



# *Analytical and numerical study of a realistic model for fish schools*



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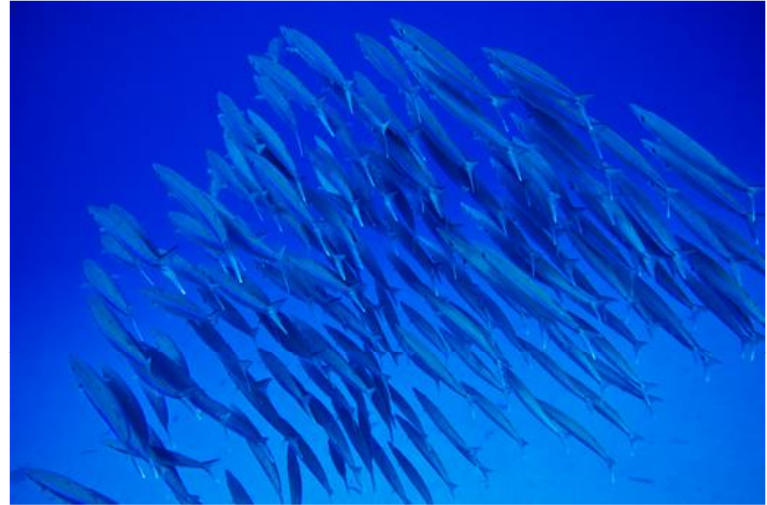
**[www.lpt.ups-tlse.fr](http://www.lpt.ups-tlse.fr)**

**Guy Theraulaz, Daniel Calovi, Ugo Lopez, J. Gautrais  
(CRCA, Toulouse)**

**Hugues Chaté, Sandrine Ngo  
(CEA, Saclay)**

# *Collective motion in fish schools*

Swarming, schooling, milling



# Introduction

- Several models reproduce qualitatively the collective behaviors in fish schools, wild insect swarms, flocks of birds...
- The **Vicsek Model** (1995)

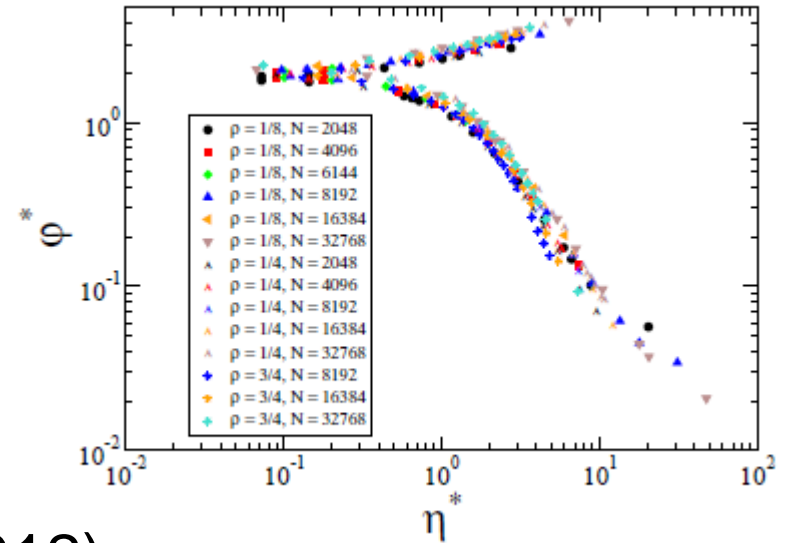
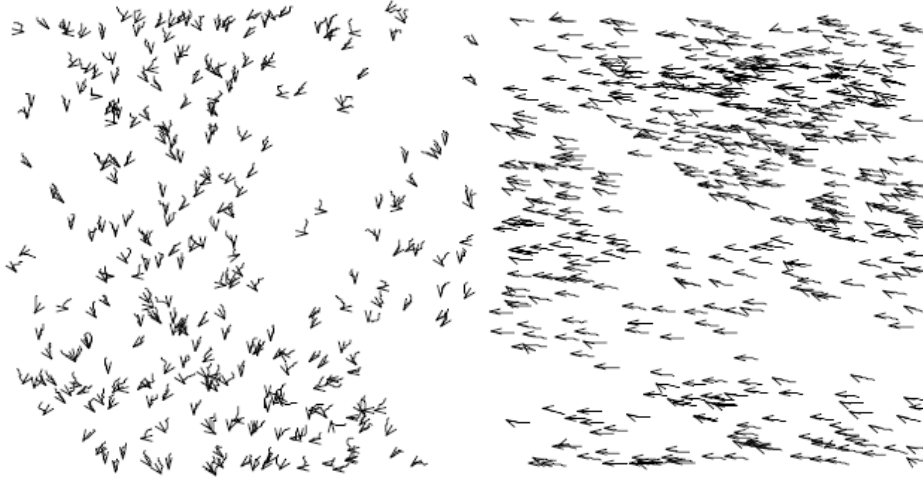
$$\phi_i(t+1) = \arg \sum_{\langle i, j \rangle_{R_0}}^N e^{i\phi_j(t)} + \eta \xi_i(t)$$

$$\mathbf{r}_i(t+1) = \mathbf{r}_i(t) + v_0 \mathbf{e}_{\phi_i(t+1)}$$

$\eta$ ,  $R_0$ ,  $v_0$  are the noise intensity, interaction radius, and velocity  
Fixing  $R_0$  and  $v_0$ , the control parameters are  $\eta$  or the density  $\rho$

