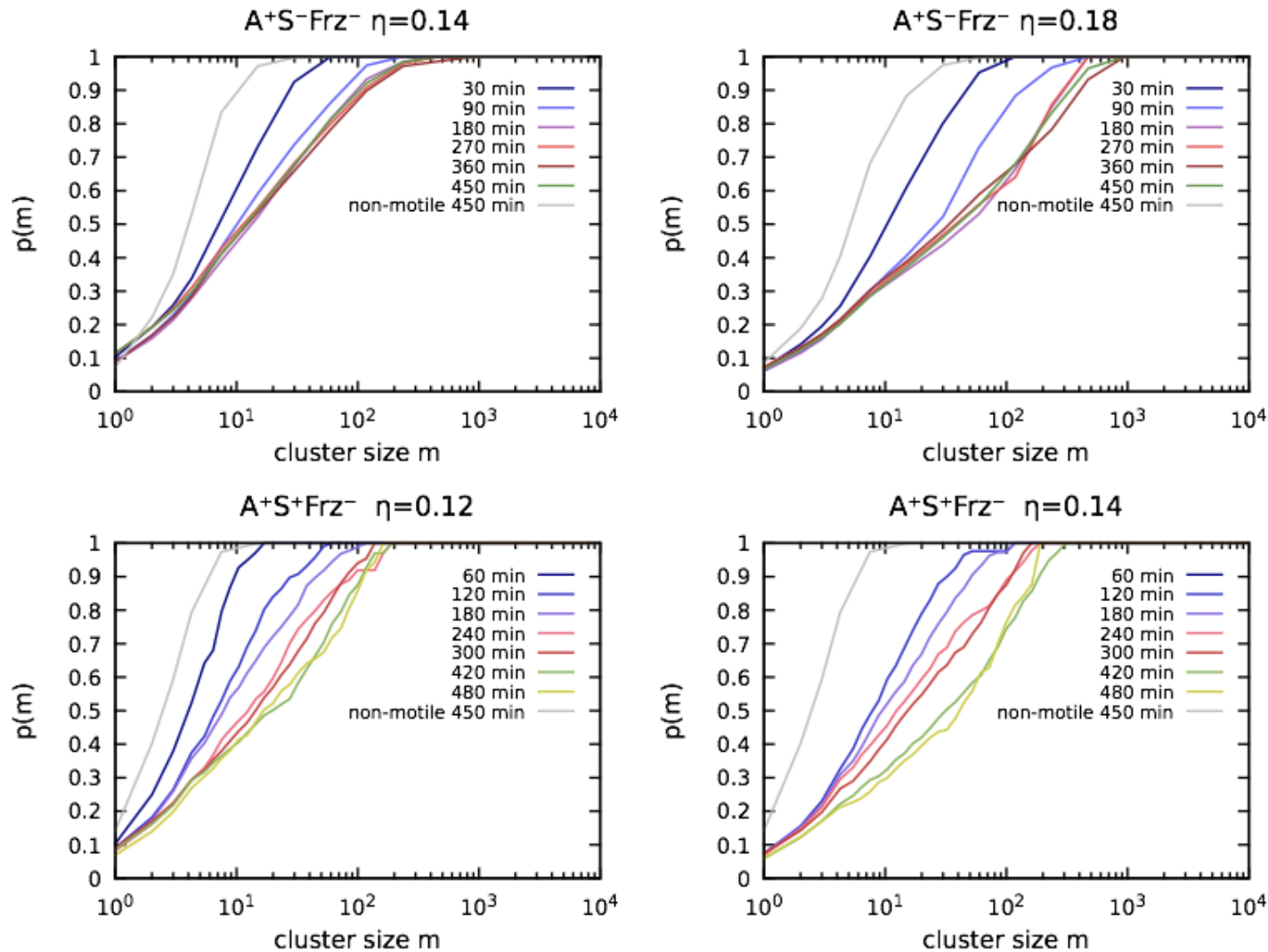


Moving clusters of bacteria are formed:



Spatial self-organization of myxobacteria

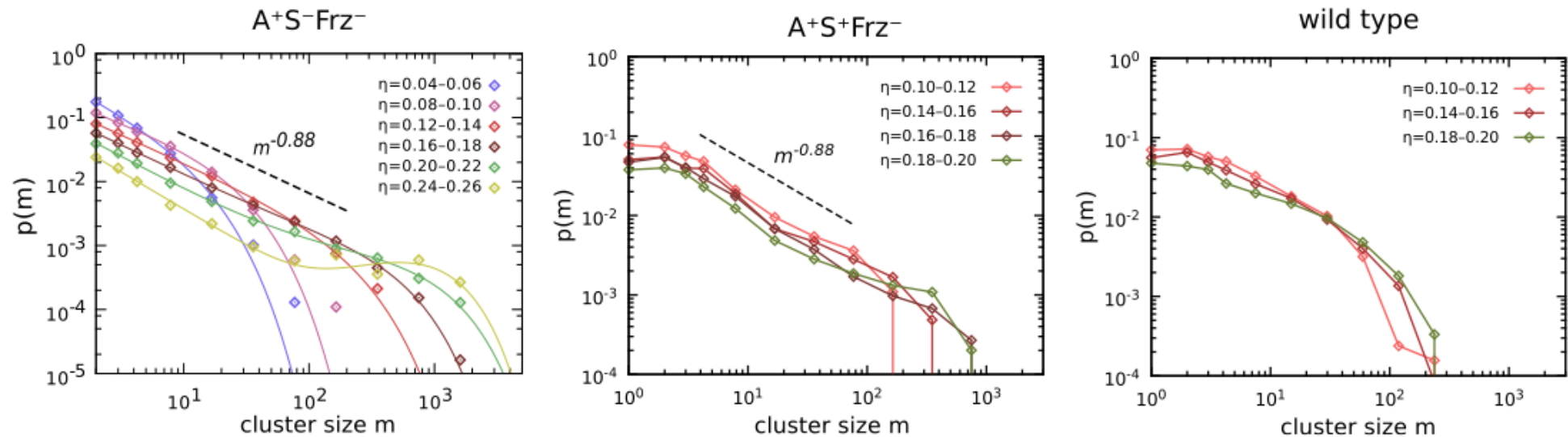
- Convergence with time:



