

Key behavioural factors in a self-organised fish school model

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The dynamics of a self-organised model of shoaling fish are explored within a Lagrangian (or individual based) framework in order to identify the key behavioural factors that shape its dynamic landscape. By exploring systematically all possible initial states we identify the transitions to and between the different possible stationary states (schooling vs. swarming or milling). The route to these stationary states is explained from an individual perspective. On the behavioural level we discuss in particular the decisive impact of two traits, the perception angle and the manoeuvrability of the fish. A key result of this study is that the fish density in certain stationary states reaches values where each fish perceives each other; local interactions actually become global interactions. We further discuss the specific value of such Lagrangian studies in comparison to analytical approaches, in particular the freedom to include any important biological trait and the importance of an exhaustive numerical investigation.

Introduction

One of the most fascinating features of collective fish behaviour is their ability to move around in closed groups (Keenleyside 1955, Radakov 1973, Giske *et al.* 1998, Becco *et al.* 2006). About half the fish species are known to form such aggregation patterns at least at one stage of their life history. This collective behaviour can be found at the larval stage and can remain an obligate behavioural feature throughout their lifespan (Pitcher & Parrish 1993). Moreover, aggregation behavior provides protection against predators and in some cases increases foraging efficiency and reproduction rates (Pitcher & Parrish 1993, Hoare *et al.* 2004).

Fish can form loosely structured groups (called shoals) or highly organised structures (called schools) with synchronized movements and correlated headings (Pitcher 1983). Fish schools can be understood as self-organised systems since they do not need leaders or external stimuli to avoid splitting up, move cohesively and adopt a common direction (Hammer & Parrish 1997, Parrish & Edelman-Keshet 1999). School dynamics emerges from numerous mutual interactions between individuals that are within a limited perception range. The individual movement decision only depends on its neighbours' positions and headings.

Based on optomotor reaction schemes, fish can consistently maintain the parallel orienta-

tion with neighbours, whether they are at the head, the middle or the rear end of the school (Shaw & Tucker 1965). This visual detection is complemented by a specific sensory device, the lateral line, which is sensitive to variations of water pressure around the body of the fish, and can provide information about movement speed and orientation of close neighbours (Partridge & Pitcher 1980).

While only few studies have tried to disentangle the underlying behavioural mechanisms (Aoki 1980, Parrish & Turchin 1997, Rees 2001, Suzuki 2003, Grünbaum *et al.* 2004, Tien *et al.* 2004), many theoretical models have emerged to build a conceptual framework in order to identify the involved mechanisms at least qualitatively (Aoki 1982, Huth & Wissel 1993, for a good review *see* Parrish *et al.* 2002). Thanks to such theoretical studies one can then design experimental setups to test and to quantify the underlying hypothesis.

There are two classes of models at hand (Levin 1997, Topaz 2006). The first one adopts an Eulerian approach where the movement dynamics are described by differential equations that represent a mean field approximation of the individual behavioural decisions as a function of their available information, which is in particular the position and the heading of conspecifics in some zone of perception. While there are some analytical tools to study the dynamics of such models (Grünbaum 1994, 1998, Niwa 1996, 1998, Toner & Tu 1998, Tu 2000, Adiou *et al.* 2003), there exists usually no analytical solution; they have to be solved numerically (Mogilner & Edelstein-Keshet 1996, Levine & Rappel 2000, Mogilner *et al.* 2003). Furthermore, many biologically relevant features cannot be incorporated into such models, for example the presence of a blind perception zone behind each fish. This is where the second class of models comes in. They adopt a Lagrangian approach and model each individual as an independent unit with its own behaviour and interactions with other units or the environment (Vicsek *et al.* 1995, Grégoire *et al.* 2003). These individual based models (IBM) are analytically even less tractable and their analysis relies on fast and efficient numerical simulation, but they leave much more room to include biologically important features

(Aoki 1982, Romey 1996, Inada & Kawachi 2002, Viscido *et al.* 2005). Recent computer power has increased these models' popularity and efforts are underway to unify their usage and description (Grimm & Railsback 2005). The present study will rely on such an IBM in order to deepen our understanding of what particular behavioural traits drive the collective properties of a fish shoal.

Most modelling studies of fish schooling describe the collective state with some global measure, e.g. group polarization or angular momentum, density (characterized by the mean nearest neighbour distance) or fragmentation (Viscido *et al.* 2005). These measures are well defined at the stationary state, which is the state where the collective dynamics converge from a given initial condition. They characterise this stationary state for the particular model hypotheses (e.g. the size of the perception radius) and permit to test the model's sensitivity with respect to them. However, the computing power necessary to run these simulations often limits the extent of a sensitivity analysis. Furthermore, there is a multitude of different IBM's teeming in the literature (Parrish *et al.* 2002), it is therefore difficult to identify the crucial factors at the base of some particular collective phenomenon. We therefore use in this study the most widespread model where fish interactions are limited to a short-range repulsion, a middle-range alignment and a far-range attraction (Couzin *et al.* 2002), and the aim is to gain further insight into this model's dynamic behaviour by doing a combined sensitivity analysis on both model parameters and initial conditions.