**Order parameter**  $\phi = \frac{1}{N} \left| \sum_{i=1}^N \mathbf{e}_{\phi_i} \right|$

# Vicsek Model

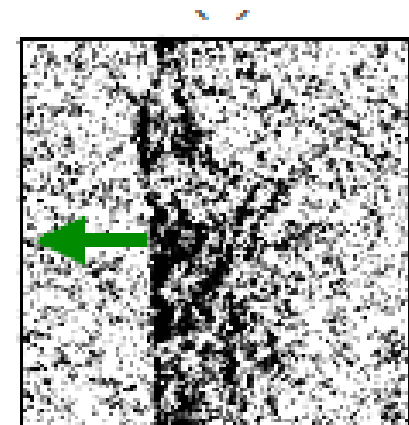


$$\phi(\eta) \sim |\eta - \eta_c|^\beta \quad (\text{Baglietto et al. 2012})$$

$$\beta \approx 0.45(3), \quad \nu \approx 1.6(3), \quad \gamma \approx 2.3(4)$$

$$\phi^* = \phi(L)L^{\beta/\nu}, \quad \eta^* = \frac{|\eta - \eta_c|}{\sqrt{\rho}}$$

Second order nature of the transition **challenged by kinetic theory**: mode instability – stripes – destabilizes the long-range order just below the onset of flocking (Grégoire *et al.* 2004, Bertin *et al.* 2006, Chaté *et al.* 2007, Ihle 2010)



# *Experiments by the CRCA team*

- Need for **realistic models** based on constraining and validating **experiments**
- These experiments (1, 2, 5... up to 30 fish) permit to identify “**individual laws**”, “**elementary interactions**”, and “**microscopic parameters**”



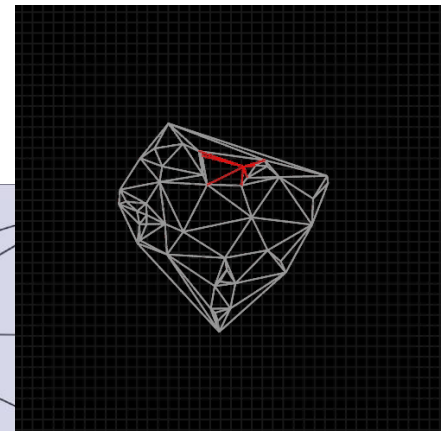
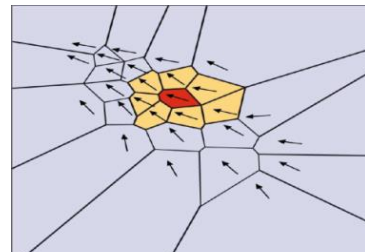
# *Some important aspects*

- Forces mediated by **vision** are in general **not conservative** (no law of action-reaction)



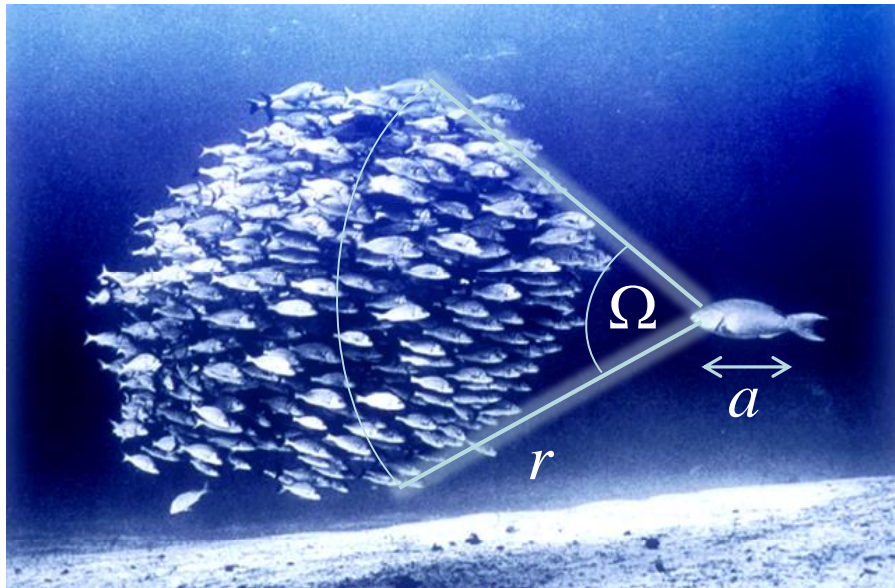
- Are forces really **additive** (a finite amount of information can be treated)? Instead, forces may be an **average** over the local environment

- Do fish (or birds) interact through **metric** or **topologic** (Voronoi diagram) forces? (not crucial in a tank)



# Long-range attractive interactions?

- Additive (?) attractive force are mediated by **vision** and should be a linear function of the **(solid) angle spread** of the (group of) fish



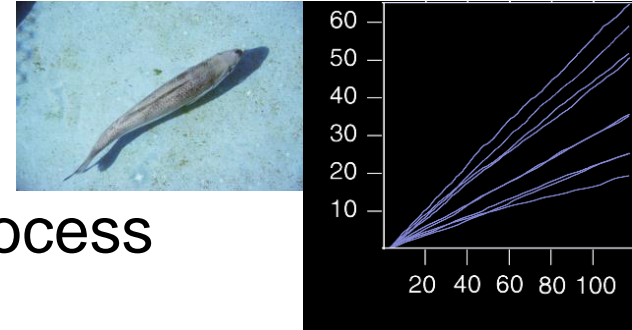
$$F(r) \sim \Omega \sim \left( \frac{a}{r} \right)^{d-1}$$

- **Long-range** attractive (~gravitation) force...  
but **screened** by obstacles

# Basic model validated by CRCA experiments

on Barred Flagtail (*Kuhlia Mugil*), and more recently, *Hemigrammus*  
*J. Gautrais et al., J. Math. Biol. (2009); Plos Comput. Biology (2012)*