There is a steady state cluster size distribution

Spatial self-organization of myxobacteria

- Steady state cluster size distribution is a function of the density



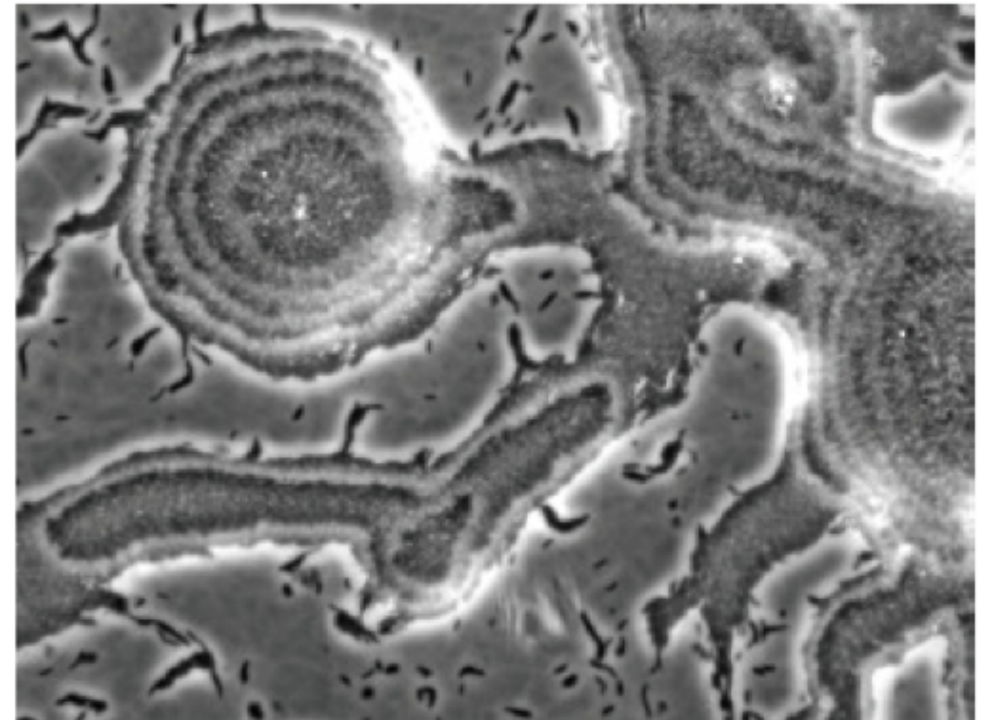
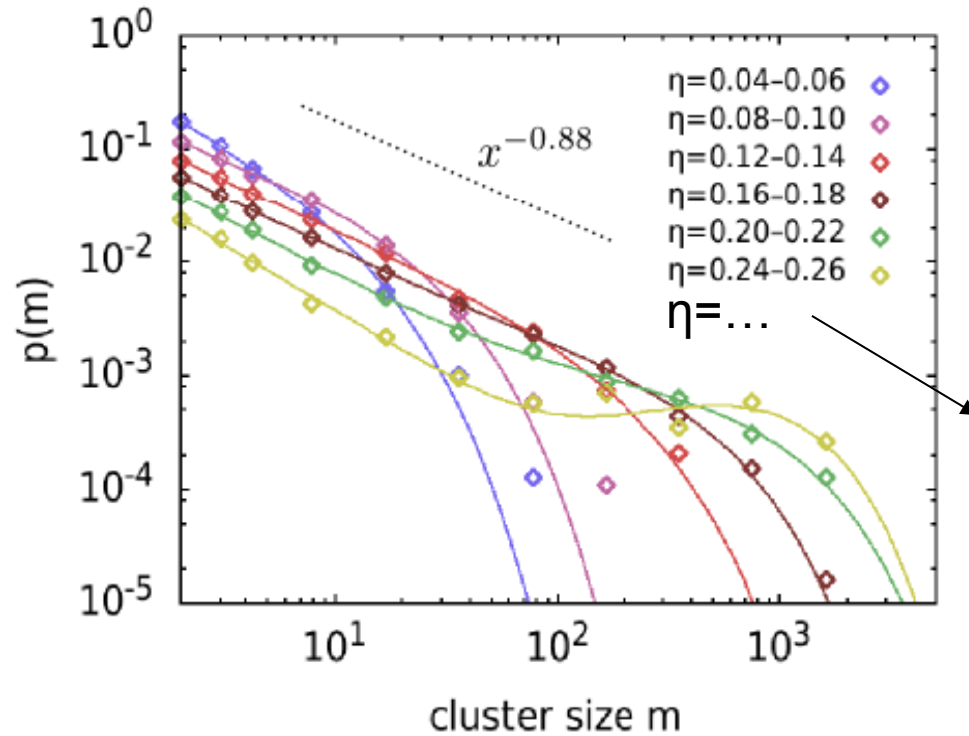
CSD in non-reversing mutants:

- low density – exponential (*mono-dispersed phase*)
- at critical density – power-law
- large density – peak at large m (*collective m . phase*)

- ↓
- Always exponential
 - Here there is a percolation transition at high densities.

Spatial self-organization of myxobacteria

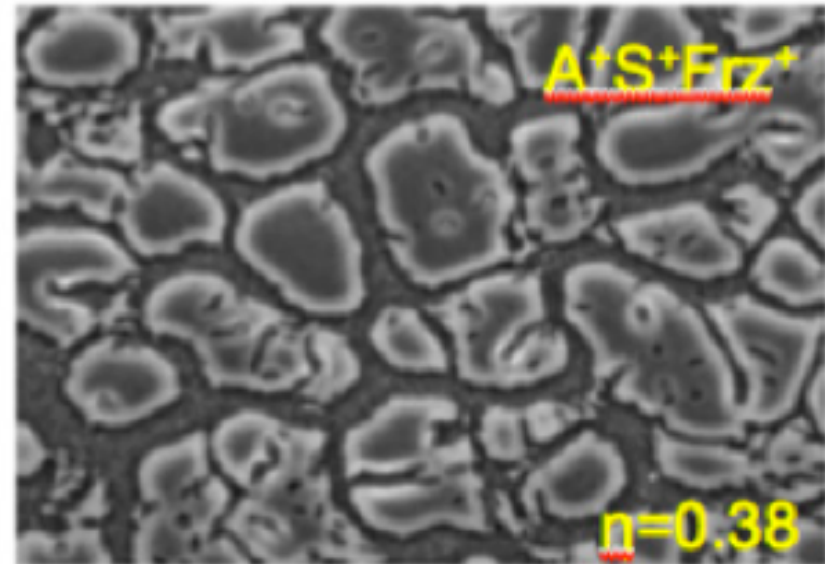
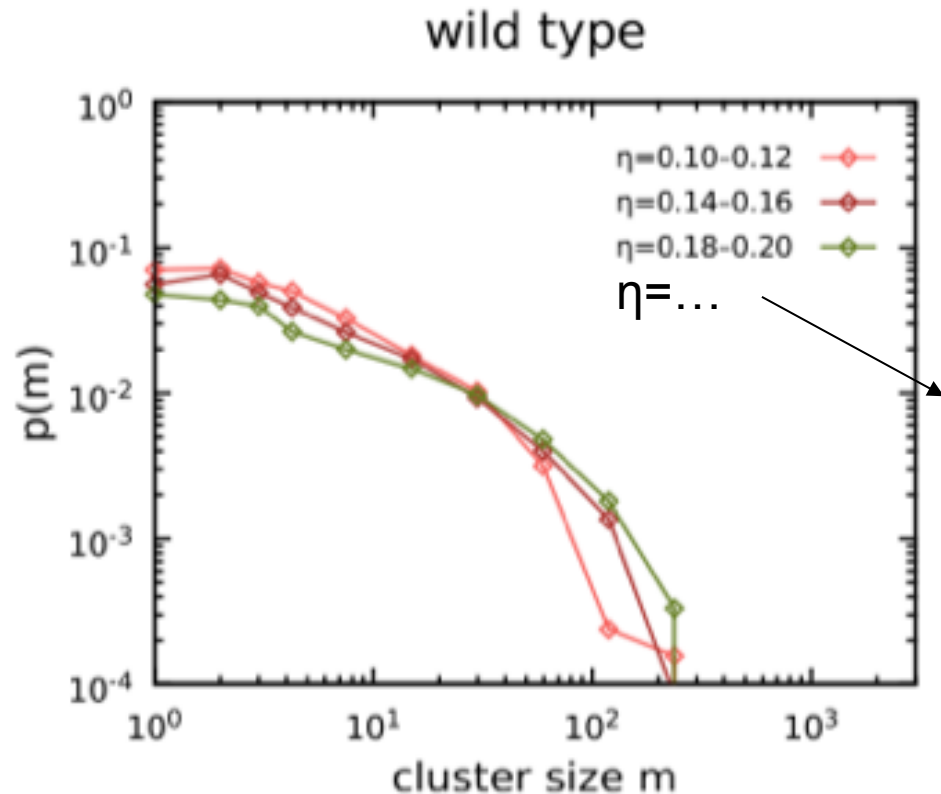
- Steady state cluster size distribution is a function of the density



