From individual to collective information processing in fish schools

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Mathematical Modeling and Applications
Meiji University, Tokyo, January 11, 2015

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From individual to collective information processing in fish schools

Scomber scombrus

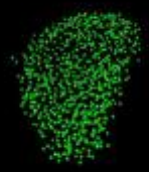
- To coordinate their actions fish have to exchange some information and perform some specific actions (controlling linear and turning velocities) in response to this information

© Christopher Swann

Collective motion in biological systems

Collective motion in bird flocks

Sturnus vulgaris (© *C. Carrere*)



Ballerini, M. *et al.*, *PNAS* (2008); Cavagna, A. *et al.*, *PNAS* (2010); Bialek, W. *et al.*, *PNAS* (2012)

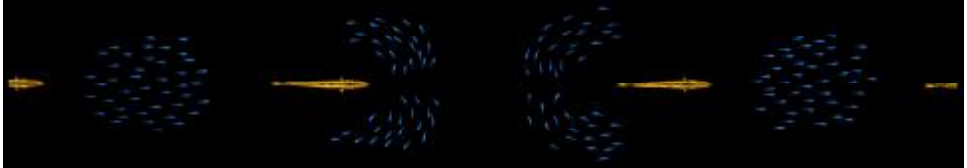
Collective motion in fish schools

Océans, (2010)
Directed by
Jacques Perrin,
Pathé Distribution

Sphyraena barracuda

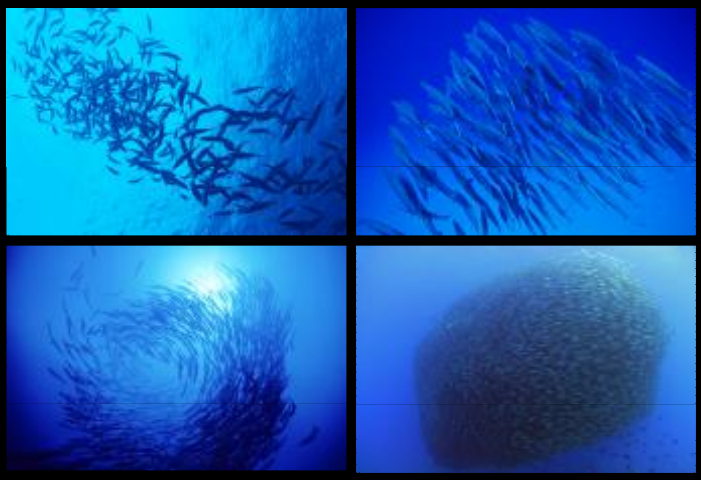
Collective motion in fish schools

Schooling manoeuvres in response to predator attacks



Collective motion in fish schools

Collective patterns arising from interactions between fish



What are the interactions rules and behavioral mechanisms involved in the coordination of collective motion?

Determining interactions rules

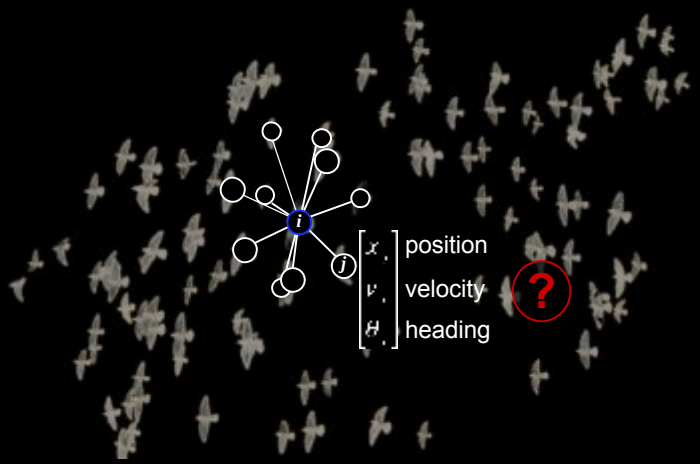
What kind of information is collected?

Determining interactions rules

What kind of information is collected?

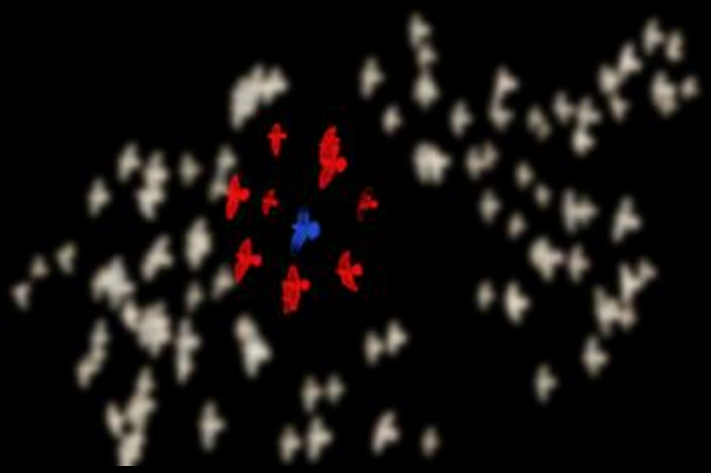
Determining interactions rules

What kind of information is collected?



Determining interactions rules

What are the neighboring partners involved in the interaction?



Determining interactions rules

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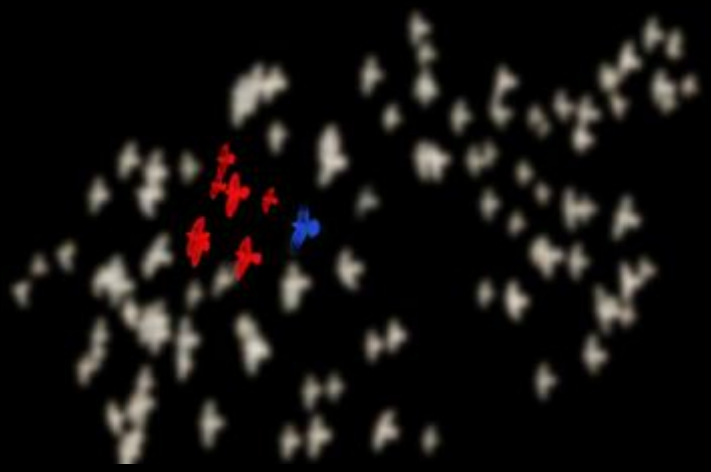
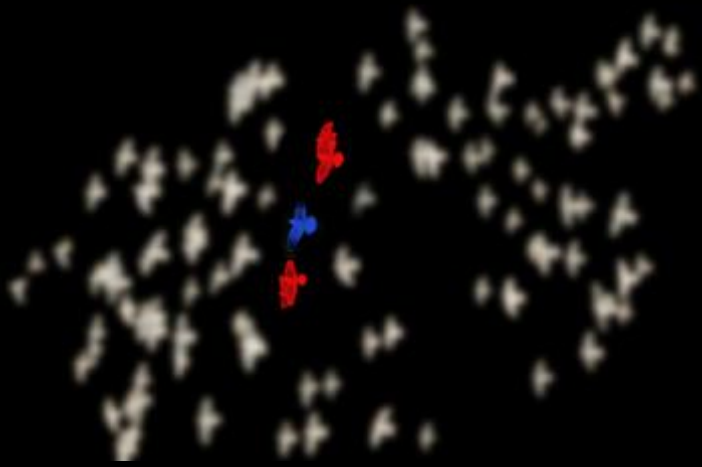


Determining interactions rules

What are the neighboring partners involved in the interaction?