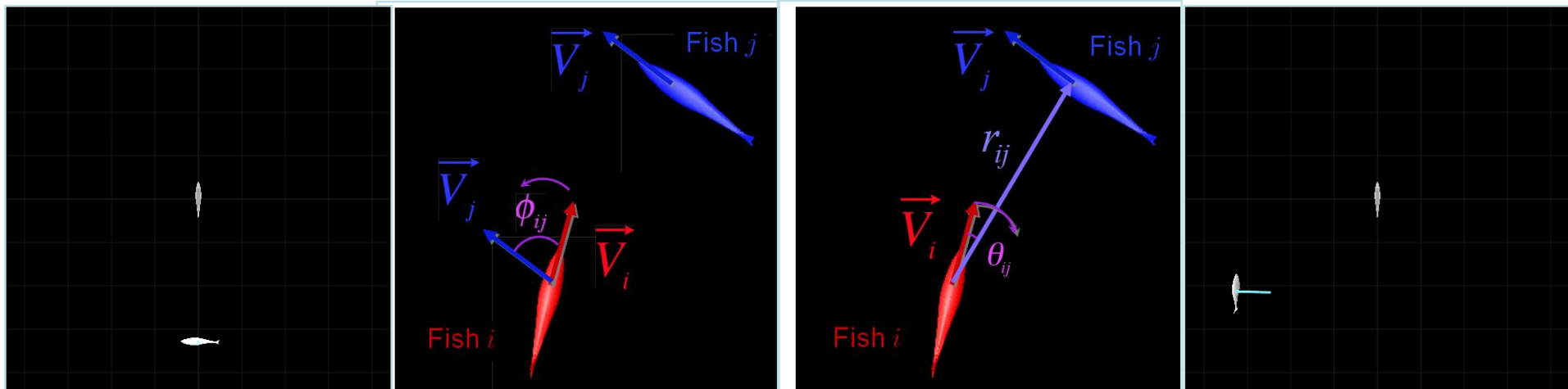
- **Constant velocity**  $v \sim 0.1 - 0.6$  m/s
- Individual (2D) angular velocity evolving according to an **Ornstein-Uhlenbeck** process



$$\frac{d^2 \phi_i}{dt^2} = \frac{d\omega_i}{dt} = -\frac{1}{\tau}(\omega_i - \omega_i^*) + \sigma \eta(t), \quad \frac{d\mathbf{r}_i}{dt} = v \mathbf{e}_{\phi_i}$$

$(\tau \sim \xi / v; \sigma \sim \hat{\sigma} v)$

- The target angular velocity includes the effect of **alignment** and **attraction** (metric/topological) forces

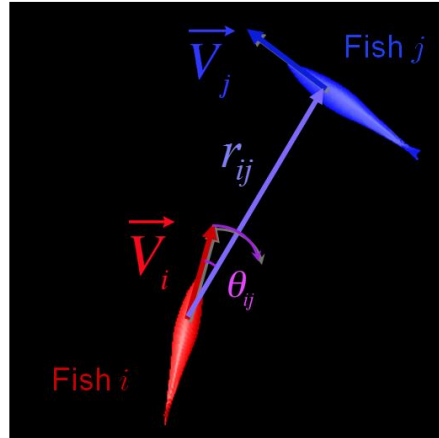
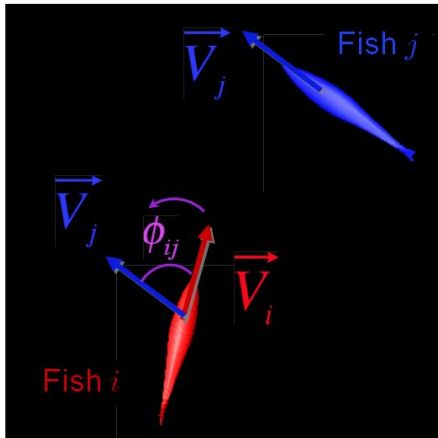




# Basic model validated by CRCA experiments

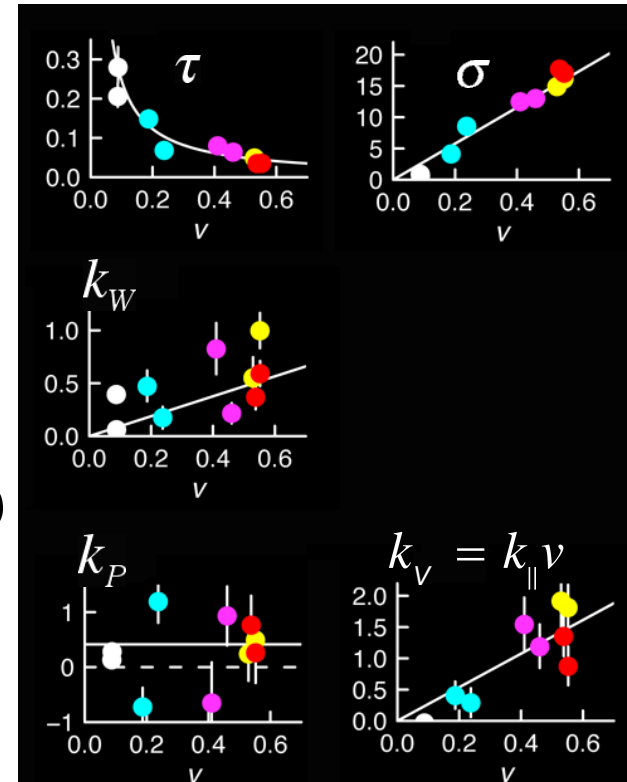
- Topological **alignment** force  $\sim v$  and **attraction** force  $\sim r_{ij}$
- Phenomenological effect of **vision angle**

$$\omega_{j \rightarrow i}^* = \left[ k_{\parallel} v \sin(\phi_j - \phi_i) + k_P r_{ij} \sin(\theta_{ij}) \right] \times \left[ 1 + \varepsilon \cos(\theta_{ij}) \right]$$