The first behavioural priority in this model is the avoidance of collisions: when a neighbour comes within a zone of repulsion the individual turns away at maximal speed. For neighbours outside this zone individuals tend to align their speed vector if these neighbours are still within a zone of orientation, or to approach them if they are farther away but still within the perception radius (zone of attraction). This is probably a minimal model that ensures both staying together and moving ahead. This model (or close variants of it) was the subject of most theoretical studies within the last twenty years (Parrish *et al.* 2002). The principal stationary dynamics

(Fig. 1) are swarming (high density but uncorrelated speed vectors), milling (turning around in donut form) or schooling (moving collectively straight ahead at maximal speed). Couzin *et al.* (2005) showed that even this minimal model enables the group to make elaborated self-organised collective choices.

The sensitivity of the collective phenomena to the initial conditions is rarely addressed in the aforementioned studies. However, in order to discover all possible dynamics or dynamic changes one has to explore various initial states. Studying the system evolution from one fixed initial condition only gives a partial view of the model capabilities. For instance, Couzin *et al.* (2002) and Viscido *et al.* (2005) computed the collective behaviour landscape starting from an initial condition close to swarming (random orientation and position). Hence, they answered the question of which sizes of the zones of attraction and alignment let a schooling behaviour emerge from random alignment at a given density. This landscape may be very different with other initial conditions (e.g. with schooling individuals to explore which sizes let a swarming group emerge from a schooling one or whether schooling is a stationary state).

Varying initial conditions is particularly important when multiple stationary states exist for the same rules and parameter values. In such a case, the final stable pattern will strongly depend on the initial conditions (e.g. the density and polarization at some earlier time). Taking again the example of Couzin *et al.* (2002), they showed that two opposite collective patterns (swarming vs. schooling) can emerge with the same rules, depending on the collective state of the group about 200 seconds earlier. They also showed that hysteresis can arise when the zone of orientation is changed smoothly step by step every T seconds (with T of the same order as the relaxation time), which is a formal illustration that the final pattern depends on initial conditions.

In this paper we will explore the model's complete system dynamics, focusing on the two most relevant macroscopic characteristics: alignment (or polarization) and density. The only restriction on initial conditions will be to avoid that the group splits up (which systematically happens when the density is too low). We will test in par-



Fig. 1. The three types of collective behaviour observed in this study (simulation snapshots): swarming behaviour without any correlation between fish orientation, milling behaviour where fish tend to be inversely aligned with their farthest neighbour, and schooling behaviour where all fish are swimming in the same direction and the group is moving at maximal speed.

ticular the sensitivity of polarization with respect to several model parameters: the size of the zone of orientation, curvature and speed of individual trajectories, the size of a blind rear zone, weighting the influence of neighbours by their distance, and the level of noise in the system.

Methods

The model

We used in all simulations $N = 100$ individuals that move in a 3-dimensional continuous (off-lattice) unbounded space. Time was discretized in steps of length $\tau = 0.1$ s. Each individual i is characterized at time t by its 3-coordinates position vector $\mathbf{P}_i(t)$ and its 3-dimensional unit speed vector $\mathbf{V}_i(t)$ (see Fig. 2). The evolution of the group is given by

$$\mathbf{P}_i(t + \tau) = \mathbf{P}_i(t) + v\tau \mathbf{V}_i(t),$$

where v is the (constant) speed expressed in body lengths per second (BL s^{-1}). Individual behavioural decisions only affect the vector $\mathbf{V}_i(t)$ and define its value $\mathbf{V}_i(t + \tau)$.

We assume that the body of each individual is perfectly aligned with its speed vector, $\mathbf{V}_i(t)$ therefore defines a natural subjective coordinate system for individual i , defining in particular its front and rear directions. All the fish within a connected group (see precise definition below) are considered to be neighbours of each other. We further assume that an individual i can assess the position and speed heading of the neighbours

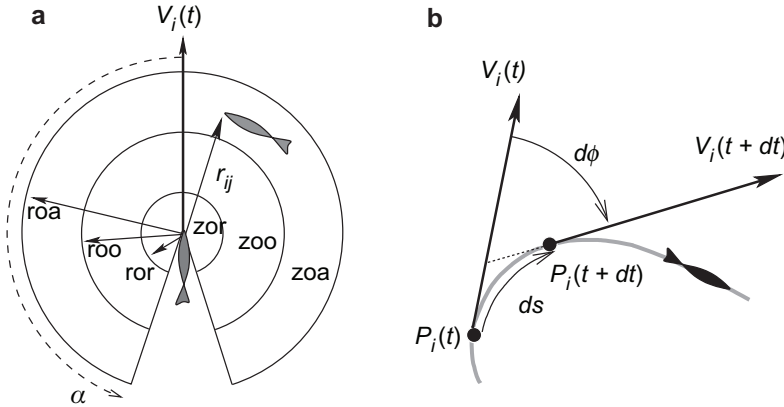


Fig. 2. — **a:** The behavioural model of the focal individual (centre) with respect to neighbours (characterized by their relative distance vector r): avoidance in the zone of repulsion zor, alignment in zone zoo and attraction in zone zoa. α denotes the perception angle. — **b:** Characterization of individual displacement by the position vector $P(t)$ and the orientation vector $V(t)$. ds and $d\phi$ represent curvilinear displacement and turning angle (respectively) during time dt .

that are within a perception sphere with the exception of a blind cone in its rear. The visual field is therefore characterised by an angle of $\pm\alpha$ degrees from the front direction to the rear.