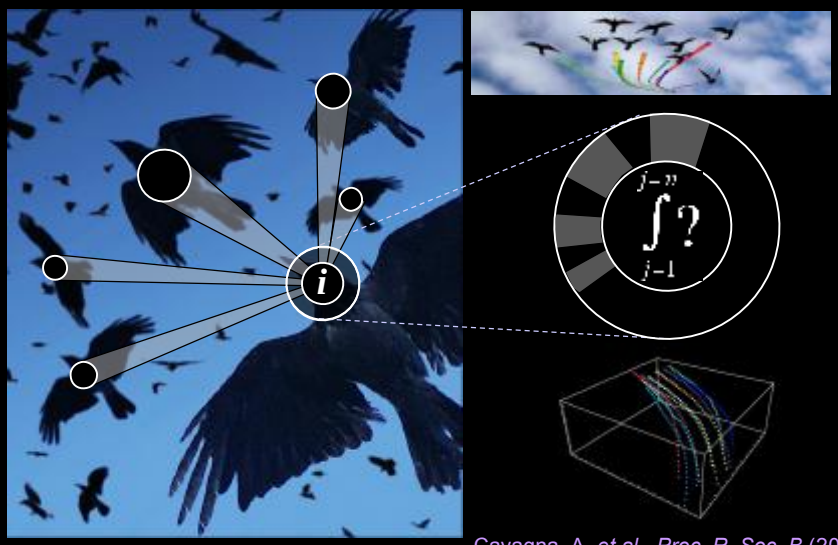


Determining interactions rules

What are the neighboring partners involved in the interaction?

Determining interactions rules

How is the information combined?



Cavagna, A. *et al.*, *Proc. R. Soc. B* (2013)

A methodology to build reliable models

Individual level

- Quantification of behaviours at different scales and in groups of different sizes
- Connecting micro-level to macro-level: how do complex patterns emerge out of local interactions among individuals?
- Trajectory analysis is used to build a model of spontaneous movement

Trajectory analysis

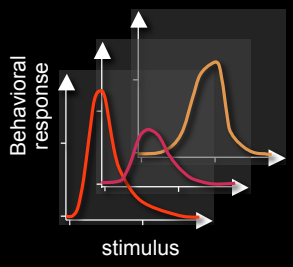
Weitz, S. *et al.*, *Plos One* (2012)
Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

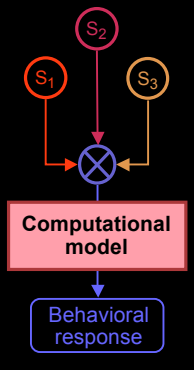
A methodology to build reliable models

Pair interactions

- Interactions between pairs of individuals are characterized
- Computational models are developed to test assumptions about the combination of information sources at the individual level and the resulting behavioural decision
- The already-determined parameters are kept unchanged and the stimulus-response function and the corresponding parameters are determined from data

Weitz, S. *et al., Plos One* (2012)
Gautrais, J. *et al., Plos Computational Biology* (2012)



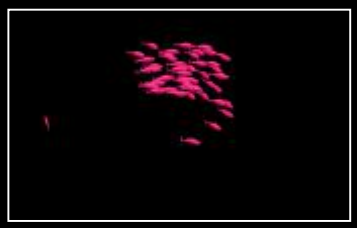


A methodology to build reliable models

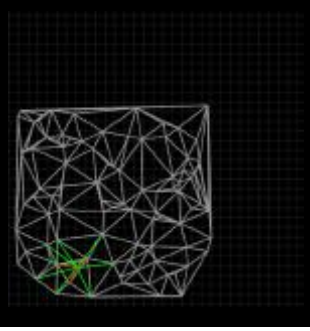
Collective level: combining many interactions

- To how many neighbors do individuals respond, and what is the relative weight given to each?
- Quantitative predictions: is the model able to accurately predict the collective dynamics and the outcome of novel situations?
- The incremental analysis allows a better understanding of the role played by each behavioral component in the observed collective pattern

Weitz, S. *et al., Plos One* (2012)
Gautrais, J. *et al., Plos Computational Biology* (2012)



Dynamics of interaction network



Empirical investigation of fish schooling

Study site

Empirical investigation of fish schooling

Study species: the barred flagtail

Khulia mugil

Empirical investigation of fish schooling

Experimental setup and video tracking

5 Fish

4 m

30 Fish

- Single fish and groups of increasing size (N = 2, 5, 10, 15, 30) have been recorded in a 4-m wide and 1-m depth tank
- Two minutes were extracted from digital video recordings and the position of the individual's head was tracked every 1/12 s (1440 data-points per trajectory)

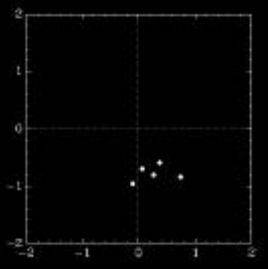
Empirical investigation of fish schooling

Experimental setup and video tracking

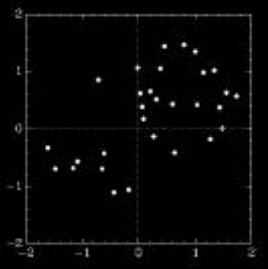
Group polarization

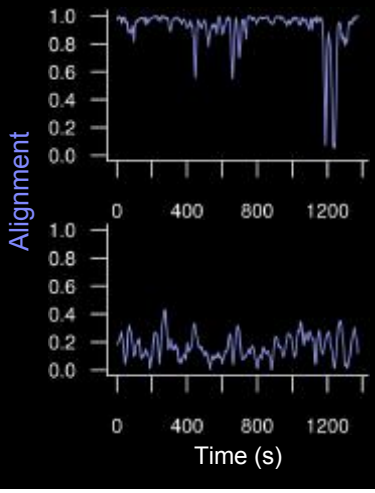
$$O_G(t) = \frac{1}{N}\left|\sum_i^N V_i(t)\right|$$

5 Fish



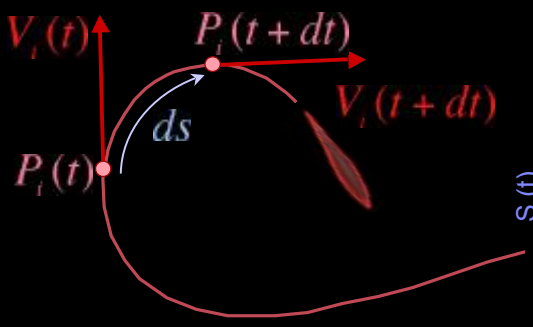
30 Fish





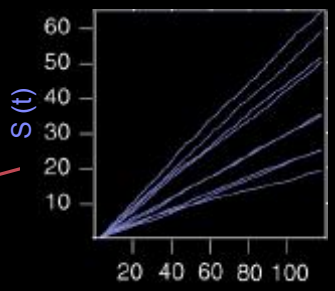
Modeling single fish behavior and wall avoidance

Spontaneous fish movement



- The swimming speed of each fish is constant

Curvilinear distance



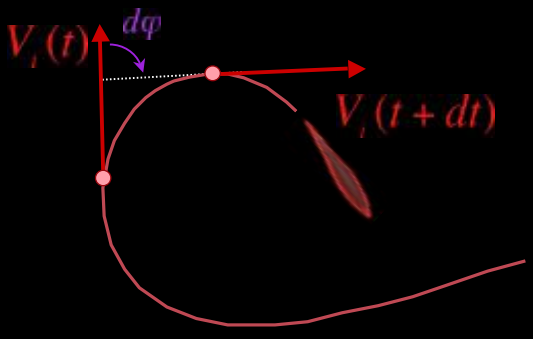
Swimming speed (m/s)

$$\frac{ds}{dt} = V(t) = c > 0$$

Gautrais, J. *et al.*, *J. Math. Biol.*, (2009)

Modeling single fish behavior and wall avoidance

Spontaneous fish movement



- The swimming speed of each fish is constant
- The observed motion results from a control of the turning speed
- There is a significant autocorrelation of the turning speed
- There is a spontaneous tendency of the fish to randomly change the turning speed