- + repulsive interaction with the **wall** ( $k_W$ )
- **Averaging**

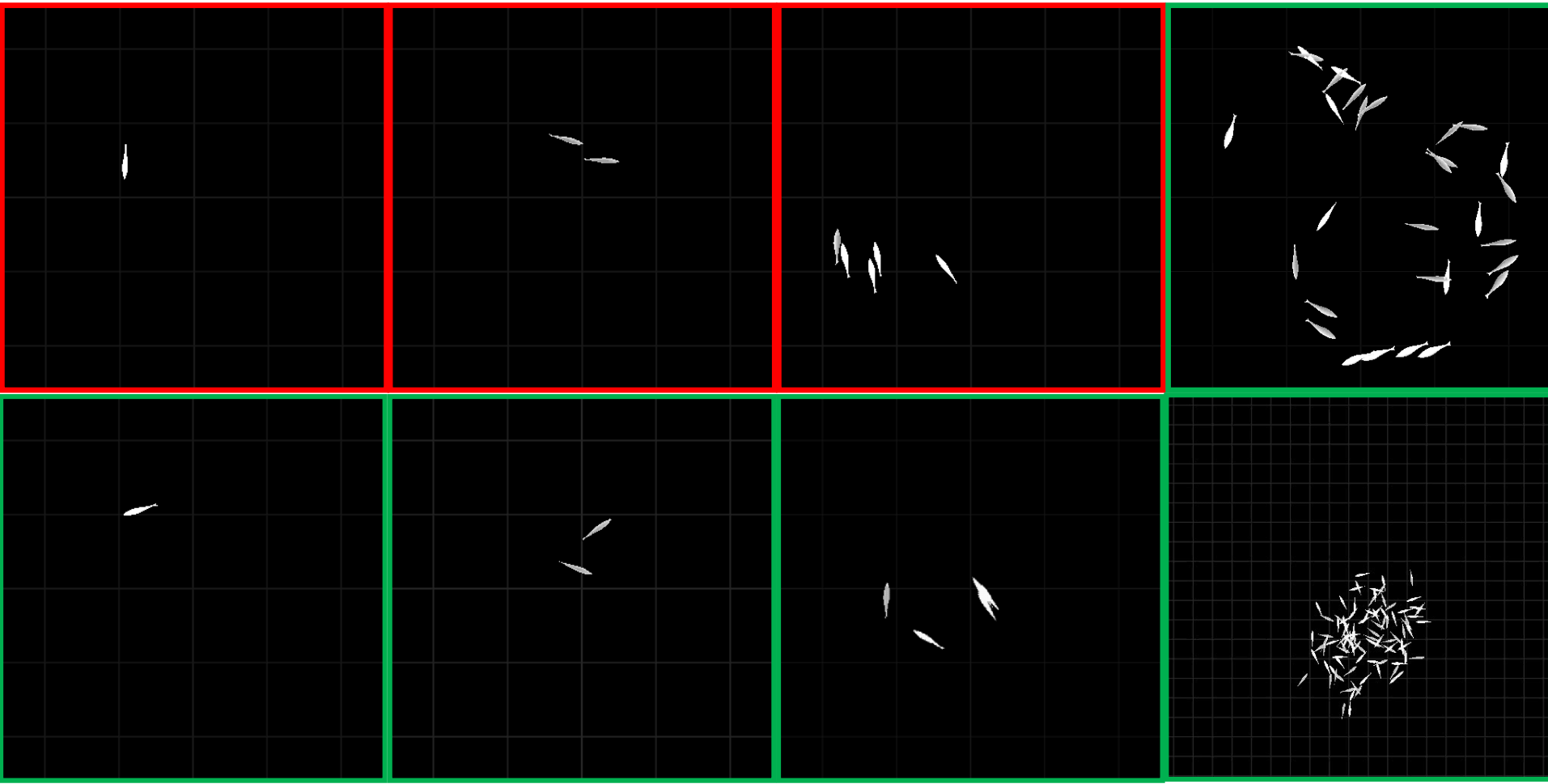
$$\omega_i^* = \frac{1}{N_i} \sum_{\langle j,i \rangle} \omega_{j \rightarrow i}^* \quad (N_i \sim 6)$$



# *Basic model validated by CRCA experiments*

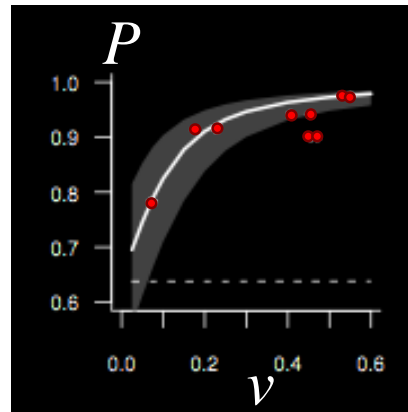
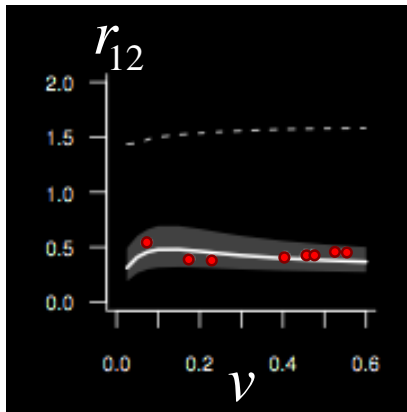
## ➤ **Experiments** vs **model simulations**

**Swarming to schooling transition** as the velocity  
(and hence, **alignment**) is increased



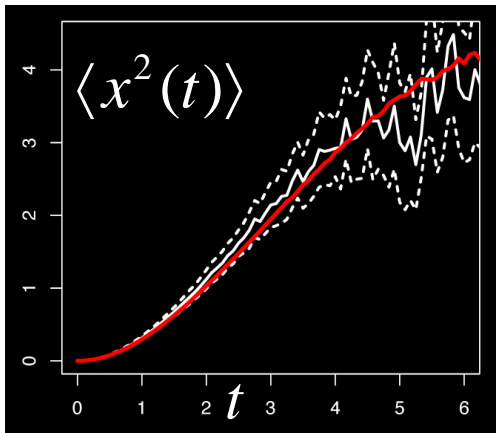
# Basic model validated by CRCA experiments