We took as a reference model the behavioural rules defined by Couzin *et al.* (2002). Adopting the same model with a complementary approach allowed us to deepen our understanding of the internal logic of this collective behaviour. The core characteristic of this model is that the behavioural response of individual i to its neighbours is mediated through a desired direction $D_i(t)$ computed from the perceived neighbours. The perception sphere within the visual field (i.e. without the blind cone) is decomposed into three non-overlapping zones of increasing range: zone of repulsion, zone of orientation and zone of attraction (Fig. 2a) with outer radii of r_{or} , r_{oo} and r_{oa} respectively. The desired direction $D_i(t)$ is now computed from the number of neighbours (respectively n_r, n_o, n_a) in each zone as follows: If there is at least one neighbour in the repulsion zone ($n_r > 0$), repulsion prevails and

$$D_i(t) = - \sum_{j \neq i}^{n_r} \frac{r_{ij}(t)}{|r_{ij}(t)|}$$

where $r_{ij}(t)$ denotes the vector from the position of the focal individual i to the position of individual j (Fig. 2a). This repulsion mechanism at the body length scale ensures that two fish bodies do not merge. If there is no neighbour in the repulsion zone ($n_r = 0$) but some neighbours

are present in the perception volume ($n_o > 0$ or $n_a > 0$), then

$$D_i(t) = \sum_{j=1}^{n_o} V_j(t) + \eta \sum_{j=1}^{n_a} \frac{r_{ij}(t)}{|r_{ij}(t)|}$$

where the $V_j(t)$ denote the unit speed vectors of neighbours j in the orientation zone which add up into an orientation matching component, and the $r_{ij}(t)$ add up into an attraction component. We introduced a factor η in order to weight both components differentially (in the original model $\eta = 1$). In all other cases $D_i(t)$ is simply ignored and $V_i(t)$ remains unaffected.

In the original model (Couzin *et al.* 2002) this deterministic value of $D_i(t)$ was blurred by a Gaussian noise added to each of its components in order to mimic the lack of precision in the perception process. Noise can significantly alter the collective pattern (e.g. the onset of the schooling structure can depend on the level of individual fluctuations, Niwa 1996) and will therefore also be included in the present work. The specific implementation will be detailed below.

Once $D_i(t)$ has been computed for all individuals at time t , each individual i rotates its speed vector $V_i(t)$ towards $D_i(t)$ with a constant turning rate θ (rad s^{-1}). This limit prevents the instantaneous adjustment of $V_i(t)$ to $D_i(t)$ (Mogilner *et al.* 1996), except when $D_i(t)$ is already very close to $V_i(t)$. Note that this movement rule enforces a constant linear speed in contrast to mechanistic models based on forces (Viscido *et al.* 2005).

The actual turning rate θ can be further decomposed into linear and angular speed,

$$\theta = \frac{d\phi}{dt} = \frac{d\phi}{ds} \frac{ds}{dt} = \kappa v$$

where $d\phi$ and ds are respectively the turning angle of $\mathbf{V}_i(t)$ and the curvilinear displacement of $\mathbf{P}_i(t)$ during dt (Fig. 2b), κ is a curvature, and v is the linear speed. The curvature κ measures the angle turned per distance unit (rad BL^{-1}) and denotes the ability of the fish to make sharp turns (e.g. the number of body lengths it has to swim to make a full U-turn is given by $ds = \pi/\kappa$).

Ror and roa were set to 1 and to 20 BL (body lengths) respectively throughout this study. In order to assess the role of alignment we varied roo from ror (i.e. no alignment, only repulsion/attraction) to roa (only repulsion/alignment, no attraction), with a step size of 0.5 for roo $\in (1, 5)$ and a step size of 1 for roo > 5 (giving overall 24 values).

Noise

Stochastic effects are likely to weaken the accuracy of the perception of distances and headings of neighbours. However, if noise is only applied to $\mathbf{D}_i(t)$, a fish undergoing no influence from its neighbours (when it is either isolated or when all its neighbours are in its blind rear cone) would keep its speed vector constant, resulting in an unrealistically perfect straight path. Noise was therefore applied to $\mathbf{V}_i(t)$ after its correction with respect to $\mathbf{D}_i(t)$. In this way noise represents the overall effect of perception errors as well as motor decision errors. In the absence of any interactions with neighbours the group would simply undergo a spatial diffusion.

In order to keep the linear speed v constant, noise was only applied to the speed vector. It is therefore an angular noise, resulting in an angular diffusion (Perrin 1928, Brillinger 1997, Caillol 2004). In order to keep the implementation independent of the time step τ , angular noise was determined by a rotational diffusion coefficient D_r ($\text{rad}^2 \text{s}^{-1}$), as in spatial diffusion ($\text{m}^2 \text{s}^{-1}$, Lombardo *et al.* 2006). The angular stochastic deviation $d\gamma$ during the time step τ was drawn randomly from a normal distribution $N(0, \sigma)$

with a variance proportional to the time step τ , $\sigma_r^2 = 2D_r\tau$. $\mathbf{V}_i(t)$ was then rotated by $d\gamma$ around a uniformly distributed random vector orthogonal to $\mathbf{V}_i(t)$. Note that this specification of angular noise allows to ensure that noise stays within the turning capacity imposed by the maximal curvature κ : for 95% of noise angle deviation to remain within the deviation permitted by maximal curvature, we must simply set

$$D_r \leq \left(\frac{\kappa v \tau}{1.96} \right)^2 \frac{1}{2\tau}.$$

with the reference values $\kappa = 0.23 \text{ rad BL}^{-1}$, $v = 3 \text{ BL s}^{-1}$ and $\tau = 0.1 \text{ s}$, we get $D_r \leq 20 \text{ deg}^2 \text{ s}^{-1}$ or $0.006 \text{ rad}^2 \text{ s}^{-1}$.