**At very high densities we observe vortex formation
in A+S-Frz- & A+S+Frz-**

Spatial self-organization of myxobacteria

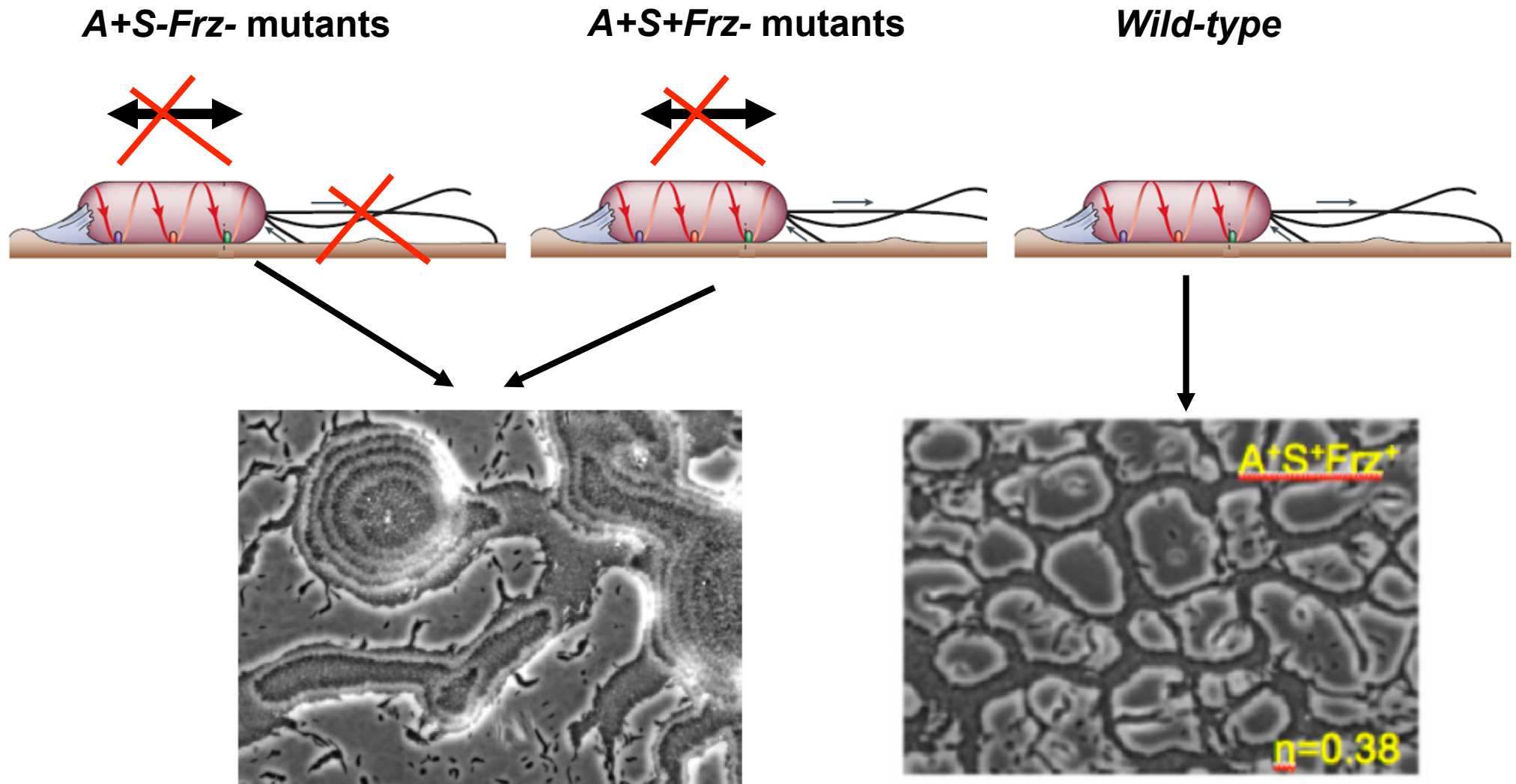
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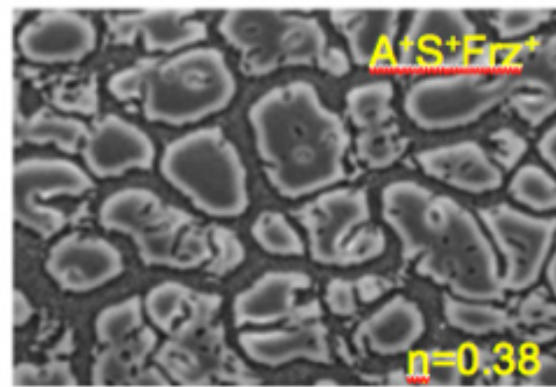
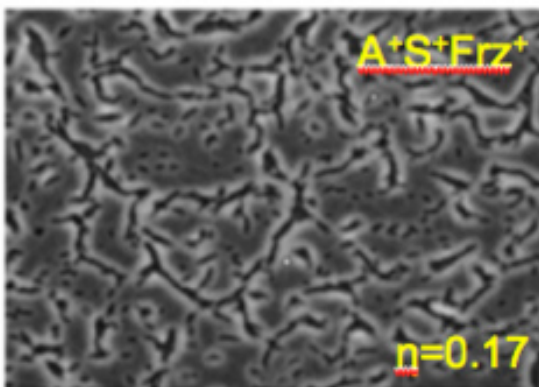
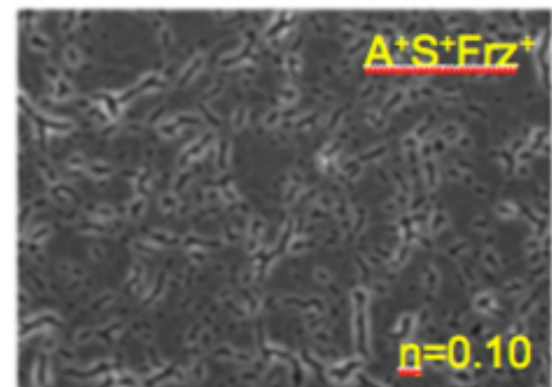
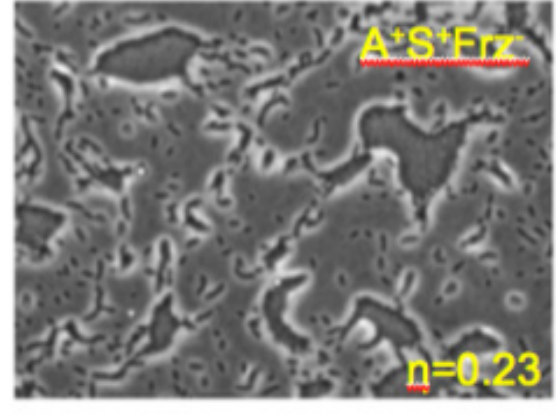
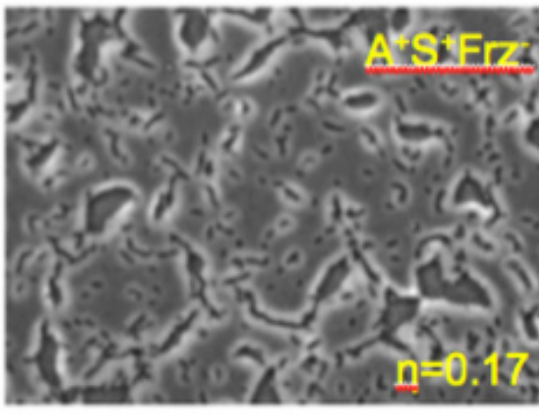
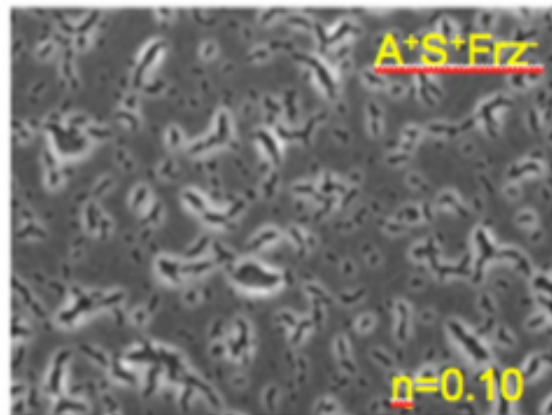
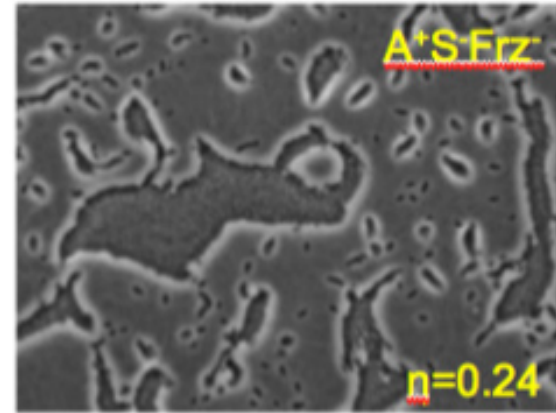
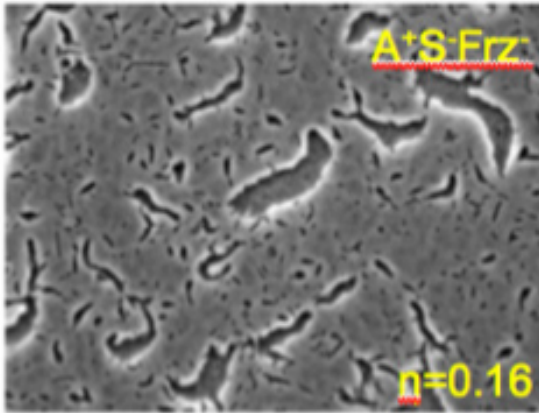
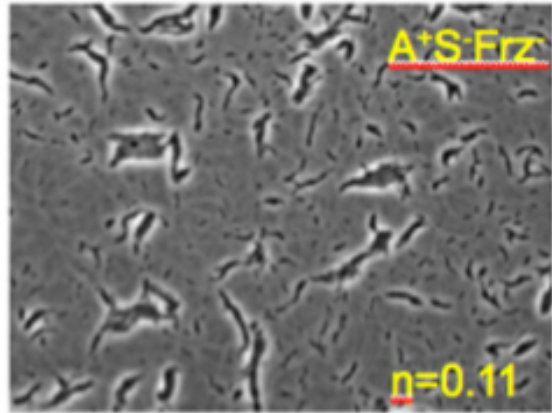
At very high densities we observe formation of mesh-like structures in the (reversing) wild-type