- Mean fish distance  $r_{12}$  and magnetization  $P$  vs velocity  $v$



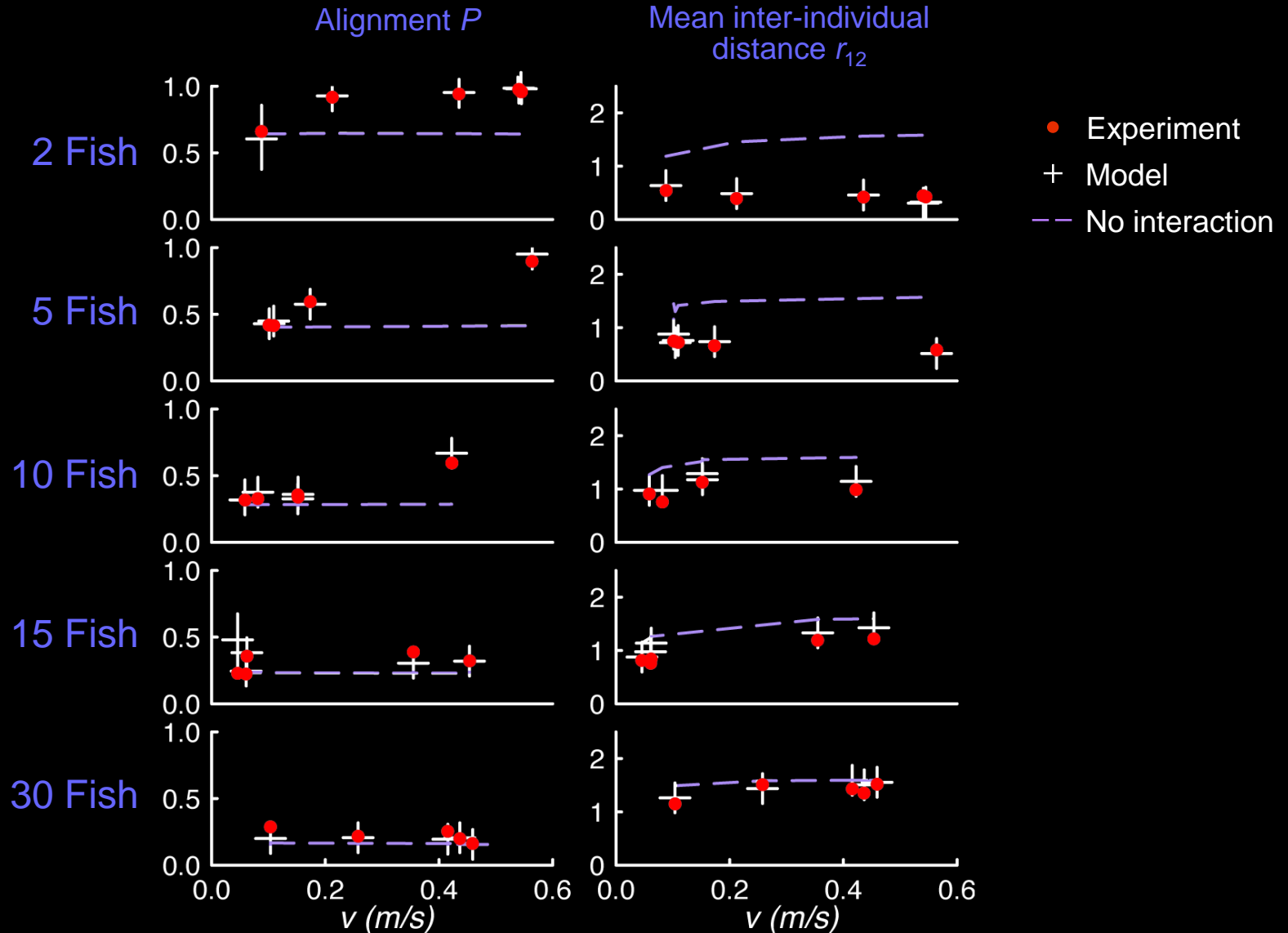
**Order parameter**  $P = \frac{1}{N} \left| \sum_{i=1}^N \mathbf{e}_{\phi_i} \right|$   
(Polarization)

- Mean square displacement in a tank



# Empirical investigation of fish schooling

Comparison between model predictions and experimental data



# Dimensionless equations of motion

$$\triangleright \alpha \frac{d^2 \phi_i}{dt^2} + \frac{d\phi_i}{dt} + \sqrt{2}\eta_i = \frac{1}{N_i} \sum_{\langle i,j \rangle} \omega_{j \rightarrow i}^*, \quad \frac{d\mathbf{r}_i}{dt} = \mathbf{e}_{\phi_i} = (\cos \phi_i, \sin \phi_i)$$

$$\omega_{j \rightarrow i}^* = \left[ \beta \sin(\phi_j - \phi_i) + \gamma r_{ij} \sin(\theta_{ij}) \right] \times \left[ 1 + \varepsilon \cos(\theta_{ij}) \right]$$

$\mathbf{r}_i$  = position of fish  $i$ ;  $\phi_i$  = angle of fish  $i$  velocity with respect to the horizontal

$\theta_{ij}$  = angle view of fish  $i$  looking at fish  $j$ ;  $r_{ij}$  = distance between fish  $i$  and  $j$

For  $v = 0.24$  m/s,  $\tau = \xi / v = 0.1$  s,  $2 / \tau_0 = (\xi \hat{\sigma})^2 \approx 0.48$  s<sup>-1</sup>

$$\alpha = \frac{\tau}{\tau_0} \approx 0.024, \quad \beta = \frac{k_{\parallel} \xi}{\alpha} \approx 2.7, \quad \gamma = \frac{k_P \xi \tau}{\alpha^2} \approx 1.7$$

$$\triangleright \text{Alignment } \omega_{j \rightarrow i}^* = -\frac{\partial V}{\partial \phi_i} (\phi_i - \phi_j), \quad \text{with } V(\phi) = -\beta \cos \phi$$

(XY model, **in-between**  $d = 2$  and **mean-field**)

**Inertial effects** on the angle dynamics are negligible

$\varepsilon = 1$  in numerical simulations (**no milling phase** for  $\varepsilon = 0$ )