Characterizing collective dynamics

Group polarization

At the collective level we characterized the dynamics in terms of polarization, computed as in Vicsek *et al.* (1995) and Couzin *et al.* (2002) by

$$O_G(t) = \frac{1}{N} \left| \sum_{i=1}^N \mathbf{V}_i(t) \right|$$

(note that $|\mathbf{V}_i(t)| = 1$ for each i). $O_G(t)$ close to 1 indicates that the individual speed vectors are close to each other (schooling) and permits the group to travel long distances while staying together. On the other hand, an $O_G(t)$ close to 0 lets the group stay in the same place (swarming or milling).

The group dynamics converge within 30 s to their stationary state; we therefore run simulations for 60 s and computed the mean O_G over the last 20 seconds. Control simulations over 8 min gave exactly the same polarizations. Results were also unaffected when setting τ to 0.01 s. We finally also verified that 60 s were enough time to move away from the initial conditions and to detect the group's dissolution in the absence of interactions.

Group connectedness

We focused on groups of fish that remain a single unit, i.e. we discarded the cases when

the group underwent a fission event. The group was assumed to remain a unique unit if each individual in the group was in contact with all other ones, either directly or indirectly. Two individuals were considered in direct contact if their inter-distance is lower than the maximal perception radius z_{oa} . Two individuals were considered in indirect contact if a chain of direct contacts through any number of neighbours could connect them. We finally assessed group connectedness by the algorithm for equivalence classes given in Press *et al.* (1992: p. 345).

Dynamics from an individual's perspective

To explore the corresponding dynamics from the individual's perspective we computed an individual density measure $\langle \lambda \rangle$ as the mean distance to the farthest neighbour and an individual polarization measure

$$O_\lambda = \frac{1}{N} \sum_{i=1}^N V_i \cdot V_{\lambda(i)},$$

where $\lambda(i)$ denotes the farthest neighbour of individual i , and the dot denotes the dot product. Since the speed vectors are scaled to unit, this dot product is the cosine of the angle between the headings of individuals i and $\lambda(i)$. In the context of connected groups the frequently measured mean nearest neighbour distance is a simple consequence of the short range repulsion distance. On the other hand, the density measure $\langle \lambda \rangle$ allows to explore whether the dynamics of a connected group happen at a larger scale than the individual interaction range, with information propagating through the group. Namely, we can distinguish the case when all the fish are within a sphere of diameter roa (everybody influences everybody, $\langle \lambda \rangle < 1$) from the case where individual fish only perceive part of the (connected) group ($\langle \lambda \rangle \geq 1$).

Systematic exploration of the initial conditions

Initial density

The N individuals were initially spread uniformly in a sphere of radius

$$R = \sqrt[3]{N} f roa.$$

The initial sphere volume is therefore given by

$$\Gamma(R) = \frac{4\pi}{3} (\sqrt[3]{N} f roa)^3 = N \left[\frac{4\pi}{3} (f roa)^3 \right],$$

that is each individual was allocated on average a small sphere of radius $f roa$. The factor f is inversely proportional to the cube root of the initial density.

Given a cut-off distance for contact (in the present case, the maximal perception range roa), the connectedness of the group depends on its density and on the raw number of individuals. For $N = 100$ individuals we computed the probability for the group to remain connected: it falls below 0.05 for $f > 0.5$ and exceeds 0.95 for $f < 0.38$.

What are the values of f that should be explored? Note that a group has a vanishing probability to be initially connected if the individuals are given (on average) a small sphere that nearly covers their perception radius (f close to 1). We therefore stopped the exploration of density at a value where the group is initially almost surely not unique ($f_{\max} = 0.62$). On the other end we started at the highest density at which all individuals are packed into their zone of repulsion ($f_{\min} = roa/roa = 1/20$). Preliminary studies further showed that the collective behaviour is most sensitive to the initial density for low values of f . We therefore included the effect of density by varying f as a power series. A power factor of 1.07 yielded a set of 38 initial density values from f_{\min} to f_{\max} .

Initial polarization

The initial orientations of the unit speed vectors were determined by a parameter ψ ranging in $[-1, 1]$. For each individual i , V_{ix} was drawn from a uniform distribution in $[\psi, 1]$. The other speed coordinates were computed as $V_{iy} = \sqrt{1 - V_{ix}^2} \sin u$ and $V_{iz} = \sqrt{1 - V_{ix}^2} \cos u$, with u drawn from a uniform distribution in $[0, 2\pi]$. Initial speed vectors are thus fully aligned for $\psi = 1$, and fully random for $\psi = -1$. We adopted a linear series from -1 to $+1$ by steps of 0.1 (21 values).

Overall, for each of the 24 values of roo , the histogram of polarization was computed over a total of 21 initial polarizations \times 38 initial densities = 798 initial conditions, simulating one replication per initial condition. We verified that repeated replications yielded the same results. Together with the exploration of the behavioural factors a total of 170 000 simulations were run.

