Analytical and numerical study of a realistic model for fish schools

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Collective motion in fish schools

Swarming, schooling, milling
Several models reproduce qualitatively the collective behaviors in fish schools, wild insect swarms, flocks of birds...

The **Vicsek Model** (1995)

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

\[
r_i(t+1) = r_i(t+1) + \nu_0 e^{\phi_i(t+1)}
\]

\(\eta, R_0, \nu_0\) are the noise intensity, interaction radius, and velocity. Fixing \(R_0\) and \(\nu_0\), the control parameters are \(\eta\) or the density \(\rho\).

**Order parameter** \(\phi = \frac{1}{N} \left| \sum_{i=1}^N e^{\phi_i} \right| \)
Vicsek Model

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)

\[ \phi(\eta) \sim |\eta - \eta_c|^\beta \quad \text{(Baglietto et al. 2012)} \]
\[ \beta \approx 0.45(3), \quad \nu \approx 1.6(3), \quad \gamma \approx 2.3(4) \]

\[ \phi^* = \phi(L)L^{\beta/\nu}, \quad \eta^* = \frac{|\eta - \eta_c|}{\sqrt{\rho}} \]
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 (Voronoï 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** $v \sim 0.1 - 0.6 \text{ m/s}$
- Individual (2D) angular velocity evolving according to an *Ornstein-Uhlenbeck* process

$$\frac{d^2 \phi_i}{dt^2} = \frac{d\omega_i}{dt} = -\frac{1}{\tau} (\omega_i - \omega_i^*) + \sigma \eta(t), \quad \frac{dr_i}{dt} = ve_{\phi_i}$$

($\tau \sim \zeta / v; \sigma \sim \delta v$)

- The target angular velocity includes the effect of **alignment** and **attraction** (metric/topological) forces
Basic model validated by CRCA experiments

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

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

- + 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 $v$
- Mean square displacement in a tank

Order parameter $P = \frac{1}{N} \left| \sum_{i=1}^{N} e^{\phi_i} \right|$ (Polarization)
Empirical investigation of fish schooling

Comparison between model predictions and experimental data

Alignment $P$

Mean inter-individual distance $r_{12}$

- Experiment
- Model
- No interaction

$v (m/s)$
Dimensionless equations of motion

\[ \alpha \frac{d^2 \phi_i}{dt^2} + \frac{d\phi_i}{dt} + \sqrt{2} \eta_i = \frac{1}{N_i} \sum_{j \in \{i,j\}} \omega_{j \rightarrow i}^* , \quad \frac{dr_i}{dt} = e_{\phi_i} = (\cos \phi_i, \sin \phi_i) \]

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

\( \mathbf{r}_i = \) 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 \( v = 0.24 \text{ m/s}, \tau = \xi / v = 0.1 \text{ s}, 2 / \tau_0 = (\xi \hat{\sigma})^2 \approx 0.48 \text{ s}^{-1} \)

\[ \alpha = \frac{\tau}{\tau_0} \approx 0.024, \quad \beta = \frac{k_p \xi}{\alpha} \approx 2.7, \quad \gamma = \frac{k_p \xi \tau}{\alpha^2} \approx 1.7 \]

Alignment \( \omega_{j \rightarrow i}^* = -\frac{\partial V}{\partial \phi_i} (\phi_i - \phi_j) \), 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**

*(α = 0.024; ε = 1; β – γ plane)*


- **Order parameters**: Polarization
  \[ P = \frac{1}{N} \left| \sum_{i=1}^{N} e_{\phi_i} \right| \]

- **Milling**
  \[ M = \frac{1}{N} \left| \sum_{i=1}^{N} e_{\phi_i} \times e_{r_i} \right| \]

- **Alignment**
  \[ \beta_c = 2 \]

- **Attraction**

![Graphical representation of phase diagram and order parameters](image-url)
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

\[ \beta \varepsilon = 2 (\varepsilon = 0) \]

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**
  
  \[
  \mathbf{M}(r, \theta) = (M_x(r, \theta), M_y(r, \theta)) = M_0 (\cos \phi_0, \sin \phi_0)
  \]
  
  \[
  M_x(r, \theta) = \langle \cos \phi \rangle, \quad M_y(r, \theta) = \langle \sin \phi \rangle \quad \text{(averages at fixed } r \text{ and } \theta)\]

  - **Uniform schooling phase** \( (\phi_0 = 0) \): \( \mathbf{M}(r, \theta) = (M_0, 0) \)
  - **Isotropic milling phase** \( (\phi_0 = \theta + \pi / 2) \): \( \mathbf{M}(r, \theta) = M_0 (-\sin \theta, \cos \theta) \)
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 ($\varepsilon=0$)

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

$$\frac{dr}{dt} = e_\phi - M_0 e_{\phi_0}, \text{ with } M_0 e_{\phi_0} = \langle e_\phi \rangle_{r,\theta}$$

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

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

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

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

$$- \frac{\partial}{\partial r} \left[ \left( \cos(\phi - \theta) - M_0 \cos(\phi_0 - \theta) \right) \rho \right]$$
**Diffusion coefficient of a single fish**

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

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

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

\[ \sim \alpha \to 0 \ 2 \]

\[ \sim \alpha \to \infty \sqrt{2\pi\alpha} \]

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

\[ D_0 = \nu^2 \tau_0 D(\alpha) = \nu \xi \frac{D(\alpha)}{\alpha} \]

(\( \hat{\sigma} \sim \) phase noise)

\[ \sim \alpha \to 0 \ 2\nu \xi \times \alpha^{-1} \to \hat{\sigma} \to 0 + \infty \quad \text{Weak phase noise} \Rightarrow \text{large} \ D_0 \]

\[ \sim \alpha \to \infty \sqrt{2\pi \nu \xi \times \alpha^{-1/2}} \to \hat{\sigma} \to \infty 0 \quad \text{Strong phase noise} \Rightarrow \text{small} \ D_0 \]
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

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