Spatial self-organization of myxobacteria

- Experiments with:



Spatial self-organization of myxobacteria



Spatial self-organization of myxobacteria

Number fluctuations

Average number:

$$\langle n(L) \rangle = \rho L^2$$

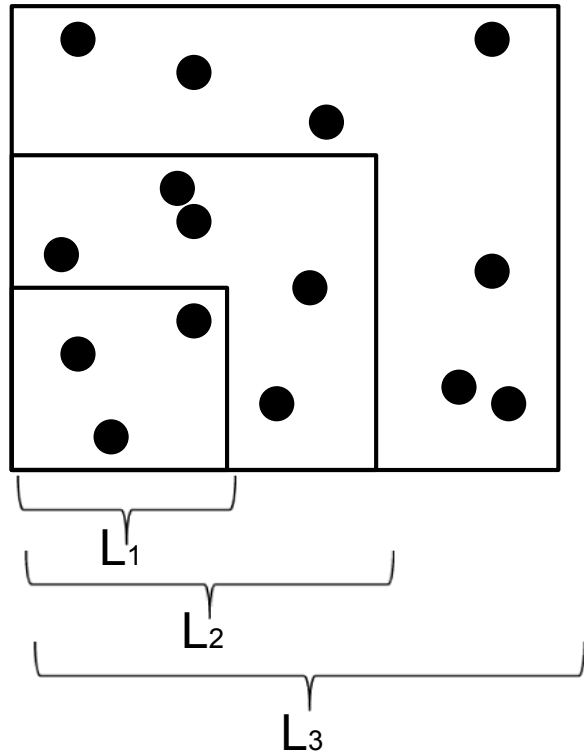
Average square number:

$$\Delta n^2 = \langle [n(L) - \langle n(L) \rangle]^2 \rangle$$

$$\Delta n = \left(\langle [n(L) - \langle n(L) \rangle]^2 \rangle \right)^{1/2} = \langle n(L) \rangle^{\beta}$$