Results

The reference model and its dynamics

The systematic variation of initial conditions confirms that the radius of the orientation matching area, roo , has an important influence on the stationary dynamics of our fish model (Fig. 3, compare with Couzin *et al.* 2002). One can identify two major qualitative behaviours in terms of the group alignment parameter O_G : (1) for a small roo the group stays in the same place, with individuals swarming or milling around the centre of mass of the group, (2) for a large roo individuals align with each other and adopt a common direction, with a cruising speed close to the individual linear speed (schooling). The hysteresis effect described by Couzin *et al.* (2002) could be obtained by varying roo continuously from 5 to 10 BL and back (Fig. 3). Note that the transition between swarming and milling occurs continuously and these two collective states cannot be qualitatively distinguished. Milling is in fact simply a swarming behaviour which is constrained by the limited turning rate (curvature) that controls the short-range matching of fish headings.

The role of the individual behaviour

The emergent global behaviour should be explained in terms of the individual behaviour. The important factor is each individual's distance to its most distant neighbour (λ) within a connected group. We will therefore visualize the transitional group dynamics in terms of this distance and alignment with these distant neighbours (O_λ), an indicator of the long-range alignment of the group (Fig. 4).

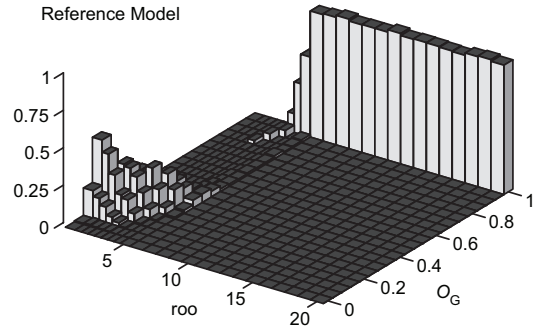


Fig. 3. The stationary dynamics of the reference model characterized by the empirical distribution of polarization O_G . For each value of the outer radius of the zone of orientation, roo , this distribution was computed from 798 systematically varied initial conditions (see text). O_G close to 1 corresponds to schooling behaviour, O_G below 0.5 to swarming or milling behaviour.

For a small ratio roo/roa (Fig. 4, upper panel, $roo = 2$ BL) the fish always end up swarming under the dominating influence of attraction. Starting from a small volume and any initial alignment (O_λ between 0 and 1) the group converges to a stationary volume where attraction becomes sufficient to balance the system's inertia (Fig. 4, upper panel, zone a). Similarly, starting from a somewhat larger volume (zone b), the group first transits in a centripetal pattern where all individuals move toward the group centre (O_λ close to -1) before converging to the same stationary volume. Finally, when the group starts with a volume exceeding a critical value, attraction is not sufficient to prevent it from splitting into subgroups (zone c). The path to swarming therefore passes through a temporal accumulation of mutual attractions between neighbours that destroy any initial alignment until it stabilizes at a stationary volume where the mean farthest neighbour distance is just below the attraction radius roa . In other words, the swarming equilibrium volume is so small that each individual is directly attracted to all others in the group. This full connectedness between all individuals explains the dominance of the swarming state: any neighbour ends up at a distance below roa , with only few individuals within roo . Hence, motor reaction is dominated by attraction; all individuals continuously try to catch up with a direction pointing towards the group centre. Perfectly aligned headings (school behaviour, $O_\lambda = 1$) only represent an unstable stationary state.

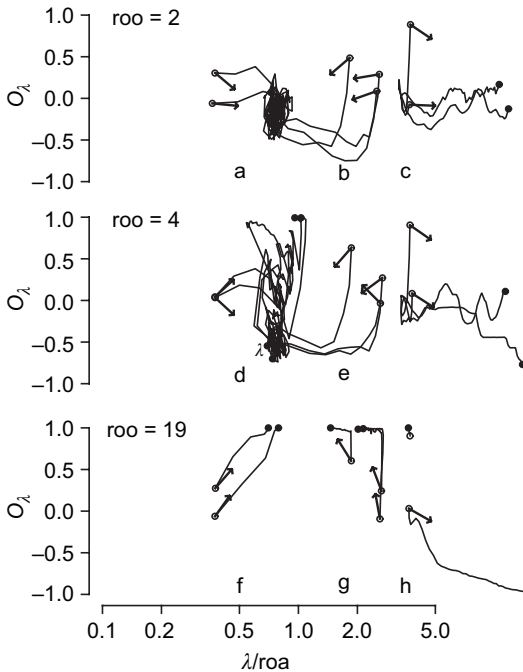


Fig. 4. Characterization of the transient dynamics towards the stationary state for $roa = 2, 4$ and 19 BL (body lengths). O_λ represents the mean polarization with respect to the farthest neighbour and λ is the mean distance to the farthest neighbour. The arrows indicate the initial conditions and point towards the stationary state. For the sake of clarity only seven representative initial conditions (out of 798 tested ones) are shown.

For a ratio roo/roa close to 1 (Fig. 4, lower panel, $roo = 19$ BL) the fish always end up in a schooling state ($O_\lambda = 1$) or split up (zone h). Starting from a small initial volume (zone f), the group first expands and then adopts a common orientation. Starting from a somewhat larger volume (zone g) the fish immediately adopt this common orientation. However, it is worth noting that the distance to the farthest neighbour can remain largely superior to roa , schooling behaviour is therefore a truly self-organized process based on the spatial propagation of local interactions between neighbours, contrary to the swarming behaviour described above.