Swimming speed (m/s)

$$\frac{ds}{dt} = V(t) = c > 0$$

Turning speed (rad/s)

$$\frac{d\varphi}{dt} = \omega(t)$$

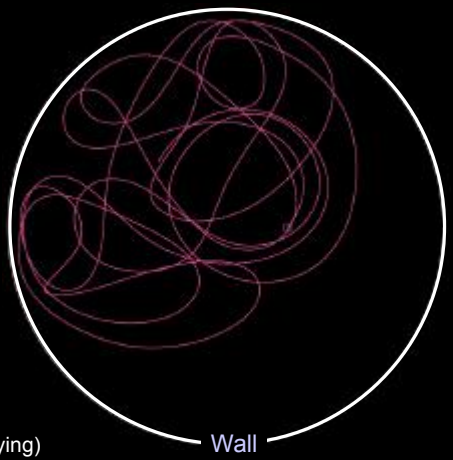
Gautrais, J. *et al.*, *J. Math. Biol.*, (2009)

Modeling single fish behavior and wall avoidance

A persistent turning walker model of fish movement

Spontaneous swimming

$$d\omega(t) = -\frac{dt}{\tau}\omega(t) + \sigma\, dW$$



τ : characteristic time of the (exponentially decaying) autocorrelation function of $\omega(t)$

Gautrais, J. *et al.*, *J. Math. Biol.*, (2009)

Modeling single fish behavior and wall avoidance

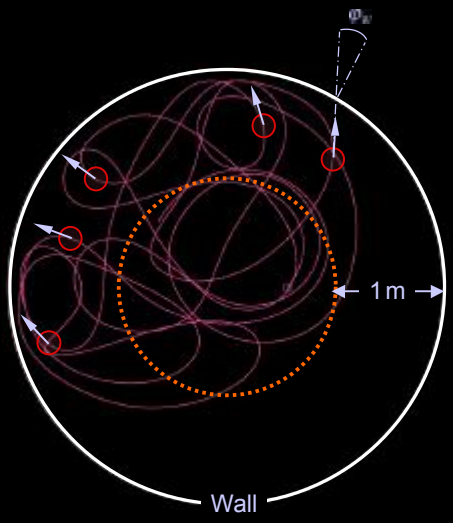
A persistent turning walker model of fish movement

Spontaneous swimming

$$d\omega(t) = -\left(\frac{dt}{\tau}\omega(t) + \sigma\, dW\right) + \sigma\, dW$$

$$\omega^*(t) = k_w \,\mathrm{sgn}(\varphi_w)/d_w$$

Wall avoidance



d_w : distance before collision

Gautrais, J. *et al.*, *J. Math. Biol.*, (2009)

Modeling single fish behavior and wall avoidance

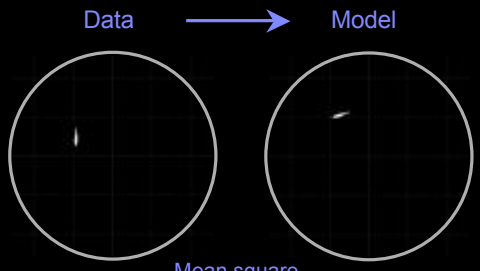
A persistent turning walker model of fish movement

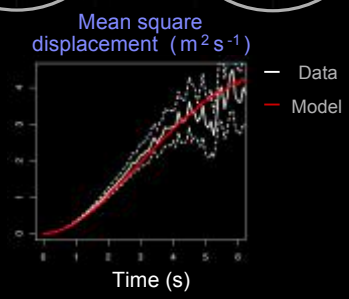
$$d\omega(t) = -\frac{dt}{\tau}\left(\omega(t) + \omega^{*}(t)\right) + \sigma\, dW$$

$$\omega^{*}(t) = k_{w}\, \mathrm{sgn}(\varphi_{w})/d_{w}$$

Wall avoidance

$$\mathrm{MSD} = \left\langle \left(x(t) - x_{0}\right)^{2} \right\rangle$$

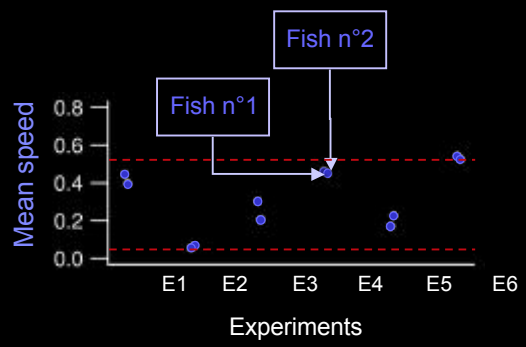




Gautrais, J. *et al.*, *J. Math. Biol.*, (2009)

Empirical investigation of fish schooling

Deciphering interactions between pairs of fish

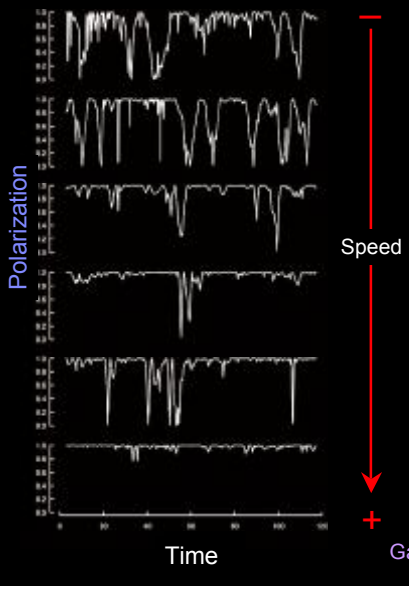


Tracking the movement patterns in groups of 2 fish

Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

Empirical investigation of fish schooling

Influence of swimming speed on coordination and alignment

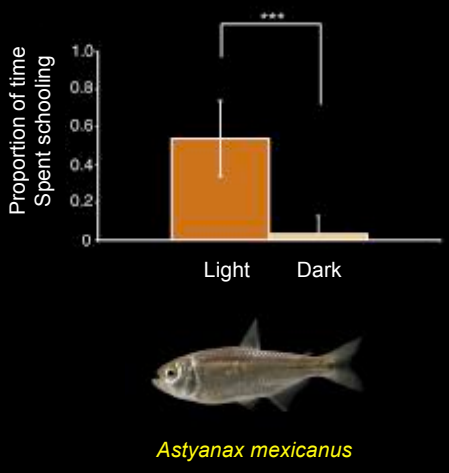


- Synchronization increases with swimming speed
- Directional information is a required component to achieve synchronization
- Positional information is likely to play a key role in the cohesion of the school

Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

Empirical investigation of fish schooling

Influence of swimming speed on coordination and alignment



Astyanax mexicanus

- The degree of synchronization increases as a result of an increase of swimming speed
- Directional information is a required component to achieve synchronization
- Positional information is likely to play a key role in the cohesion of the school

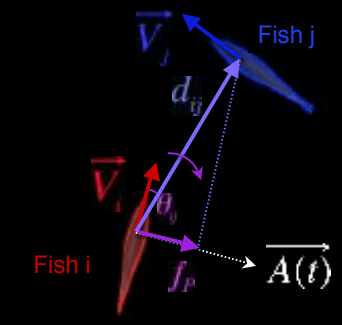
Kowalko, J.E. *et al.*, *Current Biology* (2013)