Normal number fluctuations

$$\Delta n = \langle n(L) \rangle^{1/2} !$$



$n(L)$ = number of particles
in box of size L

Spatial self-organization of myxobacteria

Number fluctuations

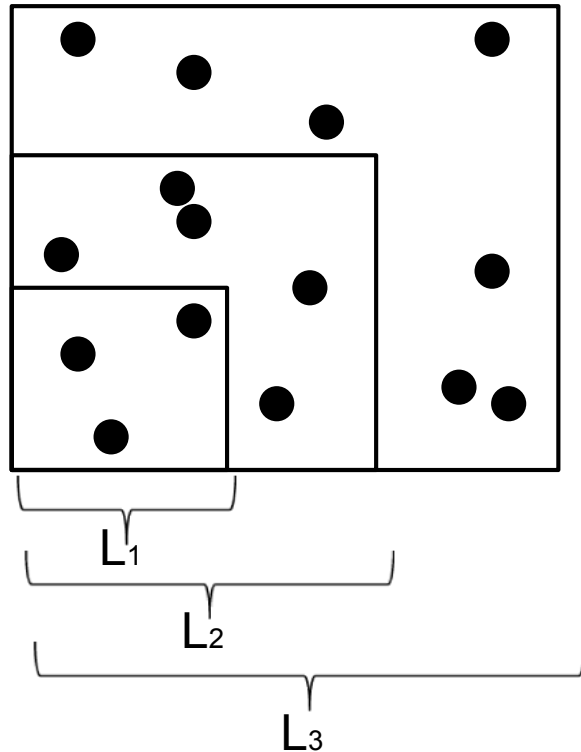
Average number:

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Average square number:

$$\Delta n^2 = \langle [n(L) - \langle n(L) \rangle]^2 \rangle$$

$$\Delta n = (\langle [n(L) - \langle n(L) \rangle]^2 \rangle)^{1/2} = \langle n(L) \rangle^\beta$$



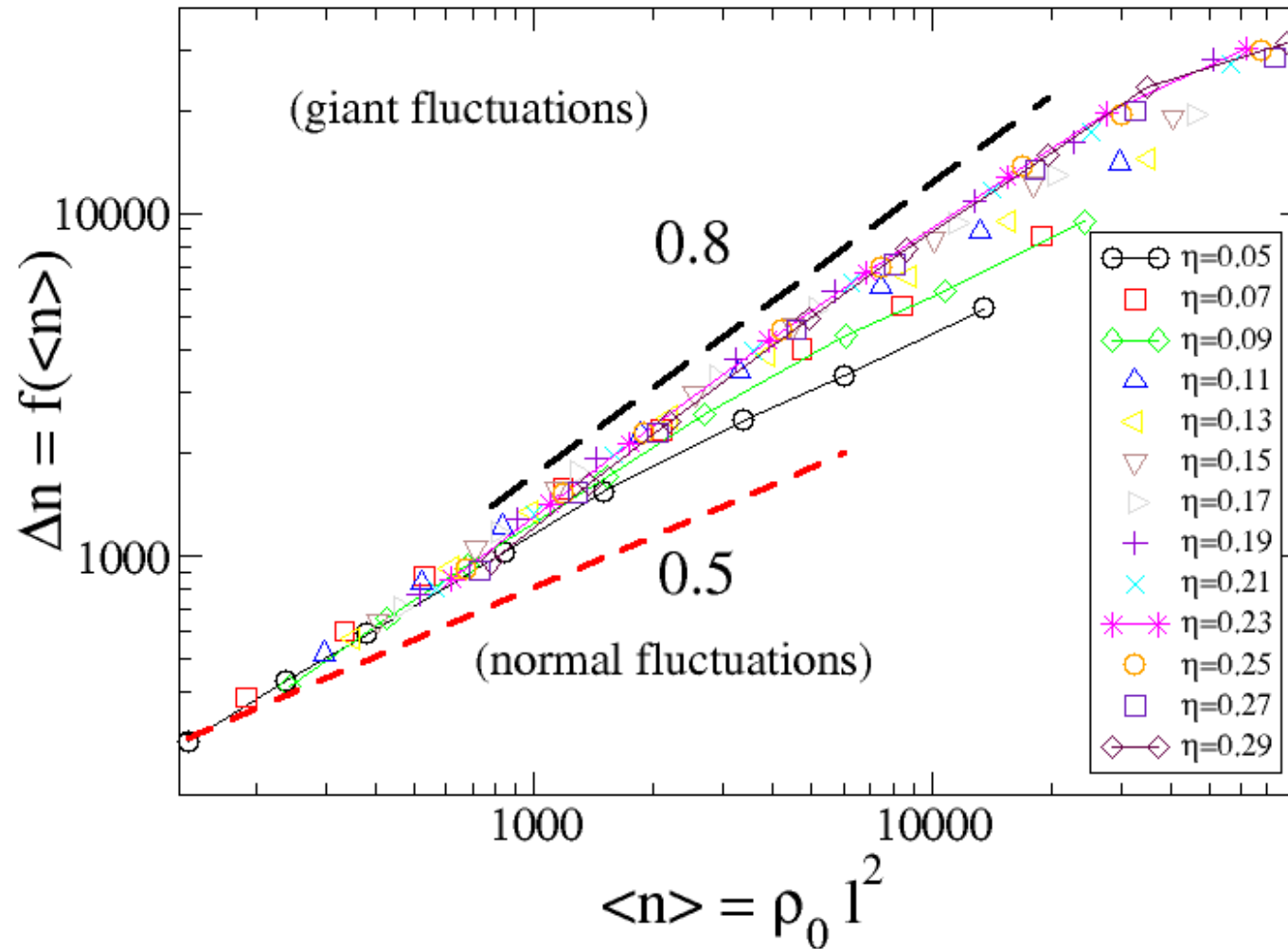
$n(L)$ = number of particles
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Giant number fluctuations