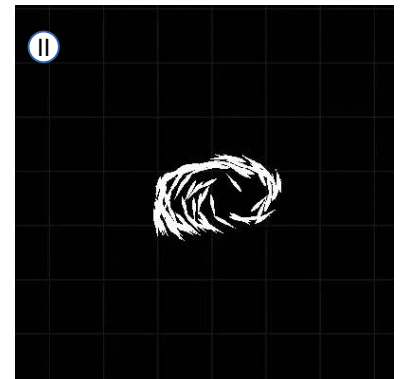
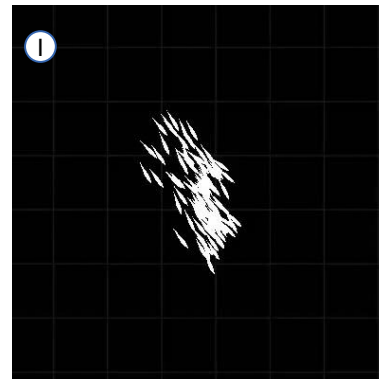
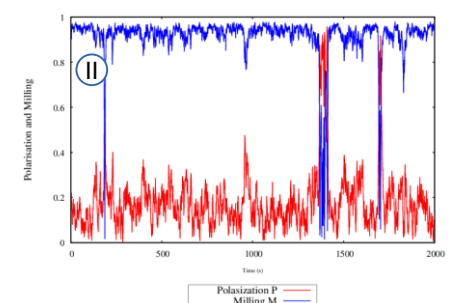
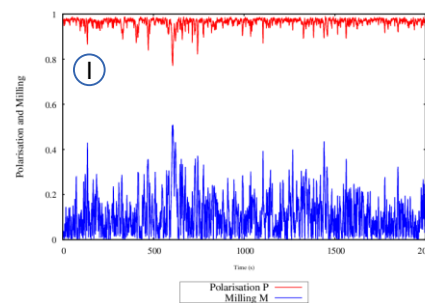
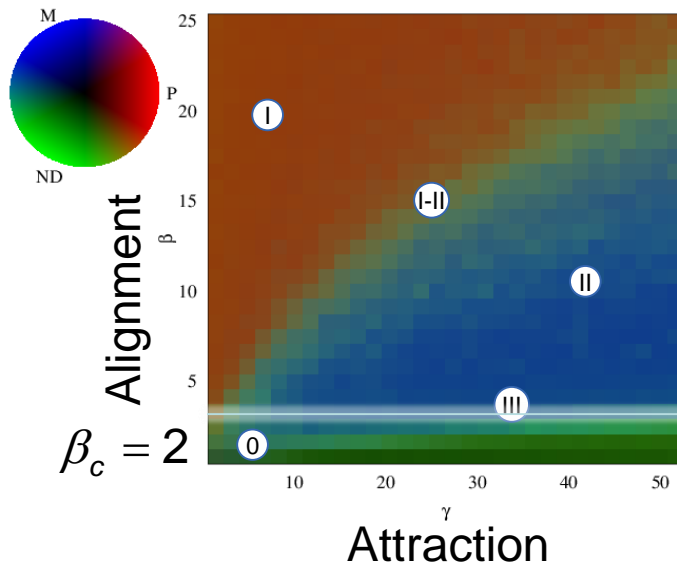
# Phase diagram without a tank

( $\alpha = 0.024$ ;  $\varepsilon = 1$ ;  $\beta - \gamma$  plane)

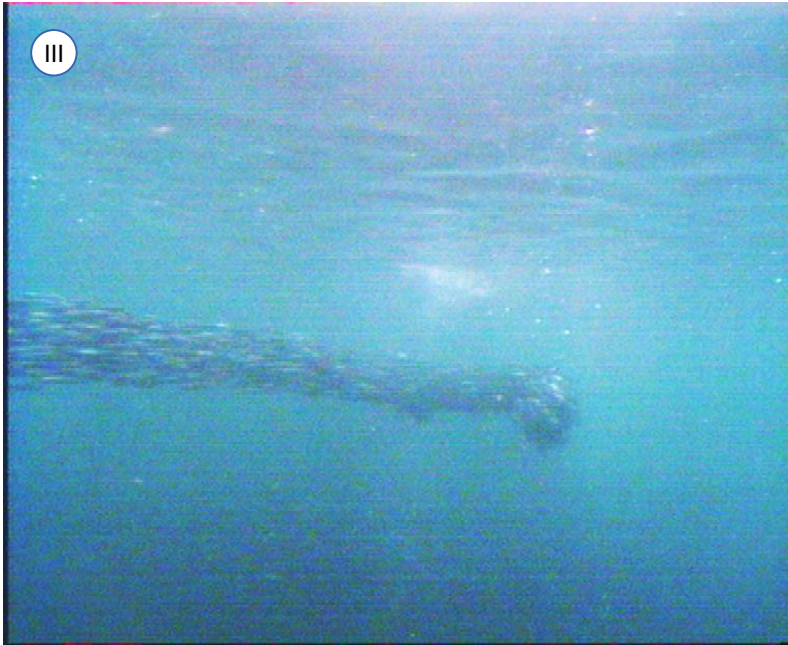
DC, UL, SN, CS, HC & GT, New J. Phys. (2014)

➤ Order parameters: **Polarization**  $P = \frac{1}{N} \left| \sum_{i=1}^N \mathbf{e}_{\phi_i} \right|$