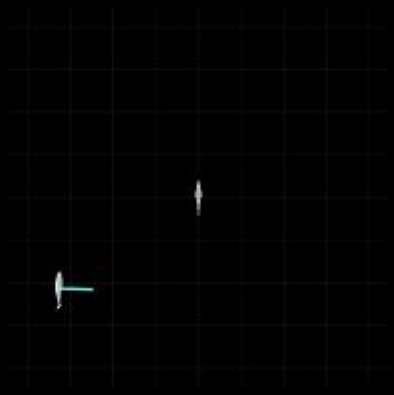
Modeling pair interactions

Characterizing interactions between pairs of fish in the model

- Positional effect (attraction): turn towards the neighbor

Short inter-distance





$$f_P\left(d_{ij},\theta_{ij}\right)=k_P\, d_{ij}\sin\theta_{ij}$$

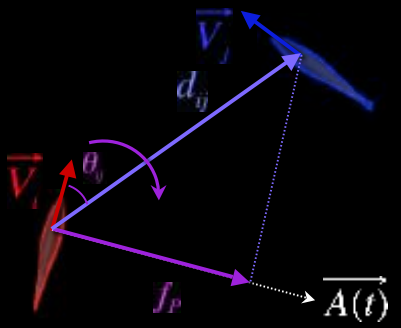
Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

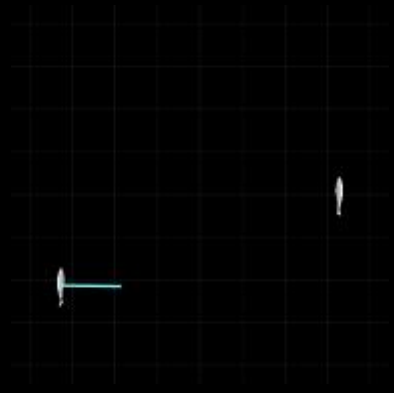
Modeling pair interactions

Characterizing interactions between pairs of fish in the model

- Positional effect (attraction): turn towards the neighbor

Large inter-distance





$$f_P\left(d_{ij},\theta_{ij}\right)=k_P\, d_{ij}\sin\theta_{ij}$$

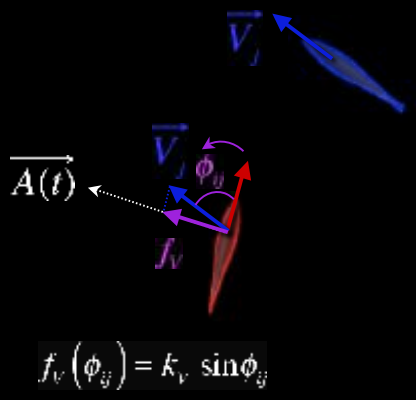
Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

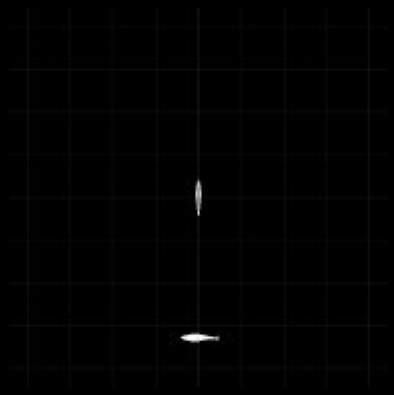
Modeling pair interactions

Characterizing interactions between pairs of fish in the model

- Directional information (alignment): turn to align with the neighbor

Low swimming speed





Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

Modeling pair interactions

Characterizing interactions between pairs of fish in the model

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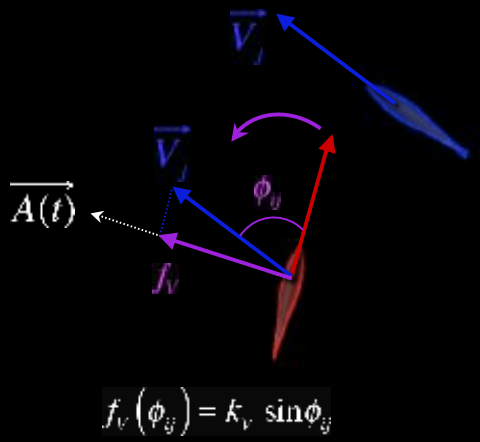
High swimming speed



Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

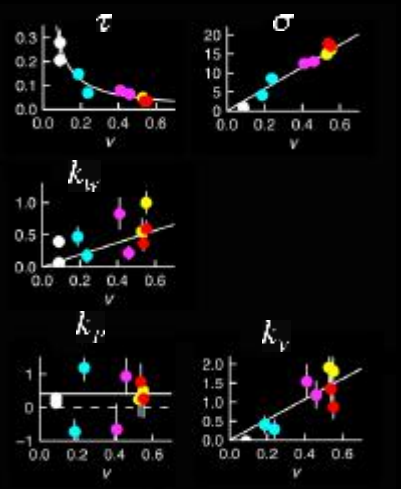
Data-driven fish school model

Modeling pair interactions

$$d\omega(t) = -\frac{dt}{\tau}\left(\omega(t) + \omega^*(t)\right) + \sigma\, dW$$

$$\omega^*(t) = \begin{cases} +k_w \,\mathrm{sgn}(\phi_{iw})/\tau_{iw} & \text{Wall effect} \\ +k_p\, d_{ij} \sin\theta_{ij} & \text{Positional effect} \\ +k_v \sin\phi_{ij} & \text{Directional effect} \end{cases}$$

Parameter estimation



Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

Data-driven fish school model

Modeling pair interactions

$$\tau = \frac{\xi}{v}$$

$$d\omega_i(t) = -v\left[\frac{dt}{\xi}\left(\omega_i(t) + \omega_i^*(t)\right) + \hat{\sigma}\, dW\right]$$

$$\omega^*(t) = \begin{cases} +\hat{k}_w \,\mathrm{sgn}(\phi_{iw})/\tau_{iw} & \text{Wall effect} \\ +\hat{k}_p\, d_{ij} \sin\theta_{ij} & \text{Positional effect} \\ +\hat{k}_v \sin\phi_{ij} & \text{Directional effect} \end{cases}$$

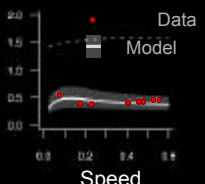
$\xi =$ 0.024 m $\hat{\sigma} =$ 28.9 $m^{-1} s^{-1/2}$

$\hat{k}_w =$ 0.94 $k_v =$ 0.41 $m^{-1} s^{-1}$ $\hat{k}_v =$ 2.7 m^{-1}

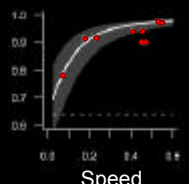
Data → Model

2 Fish

Mean inter-individual distance



Polarization

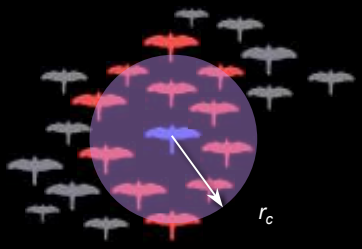


Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

Data-driven fish school model

Determining the number and position of influential neighbors

Metric interactions



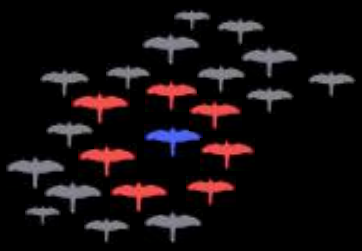
- To how many neighbors do individuals respond, and what is the relative weight given to each?
- In starling flocks each bird interacts with a fixed number of neighbors (6-7) irrespective of their distance

Ballerini, M. *et al., PNAS* (2008)
Raynaud, F. *3D Collective Behavior Models*. Ph.D. thesis, Université Paris 7 (2009)

Data-driven fish school model

Determining the number and position of influential neighbors

Topological interactions



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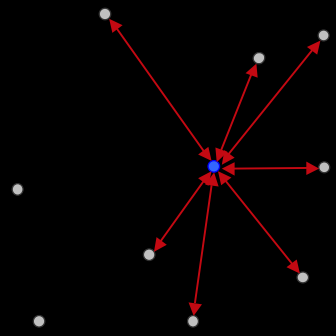
Raynaud, F. *3D Collective Behavior Models*. Ph.D. thesis, Université Paris 7 (2009)

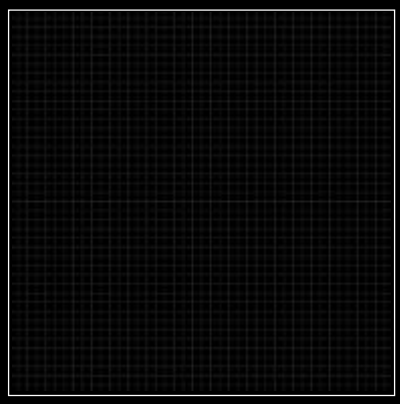
Data-driven fish school model

Determining the number and position of influential neighbors

- K Nearest Neighbors?