$$\Delta n = \langle n(L) \rangle^\beta \quad \beta > 1/2 \quad !$$

Spatial self-organization of myxobacteria

Apparent giant number fluctuations



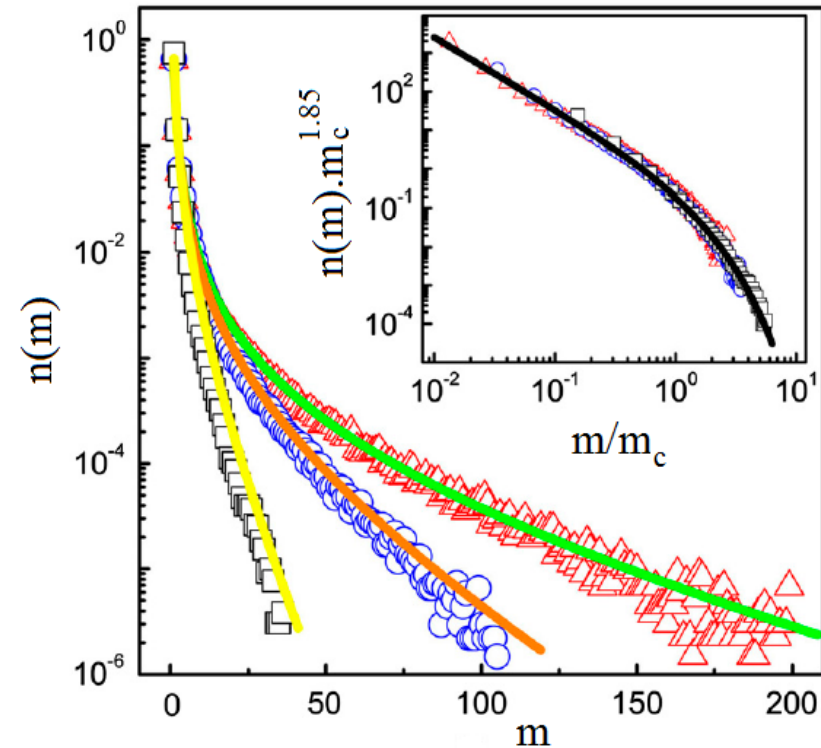
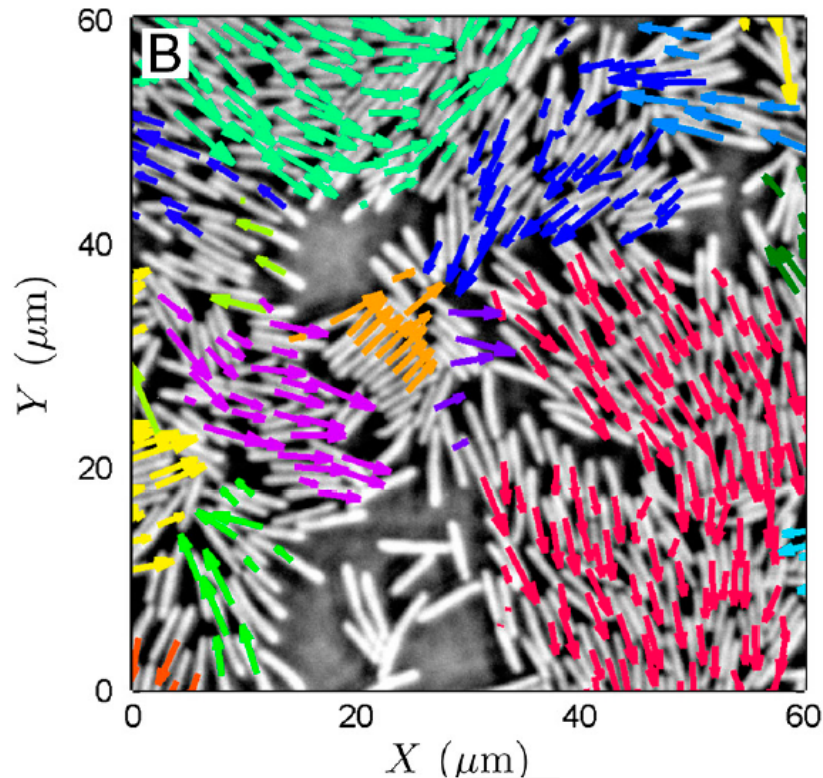
critical NF exponent: **0.8**

(Measurements performed with the A+S-Frz- cells)

Spatial self-organization of myxobacteria

Can the combination of self-propulsion and volume exclusion be a “general” mechanism for spatial self-organization in bacteria ?

Experiments with *Bacillus subtilis* – motion in a 2D thin film of flagellated cells

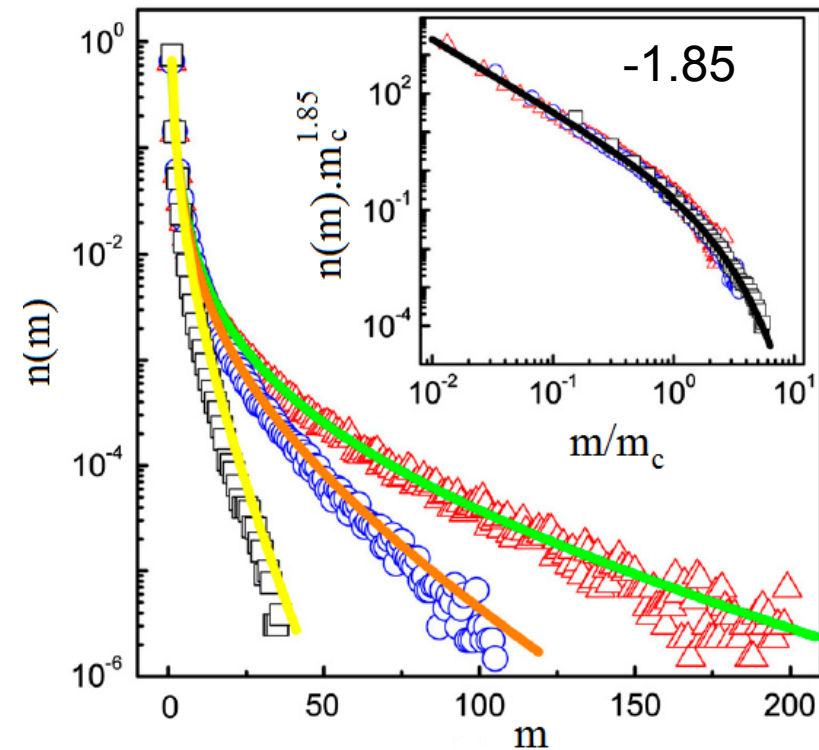
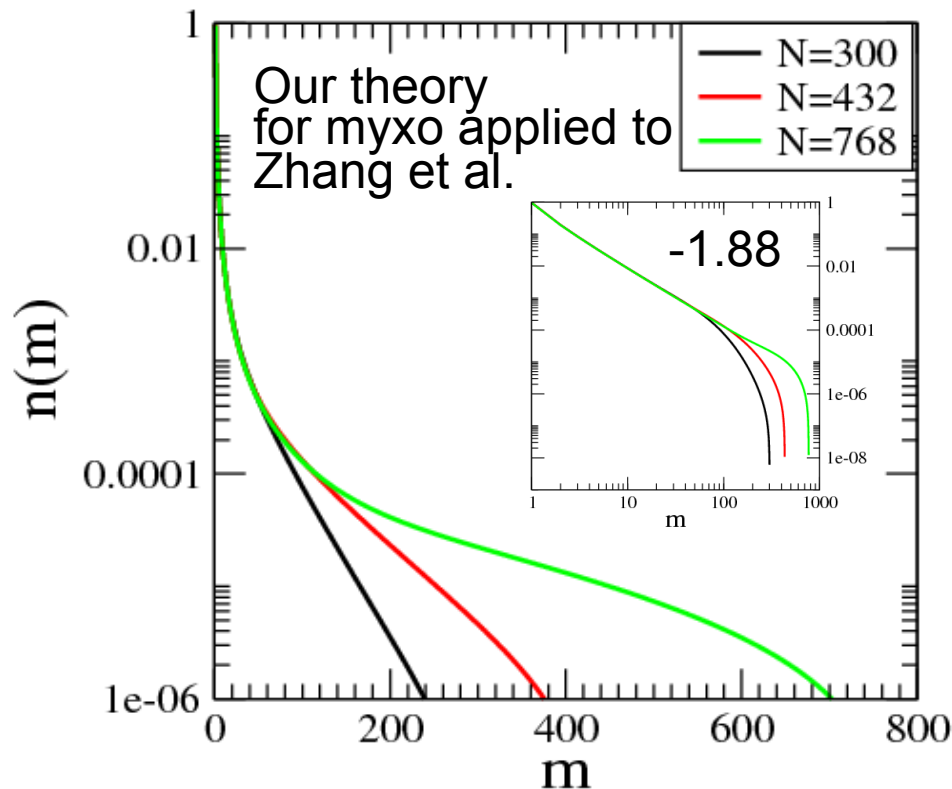