Finally, for intermediate values of roo/roa (Fig. 4, middle panel, $roo = 4$), the system is in a bi-stable state where initial conditions in zones d and e can lead either to schooling or to swarming behaviour. We could not detect any pattern that

permits to predict the stationary state from the initial conditions as characterized by the parameters O_λ and λ . Though, some tendencies exist. Starting from a small volume (zone d), high initial alignment biases the dynamics toward further alignment (schooling). However, starting from a larger volume (zone e), the opposite may occur and initially aligned states lead to swarming, whereas initially disorganised states lead to schooling. Note that even in the latter case the dynamics pass through the swarming or even milling area before reaching the schooling state. This might depend on the geometrical arrangement of the individuals, in particular whether the global shape of the group remains spherical or tends to some shape boosting alignment. This point has not been investigated in the current study but merits further attention.

In summary, the ratio roo/roa crucially determines the stationary state(s) of the system. For small ratios the fish end up in the swarming state where each fish is within the attraction zone of each other, while for ratios close to 1 the final state is schooling where individuals only interact with few neighbours. In between the system is bi-stable where the stationary state cannot be predicted from the initial state.

Critical behavioural factors

Blind zone

A blind rear zone of specific size is an often used feature in fish modelling (Aoki 1982, Couzin *et al.* 2002). In the reference model it was set to 90° ($\alpha = \pm 135^\circ$, Fig. 2a), but the global dynamics are affected by the size of this zone (Fig. 5). An intermediate increase (reducing α from $\pm 180^\circ$ to $\pm 120^\circ$) only increases the probability for a group to split up, while conserving the dynamic landscape qualitatively. But further reduction of α (down to 90°) leads to dramatic changes, swarming behaviour disappears completely and the probability to split up increases tenfold or more (Fig. 5).

The relative robustness of group behaviour with respect to small blind rear zones can be explained as follows: the collective dynam-

ics rely on the spread of information about positions and orientations of individuals. For a given individual this information flows through its perceived neighbours, which in turn collect this information from their neighbours, and so on. Hence the intensity of the information flow depends on the global density of perceptual links between the individuals. For a large α , this density varies little with a changing α (and is further smoothed by the turning movements) whereas it undergoes a non-linear drop if α is greatly reduced (e.g. down to the volume ahead for $\alpha = 90^\circ$). “Leader–Follower” behaviours can emerge depending on whether two fish are in an attracting or aligning distance from each other. In the first case the follower tends to remain within the blind rear zone of its leader, but tracking it efficiently and thus remaining together. In the second case alignment of both fish also leads to joint displacement with a constant inter-individual distance.

However, increasing the blind zone further (Fig. 5, lower panel) increases the probability for a leader to completely loose contact with its rear neighbours and to swim straight ahead. If this happens for several local leaders the group will split up. In the present model this happens for α between $\pm 120^\circ$ and $\pm 90^\circ$ which is unrealistically low for real fish.

Curvature

The curvature parameter κ determines the speed with which a fish can change its heading. This parameter turned out to be the most important factor in the present model (Fig. 6). In the reference model (Fig. 3) κ was set to 0.43 rad BL^{-1} , corresponding to a turning rate of 40° s^{-1} for a speed $v = 3 \text{ BL s}^{-1}$.

If κ is too low (Fig. 6, upper and middle panels) fish are unable to adopt quickly the desired direction $D_i(t)$. They tend to disperse more rapidly than the attraction can cope with. As a consequence, the group splits up in most cases.

Conversely, if κ is set to a high value (Fig. 6, lower panel), individuals are highly reactive to their perception and reach very easily their

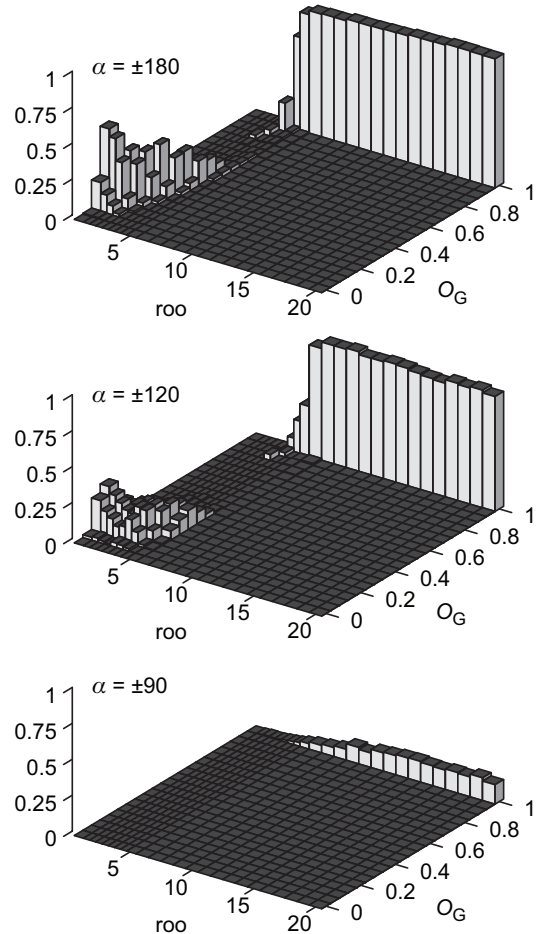


Fig. 5. The influence of a decreasing perception angle (α) on the model's stationary states (see Fig. 3 for the notations). At a low value of roo the heights of the columns do not add up to 1, indicating the occurrence of a high proportion of fissions.

desired heading. In this case the system reaches its stationary state (swarming, schooling) more rapidly and the range of ratios roo/roa where bi-stability occurs becomes negligible.