KNN = 7

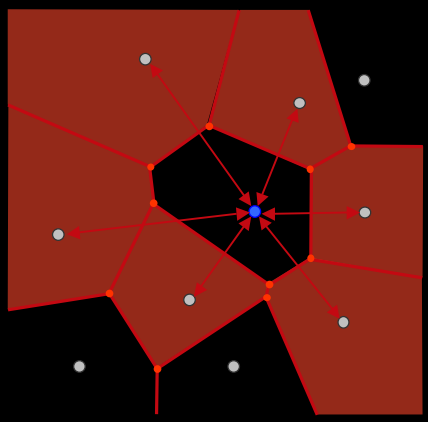


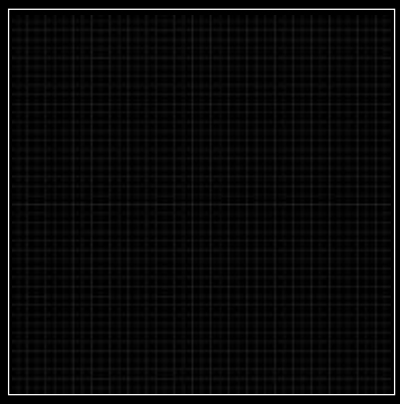


Data-driven fish school model

Determining the number and position of influential neighbors

- Approximating "visible" neighbors with a greedy triangulation





Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

Data-driven fish school model

Weighting all influential neighbors

- Simplest assumption: averaging the influence of all "visible" neighbors

$$d\omega_i(t) = -\nu\left[\frac{dt}{\xi}\left(\omega_i(t) + \omega_i^*(t)\right) + \hat{\sigma}\, dW\right]$$

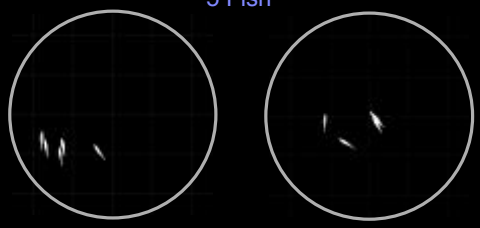
$$\omega_i^* = \hat{k}_w \frac{\mathrm{sgn}(\omega_{iz})}{\tau_{iw}} - \frac{1}{N_i}\sum_{j=1}^{N_i}\left(\hat{k}_r d_{ij} \sin\theta_{ij} + \hat{k}_v v \sin\psi_{ij}\right)$$

$\xi =$ 0.024 m $\hat{\sigma} =$ 28.9 $m^{-1} s^{-1/2}$

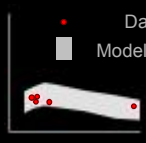
$\hat{k}_w =$ 0.94 $\hat{k}_r =$ 0.41 $m^{-1} s^{-1}$ $\hat{k}_v =$ 2.7 m^{-1}

Data → Model

5 Fish

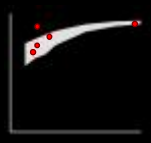


Mean inter-individual distance



Speed

Polarization

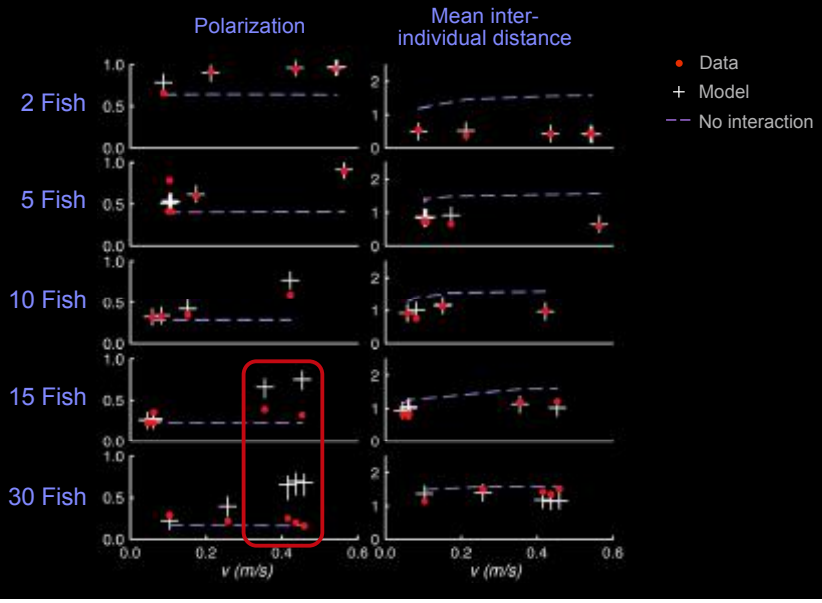


Speed

Gautrais, J. *et al.*, *Plos Computational Biology* (2012)

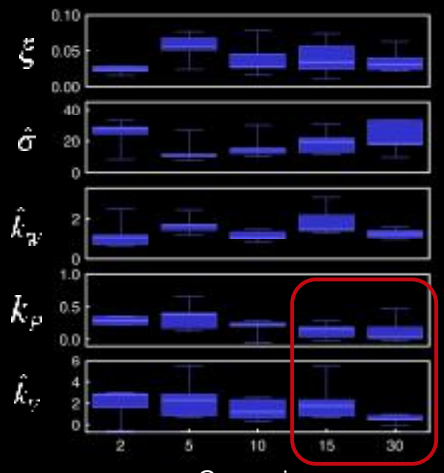
Data-driven fish school model

Comparison between model predictions and experimental data

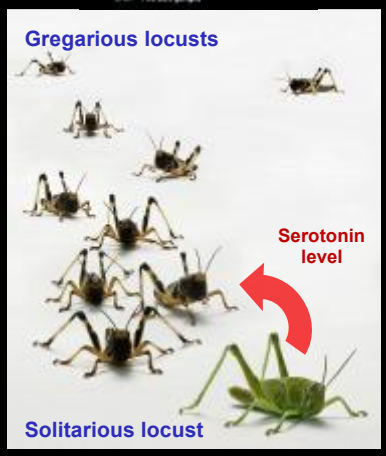


Data-driven fish school model

Quantification of group-size effect



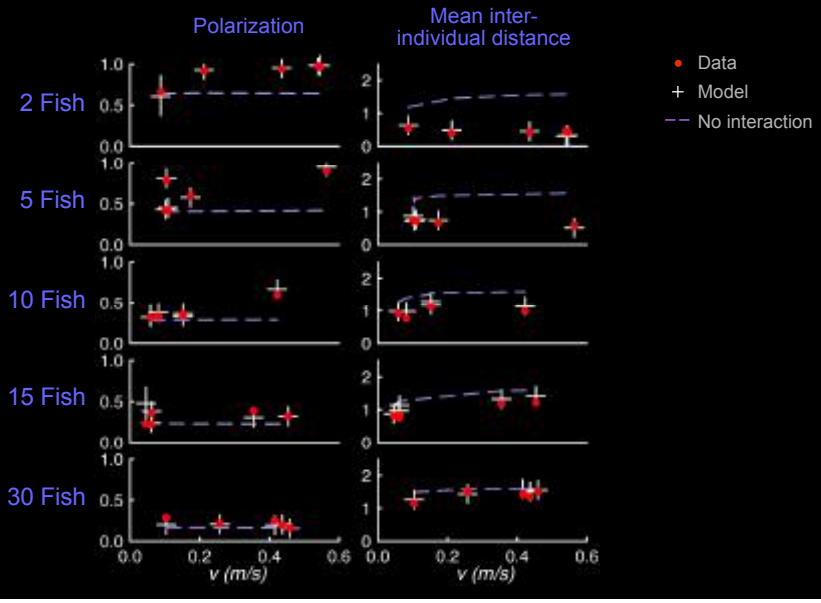
Group size



Anstey *et coll.*, *Science* (2009)