$$n(m) \sim m^{-1} p(m) \longrightarrow \text{critical exponent: } \mathbf{0.85}$$

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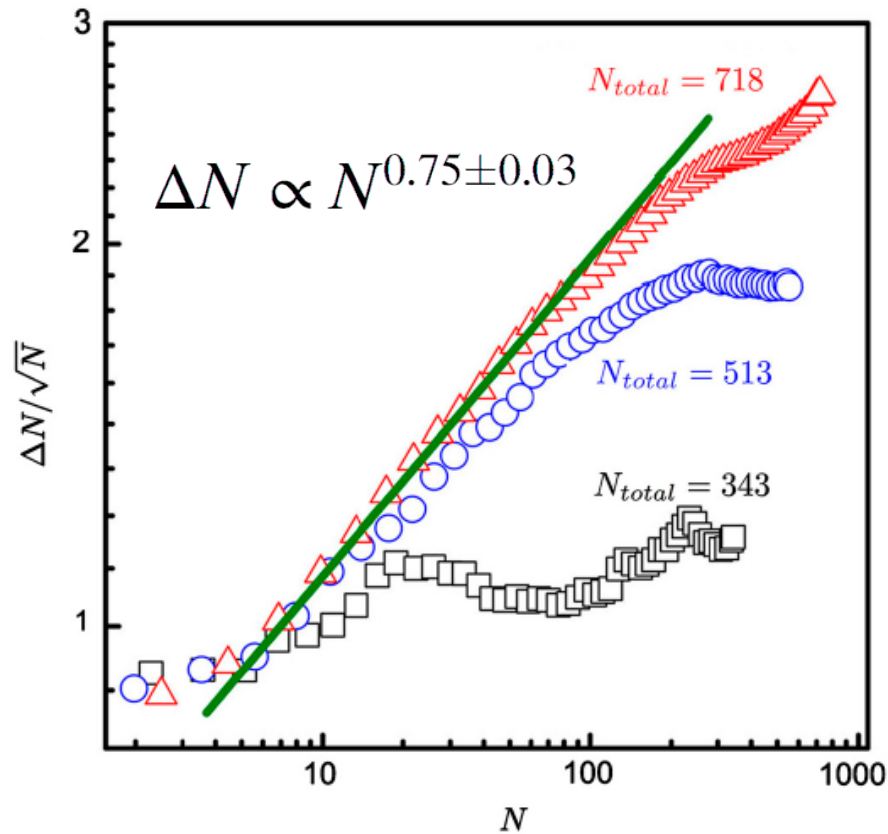
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H. P. Zhang et al., PNAS 107, 13626 (2010)

Spatial self-organization of myxobacteria

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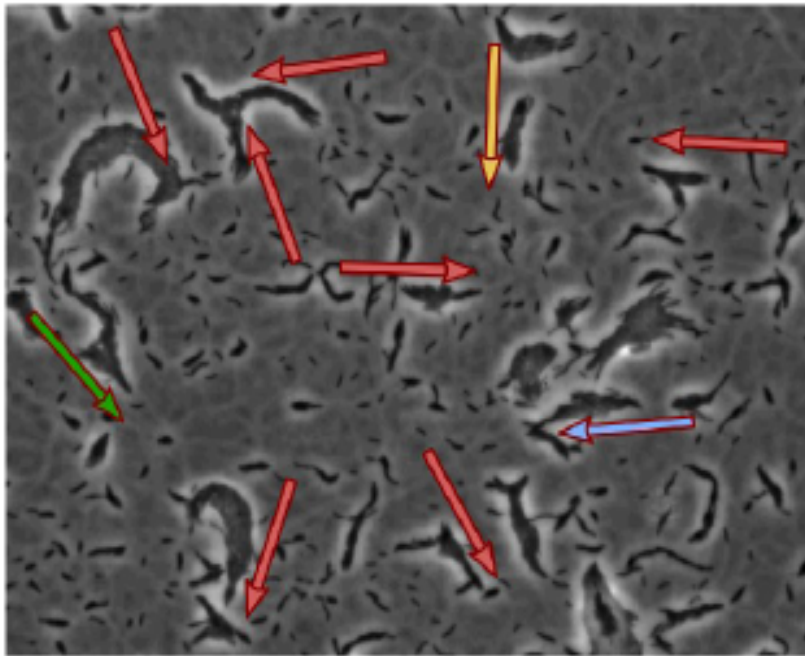


Measurement of number fluctuations:

- Giant number fluctuations reported!
- Critical NF exponent: **0.75 +/- 0.03**

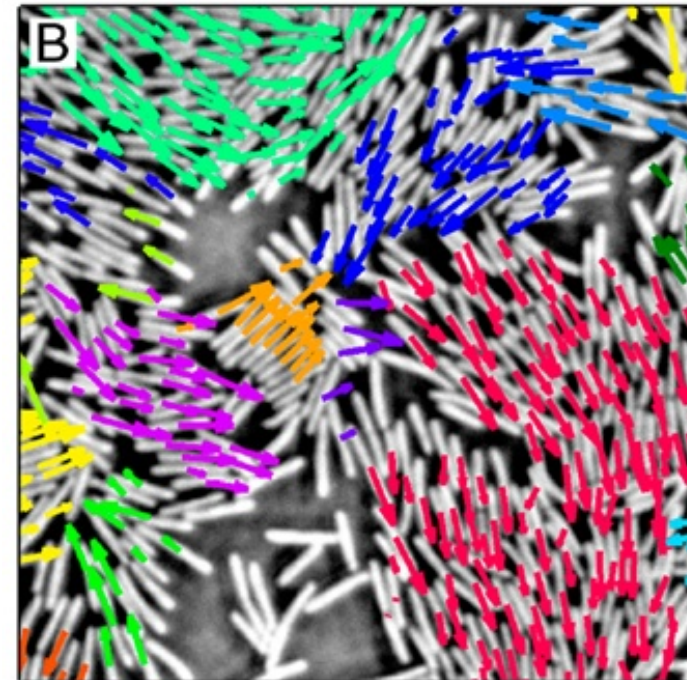
Spatial self-organization of myxobacteria