Noise

In a realistic system the effect of angular noise cannot go beyond the curvature κ , we therefore limited our exploration to values $D_r < 20$. The resulting dynamic landscapes (not shown) were indistinguishable from the reference model

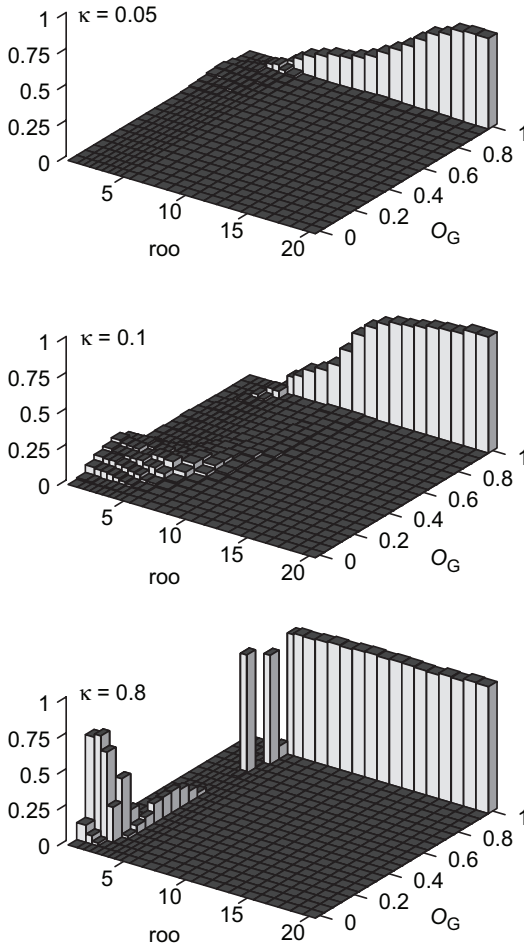


Fig. 6. The influence of maximal curvature κ on the model's stationary state (see Fig. 3 for the notations).

(Fig. 3). We can therefore conclude that the detected stationary states and their dependence on initial conditions are barely modified by noise in the present model.

Attraction weighting

Finally, increasing the weight of attraction η with respect to alignment when computing the desired direction $D_i(t)$ has two effects: it increases the range of roo/roa values for which bi-stability occurs and shifts this range to the right (Fig. 7). For a fixed value of the orientation zone (e.g. roo = 4), the modulation of the attraction weight can make the collective state switch from schooling

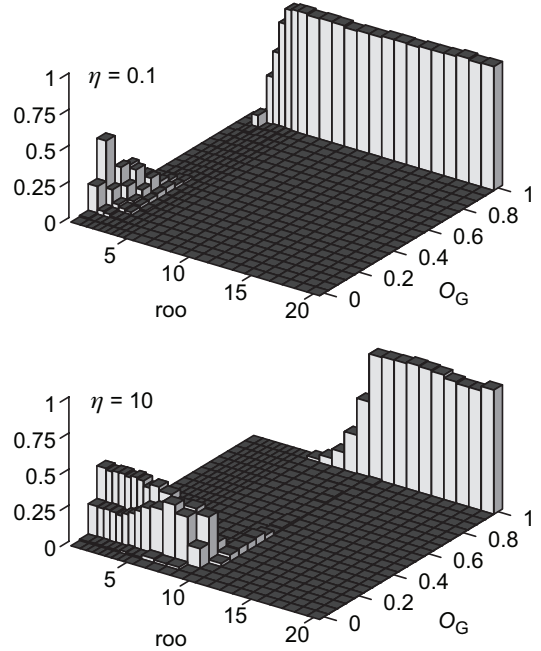


Fig. 7. The influence of differential weighting η between attraction and alignment on the model's stationary dynamics (see Fig. 3 for the notations). Low influence of attraction (top panel) vs. high influence of attraction (lower panel).

($\eta < 1$) to swarming ($\eta > 1$) through the bi-stability ($\eta = 1$).

Factors with no effect

Alteration of the linear speed v (keeping curvature κ constant), and the further enlargement of roa were found to yield the same results as the reference case.

Discussion

The present analysis confirms the results in Couzin *et al.* (2002) that there are two major collective behaviours, schooling with the fish group moving straight ahead at maximal speed and swarming or milling where the group remains at the same spot. The former happens when alignment to neighbours dominates over attraction to them, while the latter occurs when attraction dominates. If both behaviours have equal importance a bi-stable state can occur where the initial

conditions determine the final collective state. This bi-stable state signifies that the same behavioural rules on the individual level can result in multiple collective states.

The bistability has been made apparent because relevant initial conditions (initial packing density and polarization) were systematically explored. The initial density was explored from highest densities down to a critical lowest density that still allows the group to remain connected. It is worth noting that this critical lowest density arises from a geometrical constraint and depends on the group size: a larger group must be more packed to remain connected. However, sonar measures in open sea show that the packing densities of fish seem to be independent of the size of the shoal (Misund 1993, Misund *et al.* 2003 and references therein). Note however that the density is in general quite heterogeneous inside large schools and may depend on their shape (Mogilner *et al.* 2003). With our model, the final density of the school (as measured by the mean distance to the nearest neighbour to correct for group shape) proved indeed stable for larger group sizes (up to $N = 5000$), whether the final state belonged to swarming or schooling. In all cases, the final density is far below the critical density for connectedness, the geometrical constraint therefore does not play a role at steady state. This result also shows that for large groups the swarming shape can be stable even if the fish do not perceive all others at the equilibrium volume ($\lambda > 1$).