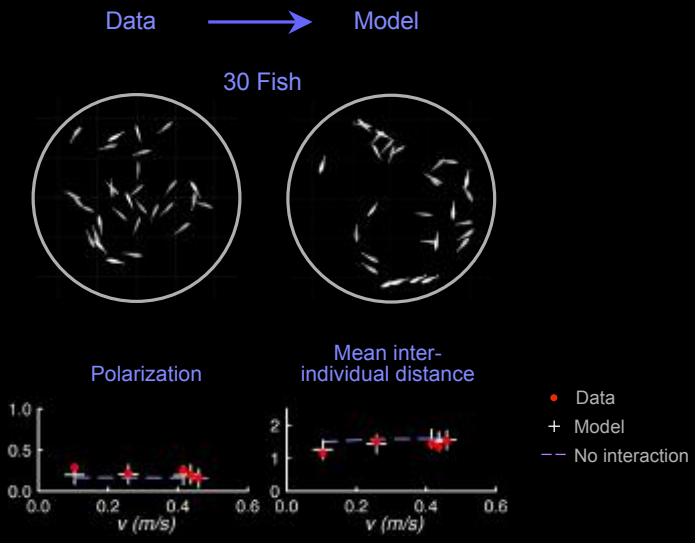
Data-driven fish school model

Comparison between model predictions and experimental data



Data-driven fish school model

Comparison between model predictions and experimental data

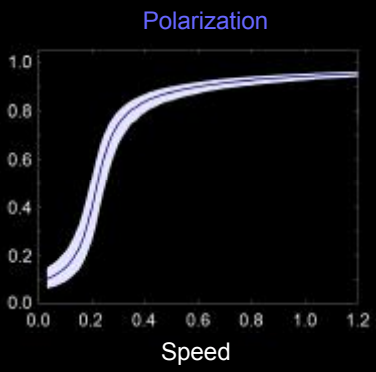


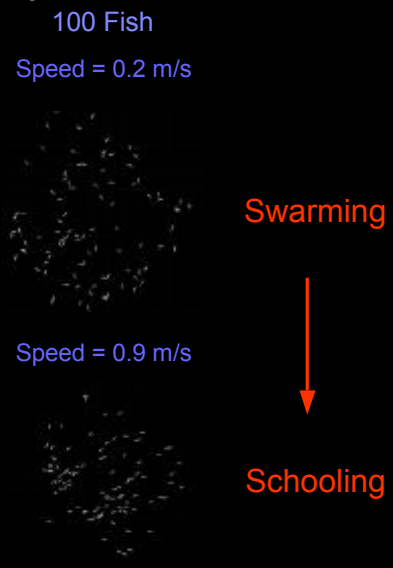
Gautrais, J. *et al., PLoS Computational Biology* (2012)

Model properties

Speed-induced transition to schooling

- What are the the model predictions for larger groups in unbounded space?





Calovi, D. *et al., New Journal of Physics* (2014)

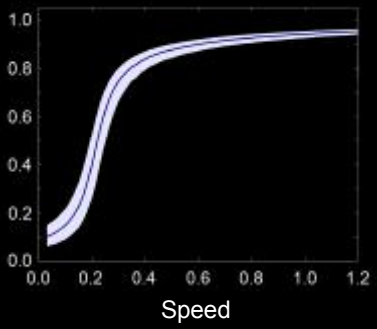
Model properties

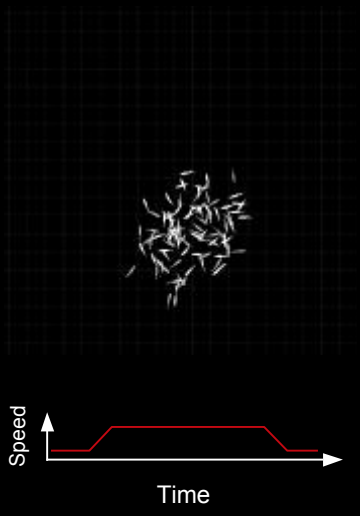
Speed-induced transition to schooling

Group polarization increases with velocity

- What are the the model predictions for large groups in unbounded space?

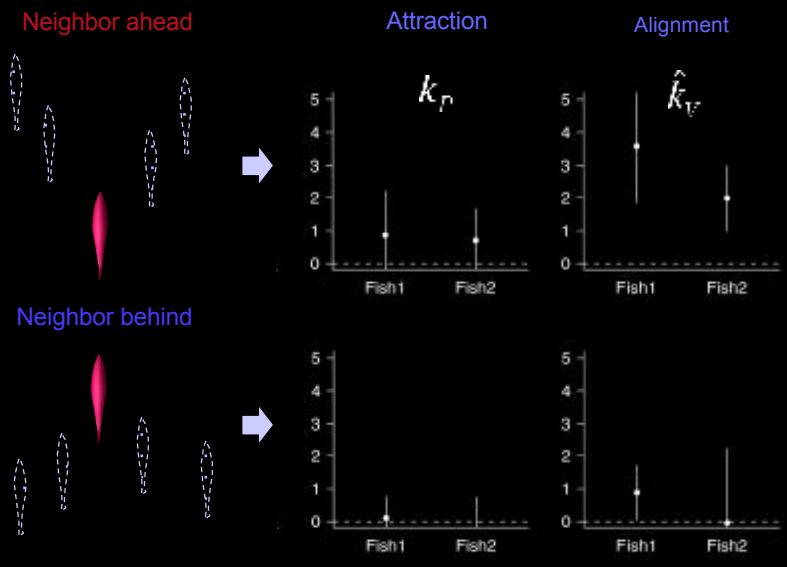
Polarization





Empirical investigation of fish schooling

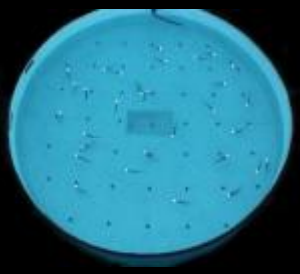
Neighbors' influence depends on their position

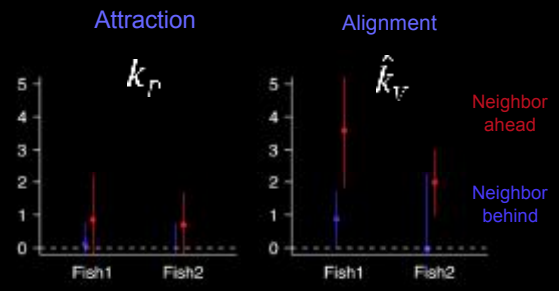


Empirical investigation of fish schooling

Neighbors' influence depends on their position

- In a confined environment the influence of the spatial modulation of interactions on collective motion patterns cannot be detected (reaction to the wall and to the density of fish)