Myxococcus xanthus



- no flagella
- no swimming, no fluid – just gliding
- speed $3.1 \mu\text{m}/\text{min}$
- $L=6.3\mu\text{m}$; $W=0.7\mu\text{m}$
- $T=480 \text{ min}$ (8hs)

Bacillus subtilis



- flagella
- swimming ?
- speed $900 \mu\text{m}/\text{min}$?
- $L=3\mu\text{m}$; $W=0.6\mu\text{m}$
- $T=1.6 \text{ min}$

Common features: **2D motion, self-propulsion, volume exclusion effects**

Critical clustering exponent: **0.88 (myxo)** and **0.85 (B. subt.)!**

Critical NF exponent: **0.8 (myxo)** and **0.75 (B. subt.)!**

**evidence of a general mechanism
for the spatial self-organization in bacteria ?**

Spatial self-organization of myxobacteria

Gliding bacteria – in absence of biochemical signal regulation or hydrodynamical interactions – exhibit a **Collective Motion (CM) phase!**

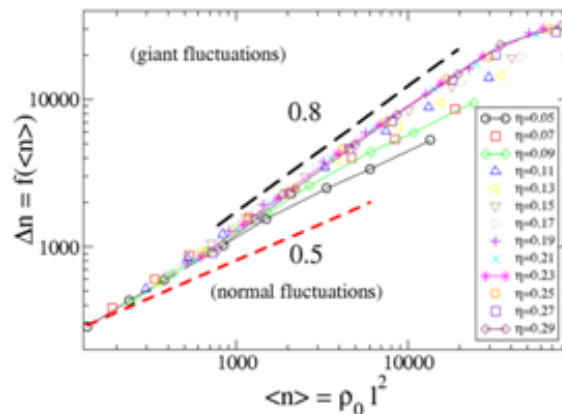
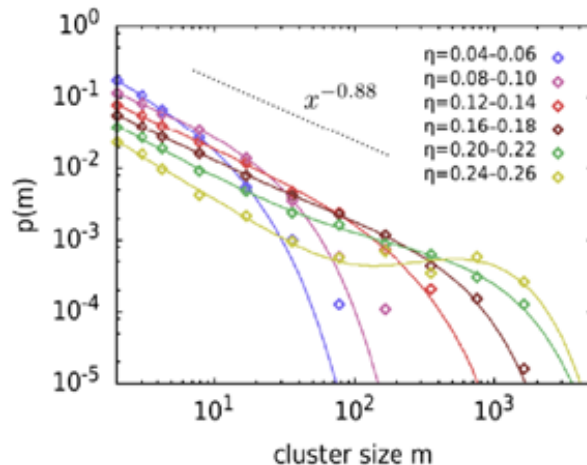
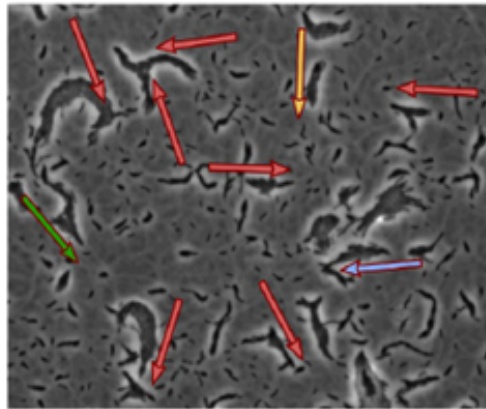
Measured statistical features of this CM phase:

- Non-monotonic CSD – existence of arbitrary large cluster sizes

- Giant number fluctuations

Onset of collective motion:

- Power-law CSD with exponent 0.88
- Apparent giant num. fluctuations with exponent 0.8



Spatial self-organization of myxobacteria

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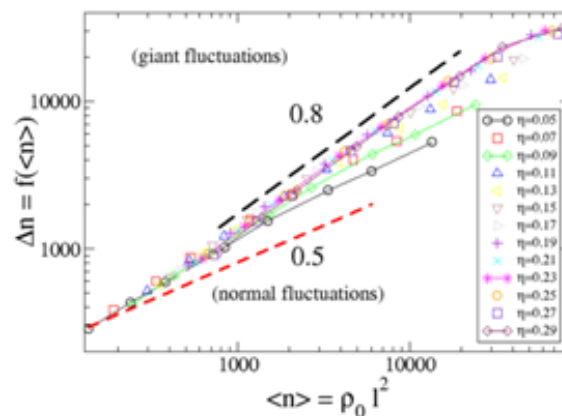
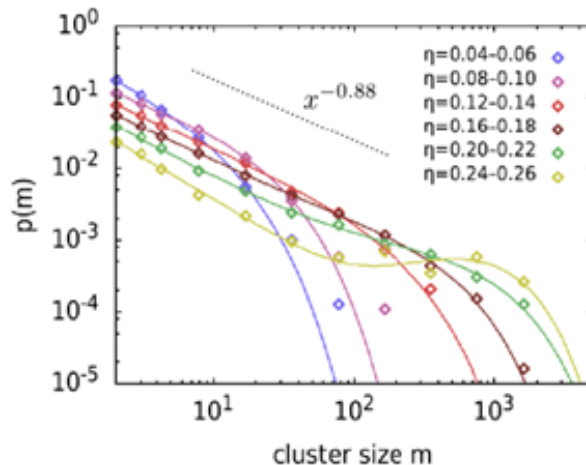
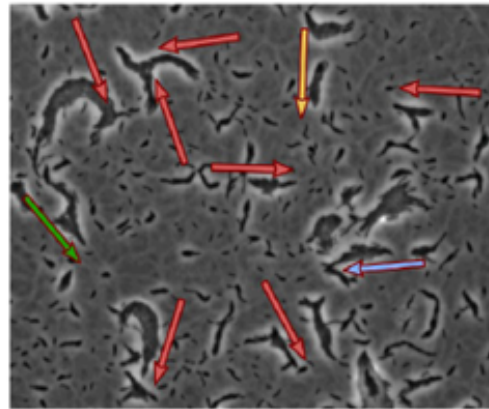
Onset of collective motion:

- Power-law CSD with exponent 0.88

- Apparent giant num. fluctuations with exponent 0.8

Similar statistical features observed in *B. Subtilis!*

SP + volume exclusion candidate to be a general mechanism in the spatial self-organization of bacteria moving in 2D





Thanks for you attention!

Some references:

FP, Starruss, Jakovljevic, Soogard-Andersen, Deutsch, Bär, PRL (2012)
Starruss, FP, Jakovljevic, Soogard-Andersen, Deutsch, Bär, Interface focus (2012)
Chepizkho, FP, unpublished (2012)