We already mentioned that the dynamics converge in all cases within the first 30 seconds. However, this convergence time depends on the linear speed (taken here as 3 BL s^{-1}) and also on the initial packing which in turn depends on the perception radius. To compare with biological data these model parameters ought to be tuned accordingly.

Note that the milling observed with the present model is characterized by a full connectedness of the group (everybody is within the attraction zone of each other). It is not necessarily of the same nature as the milling observed on much larger scales (Parrish & Edelstein-Keshet 1999). By the way, the question of the individual rules that might lead to a swarming like behaviour without splitting but where each individual

only perceives a fraction of the whole group remains an open one. In our case, the mechanism leading to swarming could also be replaced by a tendency to move towards the highest local group density, detection of each individual with its moving direction is not mandatory. However, reviewing the literature this seems not to be sufficient to obtain schooling, the moving direction of neighbours must somehow be perceived (Vicsek *et al.* 1995, Grégoire *et al.* 2003).

Instead of using fixed distance neighbourhood areas (r_{or} , r_{oo} , r_{oa}) many authors rather choose to fix the number of neighbours taken into account (Parrish *et al.* 2002, Viscido *et al.* 2005). Interestingly, the number fixed by Viscido *et al.* (2005) in order to obtain a minimum number of stragglers (defined as individuals that are more than 5 BL from their nearest neighbour, which serves as a measure of connectedness) corresponds to the average number of neighbours perceived by each individual in the schooling state with a dominance of alignment over attraction (6–12 neighbours, *see* Fig. 4 lower panel).

Critical behavioural parameters

Variation of the visual field α within a biologically relevant range only had a minor effect on the observed collective dynamics (Fig. 5). The presence of a (even rather large) blind rear zone seems to have no particular impact on schooling or swarming behaviour, frequent directional changes are sufficient for a fish to “scan” its rear and let it have an average impact on its movement. In contrast, low values of the maximum turning rate κ highly increase the risk of splitting up, and swarming behaviour becomes impossible (Fig. 6). This parameter might be under a strong selection pressure. For example, tuna-like swimmers seem to be optimized for high-speed swimming in calm waters (Sfakiotakis 1999) but they are barely capable of rapid accelerations or turning manoeuvres. For collective behaviour to emerge in such species, a large zone of orientation should be favoured over the attraction range, a prediction that longs for an experimental validation. This also implies that comparative studies about schooling behaviour should be done only between species with similar maximal κ .

Switching between different collective states

Many fish species are capable of switching between schooling and swarming/milling behaviour (Fréon and Misund 1999). Couzin *et al.* (2002) explained this by a modulation of the zone of orientation (ρ_0) that, as we have seen (Fig. 3), can indeed trigger such a change. However, the proposed mechanism how ρ_0 is changed often relies on external factors that modify the perception range (for example day/night or water turbidity). Our observation that differential weighting of attraction and orientation can also change the collective state suggests an alternative mechanism. For fixed $\rho_0 = 5$, changing the weight of attraction with respect to alignment (η) from 0.1 to 10 and back (Fig. 7) has the same hysteresis effect as described by Couzin *et al.* (2002) with changing ρ_0 . The weight η can be modulated by the animal's internal state, for example an anti-predator behaviour might involve a large η that increases the weight of attraction (Hamilton 1971, Beechaam & Farnsworth 1999, Viscido & Wethey 2002, James *et al.* 2004) and triggers swarming or milling behaviour, while η is small in the absence of predators, increasing the weight of alignment and leading to schooling behaviour.

This study only addressed the dynamics of schooling behaviour in the absence of environmental heterogeneities or restricting borders. The coupling of these dynamics with environmental effects (water streams, temperature gradients, pollution, food abundance, population dynamics ...) is not a trivial task and would require further detailed and specific studies. For example, Koltes (1985) showed that the presence of copper can significantly alter the behavioural parameters such as the linear speed and the curvature. This alteration had a clear impact on the collective behaviour towards schooling. Our model suggests that the observed alteration of the individual curvature can by itself explain the shift in the collective behaviour, with or without alteration of the linear speed.

Alternatives to individual based models

The present (Lagrangian) model describes the

change in individual behaviour (position and heading) as a combination of deterministic (influence of neighbours) and stochastic components that only depend on the current state of the system. It can therefore be interpreted in the framework of coupled Markov processes in continuous time with a master equation governing the (probabilistic) behavioural transitions. In some cases (for example spatial diffusion, *see* Patlak 1953 for the first application to animal behaviour) such an individual model can be linked to analytically more tractable partial differential equations (PDE) that describe population behaviour at a macroscopic scale. However, some behavioural approximations and simplifications are necessary to obtain these analytical expressions. In the case of fish school models these simplifications are particularly stringent, for example Vicsek *et al.* (1995) worked in a closed space (toroid) in order to skip the need for attraction, Niwa (1996) neglected curvature constraints, and blind rear zones never make it into a macroscopic model. The strength of numerical explorations of (stochastic) individual based models lies exactly in this absence of technical necessities to simplifications, all biologically relevant features with respect to the explored global behaviour can be incorporated. However, in order for these numerical simulations to be as exhaustive as the ones that can be performed with macroscopic equations one has to go beyond the interpretation of particular simulation runs and extract structural properties such as bi-stability or the conditions when individuals only perceive part of the group rather than the whole one. One of the ways to get there requires a systematic exploration of the dynamics starting from any possible relevant initial condition.

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