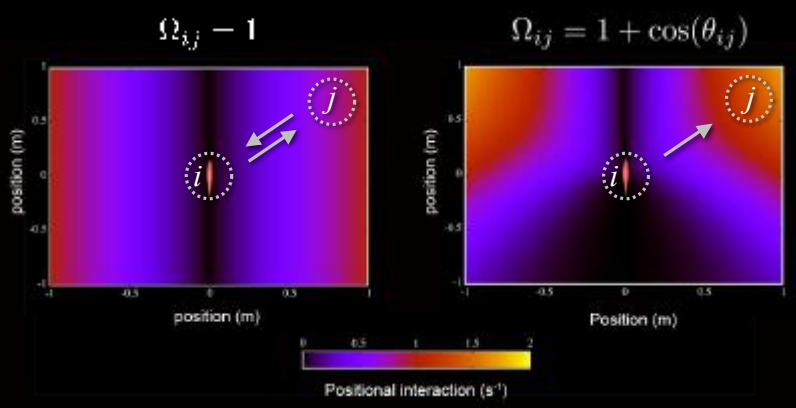




Model properties

Angular weighting of fish interactions

$$d\omega(t) = -v\left[\frac{dt}{\xi}\left(\omega(t) - \Omega_{ij}\omega^*(t)\right) + \sigma\, dW\right]$$



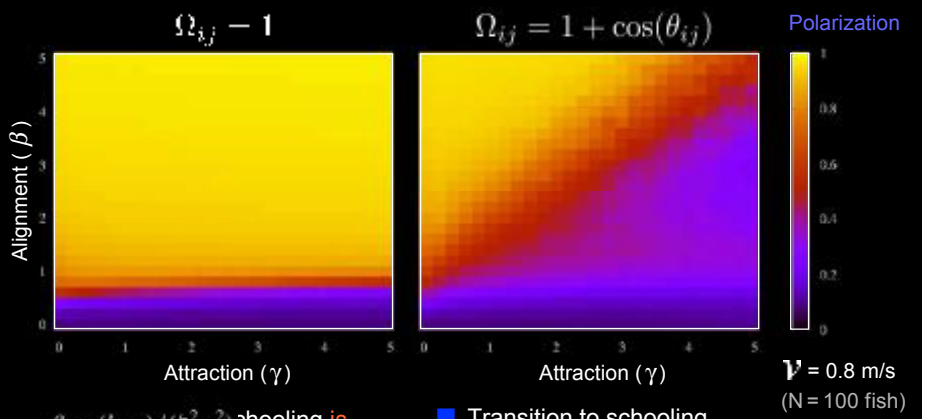
Calovi, D. *et al.*, *New Journal of Physics* (2014)

Exploring the parameter space

Parameter space effect on polarization (schooling)

- Polarisation (Schooling) : Order parameter that tends to unity as fish are aligned, and zero when swarming

$$P = \frac{1}{N}\left|\sum_{i=1}^{N}\frac{\vec{v}_i}{v}\right|$$



$\beta = (k_V v)/(\xi^2\sigma^2)$ chooling is
$\gamma = (k_P v)/(\xi^4\sigma^4)$ f the attraction

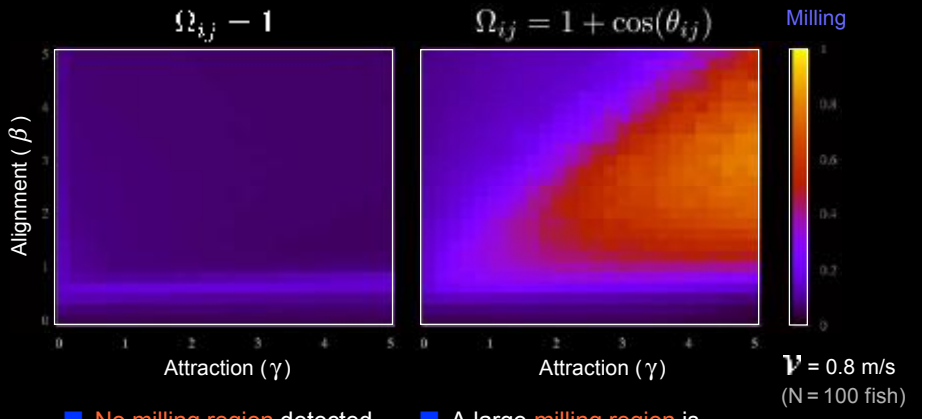
- Transition to schooling depends on the attraction

Exploring the parameter space

Parameter space effect on angular momentum (Milling)

- Angular momentum (Milling) : Order parameter that tends to unity as fish are swimming in a perfect circle

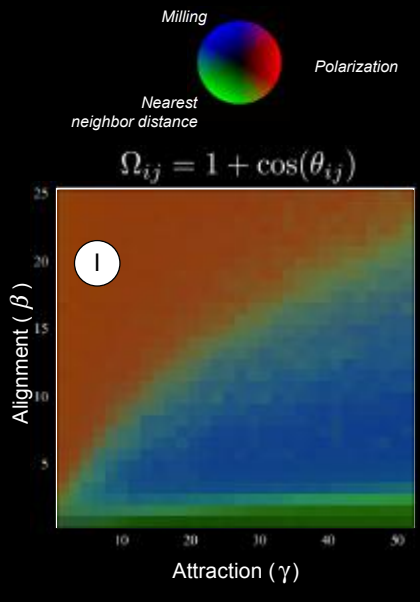
$$M = \frac{1}{N}\left|\sum_{i=1}^{N}\frac{\vec{r}_i \times \vec{v}_i}{|\vec{r}_i| v}\right|$$

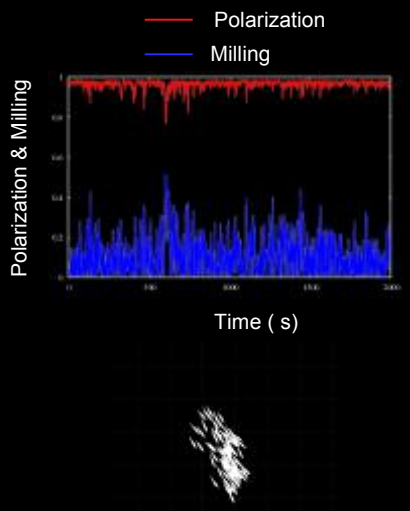


- No milling region detected
- A large milling region is observed

Exploring the parameter space

Region I: Schooling

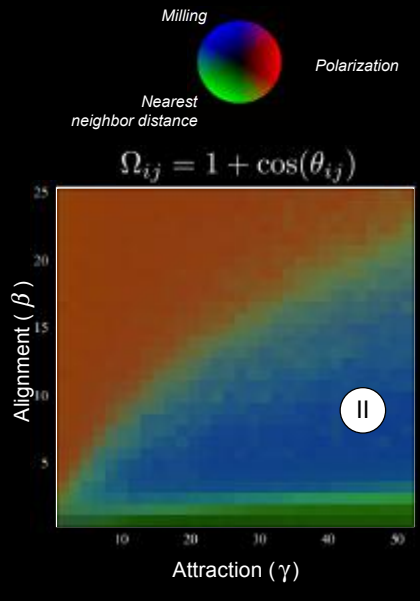


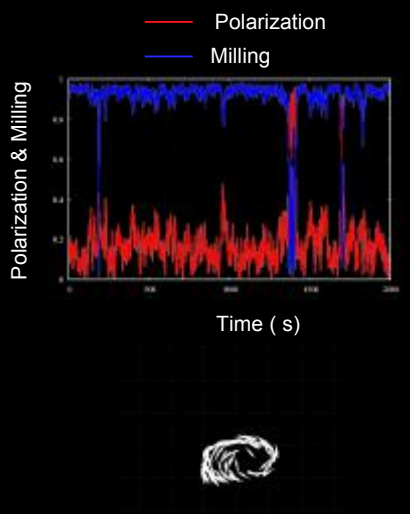


Calovi, D. *et al.*, *New Journal of Physics* (2014)