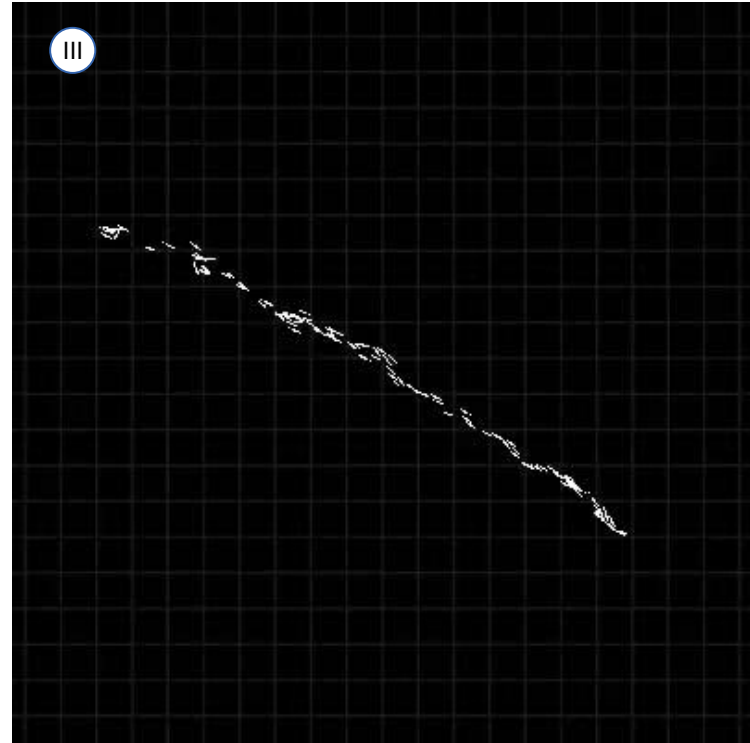
**Milling**  $M = \frac{1}{N} \left| \sum_{i=1}^N \mathbf{e}_{\phi_i} \times \mathbf{e}_{\mathbf{r}_i} \right|$



# ***Existence of a third narrow elongated phase for $\gamma \gg \beta$ ; observed in some fish schools***



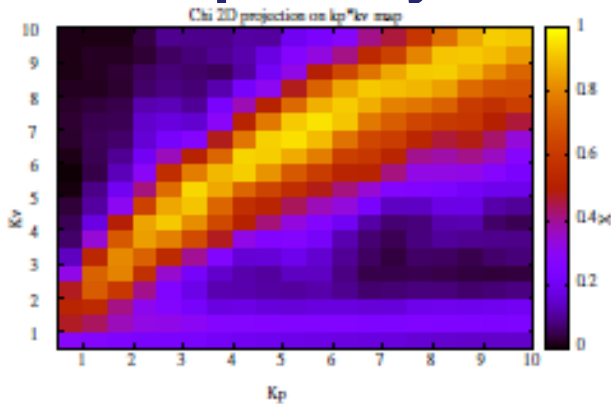
School of Atlantic herring (*Clupea harengus*)  
Photo courtesy of P. Brehmer - IRD



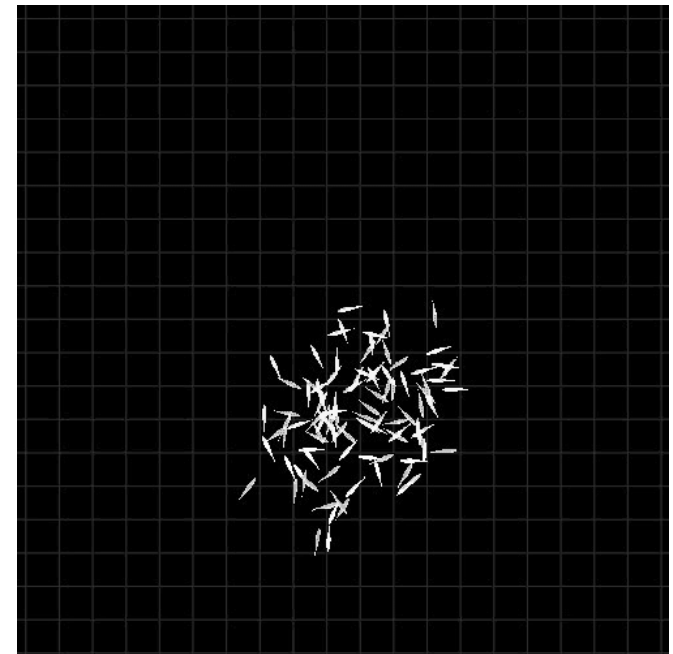
# Phase diagram without a tank

( $\alpha = 0.024$ ;  $\varepsilon = 1$ ;  $\beta - \gamma$  plane)

- Experimental parameters  $\beta \approx 2.5$ ,  $\gamma \approx 1.7$  lie not far from the **transition line**: real fishes can slightly modify their velocity to go **from swarming to schooling** (notably in the presence of a **predator**)
- Divergence of the polarization **susceptibility** near the transition line



With P. Schumacher (CRCA)



- Swarming transition near the **mean-field transition line** (see hereafter)  $\beta_c = 2$  ( $\varepsilon = 0$ )



# Mean-field theory

## ➤ Variables:

Coordinates  $\mathbf{r} = (r, \theta)$  vs the center of mass of the school

Velocity angle  $\phi$

Continuous density distribution of fish  $\rho(r, \theta, \phi)$

## ➤ Local order parameter

$$\mathbf{M}(r, \theta) = (M_x(r, \theta), M_y(r, \theta)) = M_0(\cos \phi_0, \sin \phi_0)$$

$$M_x(r, \theta) = \langle \cos \phi \rangle, M_y(r, \theta) = \langle \sin \phi \rangle \quad (\text{averages at fixed } r \text{ and } \theta)$$

$$\text{Uniform schooling phase } (\phi_0 = 0): \quad \mathbf{M}(r, \theta) = (M_0, 0)$$

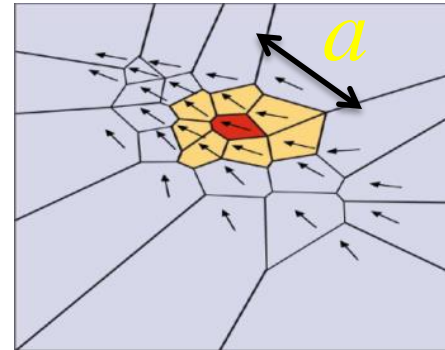
$$\text{Isotropic milling phase } (\phi_0 = \theta + \pi / 2): \quad \mathbf{M}(r, \theta) = M_0(-\sin \theta, \cos \theta)$$

# Mean-field theory (attraction force)

- If the density is smooth enough, the attractive force between fishes acts as an effective attraction force toward the center of mass ( $\varepsilon = 0$ )

$$\omega_A^*(\mathbf{r}) = \gamma \frac{\int_{r' < a} r \sin(\theta' - \phi + \theta) \rho(\mathbf{r} + \mathbf{r}') r' dr' d\theta'}{\int_{r' < a} \rho(\mathbf{r} + \mathbf{r}') r' dr' d\theta'}$$

such that  $\langle N_i \rangle = \int_{r' < a} \rho(\mathbf{r} + \mathbf{r}') r' dr' d\theta' \approx \pi \rho_0 a^2 = 6$



Expanding the top integral and assuming  $|\nabla \rho| / \rho \sim \frac{r}{r_0^2}$ ,

$$\omega_A^*(\mathbf{r}) = \frac{3}{2\pi\rho_0 r_0^2} \gamma r \sin(\phi - \theta)$$

which tends to **align the velocity to the direction  $\theta + \pi$**

# Mean-field theory equations of motion ( $\varepsilon=0$ )

$$\alpha \frac{d^2 \phi}{dt^2} + \frac{d\phi}{dt} + \sqrt{2}\eta = \omega^* = \beta M_0 \sin(\phi_0 - \phi) + \gamma(r) \sin(\phi - \theta)$$

$$\frac{d\mathbf{r}}{dt} = \mathbf{e}_\phi - M_0 \mathbf{e}_{\phi_0}, \text{ with } M_0 \mathbf{e}_{\phi_0} = \langle \mathbf{e}_\phi \rangle_{r,\theta}$$

$$\frac{dr}{dt} = \cos(\phi - \theta) - M_0 \cos(\phi_0 - \theta), \quad r \frac{d\theta}{dt} = \sin(\phi - \theta) - M_0 \sin(\phi_0 - \theta)$$

$$\alpha_{Exp.} \approx 0.024, \quad \beta_{Exp.} \approx 2.7, \quad \gamma(r)/r \sim \gamma_{Exp.} \approx 1.7 \quad (+\text{wall of the tank})$$

## Fokker - Planck equation ( $\alpha = 0$ )

$$\begin{aligned} \frac{\partial \rho}{\partial t} = & \frac{\partial^2 \rho}{\partial \phi^2} - \frac{\partial}{\partial \phi} \left[ \omega^* \rho \right] - \frac{1}{r} \frac{\partial}{\partial \theta} \left[ (\sin(\phi - \theta) - M_0 \sin(\phi_0 - \theta)) \rho \right] \\ & - \frac{\partial}{\partial r} \left[ (\cos(\phi - \theta) - M_0 \cos(\phi_0 - \theta)) \rho \right] \end{aligned}$$

# Diffusion coefficient of a single fish

$$\alpha \frac{d^2 \phi}{dt^2} + \frac{d\phi}{dt} + \sqrt{2}\eta = 0, \quad \frac{d\mathbf{r}}{dt} = \mathbf{e}_\phi$$

$$C(t) = \frac{1}{2} \langle [\phi(t) - \phi(0)]^2 \rangle = t - \alpha [1 - \exp(-t / \alpha)]$$

$$D(\alpha) = \lim_{t \rightarrow \infty} \langle [\mathbf{r}(t) - \mathbf{r}(0)]^2 \rangle / t = 2 \int_0^\infty \exp[-C(t)] dt$$

$$\sim_{\alpha \rightarrow 0} 2$$

$$\sim_{\alpha \rightarrow \infty} \sqrt{2\pi\alpha}$$

Expressing length and time in the original units with  $\alpha = \frac{\tau}{\tau_0} = \frac{\tau(\xi \hat{\sigma})^2}{2}$

$$D_0 = v^2 \tau_0 D(\alpha) = v \xi \frac{D(\alpha)}{\alpha} \quad (\hat{\sigma} \sim \text{phase noise})$$

$$\sim_{\alpha \rightarrow 0} 2v\xi \times \alpha^{-1} \rightarrow_{\hat{\sigma} \rightarrow 0} +\infty$$

**Weak phase noise  $\Rightarrow$  large  $D_0$**

$$\sim_{\alpha \rightarrow \infty} \sqrt{2\pi} v \xi \times \alpha^{-1/2} \rightarrow_{\hat{\sigma} \rightarrow \infty} 0$$

**Strong phase noise  $\Rightarrow$  small  $D_0$**

# Mean-field theory

- **Exact solution for  $M_0 = 0$  (swarming)**

$$\rho(r, \theta, \phi) = \frac{1}{Z} r \exp \left[ -\int_0^r \gamma(r') dr' \right]$$

- **Exact solution for  $\gamma(r) = 0$   
(space irrelevant; schooling / swarming)**

$$\rho(\phi) = \frac{1}{Z} \exp[\beta M_0 \cos \phi], \quad M_0 = \langle \cos \phi \rangle$$

Complete analogy with the **HMF model** (Antoni & Ruffo 1995)  
*i.e.* the XY model with all spins interacting with each other

$$M_0 \sim \sqrt{(\beta - \beta_c)}, \quad \text{with } \beta_c = 2$$

# Conclusion

- Realistic model for fish schools **validated by experiments**
- The general issue of **topologic/metric** force: relevance of **long-range interactions?** (~self-gravitating Brownian particles → school cohesion at low noise; Chavanis & CS)
- The **milling phase** is present when **vision effects** are taken into account, along with a narrow **elongated phase**
- **Biologically relevant** parameters are close to the swarming/schooling transition line, where fish can quickly adjust to their environment
- Introduction of a **mean-field theory**
  - Including the effect of vision (non conservative attractive force) to reproduce the milling phase
  - Allowing for non uniform/non isotropic order parameter
  - Time evolution (instability modes, dynamical transitions...)