Exploring the parameter space

Region II: Milling

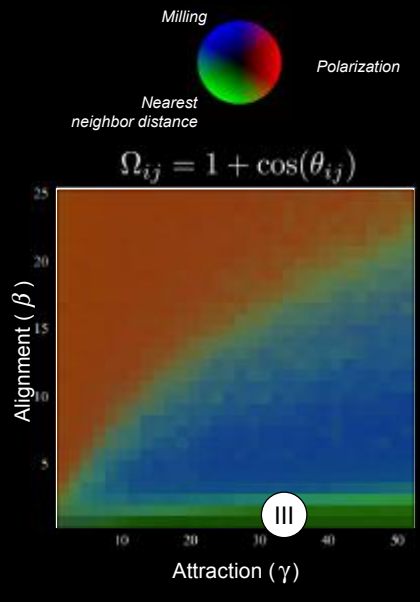


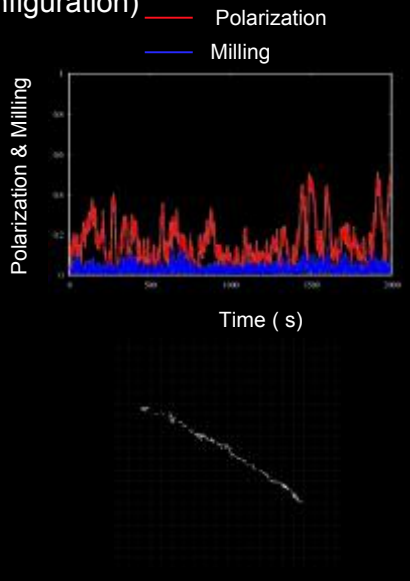


Calovi, D. *et al.*, *New Journal of Physics* (2014)

Exploring the parameter space

Region III: Winding zone (line configuration)





Calovi, D. *et al.*, *New Journal of Physics* (2014)

Exploring the parameter space

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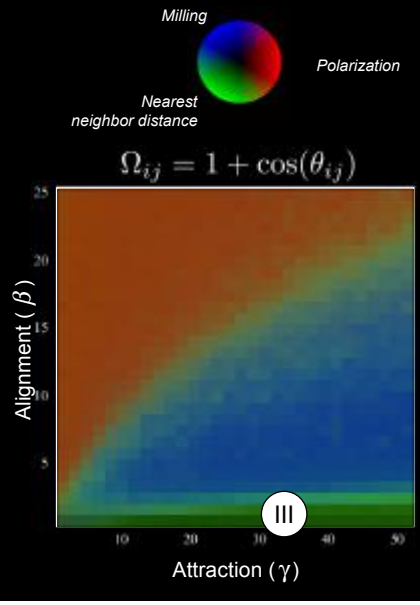
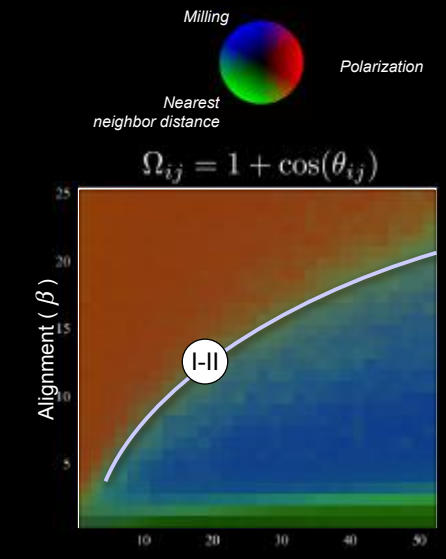


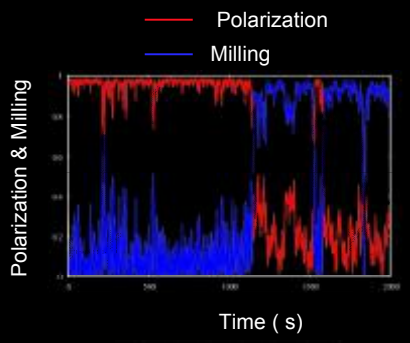
School of Atlantic herring
(*Clupea harengus*)
© P. Brehmer, IRD

Calovi, D. *et al.*, *New Journal of Physics* (2014)

Exploring the parameter space

Region I-II: Transition zone

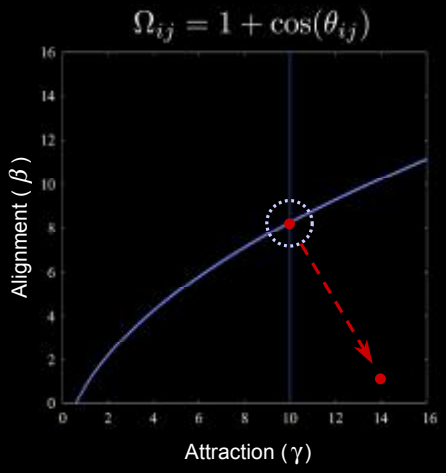


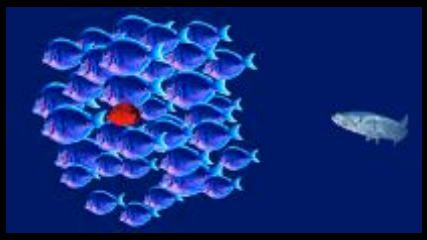


Tunstrøm, K. *et al., PLoS Computational Biology* (2013)

Model properties

Enhanced collective response to perturbations in the transition zone

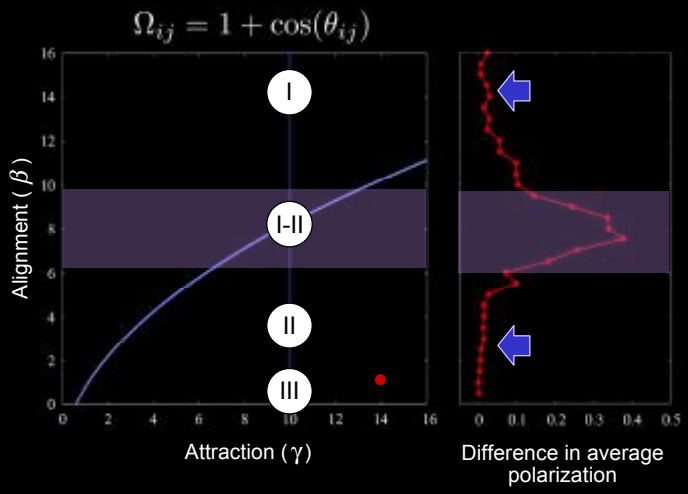




Calovi, D. *et al., Journal of the Royal Society Interface* (2015)

Model properties

Enhanced collective response to perturbations in the transition zone close to criticality



- The maximum response of the school to perturbations is reached In the transition zone between schooling and milling

Calovi, D. *et al.*, *Journal of the Royal Society Interface* (2015)

Emergent coordination in fish schools

Wrap-up: main findings

- An incremental methodology was used to build a fish behavior model completely based on interactions with the physical environment and neighboring fish
- There is a continuous balancing between attraction and alignment behavior as a function of the distance between fish

Khulia mugil

Emergent coordination in fish schools

Conclusions

- The modulation of strength of the alignment and attraction behaviors plays a key role in the kind of collective motion pattern that emerge at the school level
- By providing a high responsiveness to perturbations the transition region between milling and schooling is a highly desired state that optimizes the ability of the fish to react collectively (e.g. to a predator attack) thus increasing the survival of fish

Caranx sexfasciatum

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