



Density induced transition in a school of fish

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ABSTRACT

Collective behaviour has been studied in various fields of science. As an example, we may consider the patterns observed in living systems, whose aggregates form organized groups such as flocks of birds, herds of mammals and schools of fish. These aggregates may be formed as a consequence of an external stimulus or due to the local interaction among nearby specimens. As an example of the latter case one may think about a school of fish, where each individual bases its behaviour on its perception of the position and velocity of its nearest neighbours. As a result of these interactions, global collective behaviour may emerge, originating and maintaining the cohesion of the aggregate. In this work, we model the collective movement of a school of fish using an agent-based model which follows biologically motivated behavioural rules previously proposed. The distributions of nearest neighbour distance and relative orientations between neighbouring fishes are measured and the results are found to be in good agreement with previous experimental measurements.

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1. Introduction

Collective behaviour has attracted the interest of scientists from various areas. Particularly, pattern formation in groups of animals in motion [1–4], such as flocks of birds [2,5,6], schools of fish [7] and herds of animals [8], is a subject of interest of biologists as well as physicists. Biologists are usually concerned with the advantages that these aggregates confer to their members, such as predator avoidance [9,10], increase in the reproduction rate and forage [11], while physicists usually focus on the dynamical aspects of the appearance and maintenance of collective behaviour. The origin of these swarms may be an external stimulus or, more interestingly, a consequence of the local interaction among neighbours. Theoretically, the later option has been studied assuming each member of the swarm to be a self-propelled particle interacting with other particles moving around it.

Self-propelled particle models have become an important tool in various studies involving collective motion of groups of organisms in the presence of perturbations. In order to study some aspects of the emergence of collective motion, Vicsek et al. [12] proposed a minimal model to mimic the dynamics of biological swarms. In such model, each particle (e.g. fish or bird) is supposed to move with the same speed and the direction of motion is set, at each (discrete) time step, to the average direction of all particles in its neighbourhood. Possible “measurement” errors in the detection of the neighbours’ movement direction are taken into account through a noise term. For small enough noise, it was shown that collective behaviour appeared without any external stimulus. Since this seminal work, the study of the motion of animal groups has spread among scientists. Frequently, this model [12] or variants thereof have been employed to investigate several problems, such as, swarm models [13,14], effects of noise and scaling behaviour [15], intermittent dynamics and clustering [16], the onset of collective motion [17] and self-driven agents with avoidance of collisions [18]. Other methods have focused on the effective leadership and decision making [19] and the consequences of adaptive velocity strategies [20]. Several aspects of

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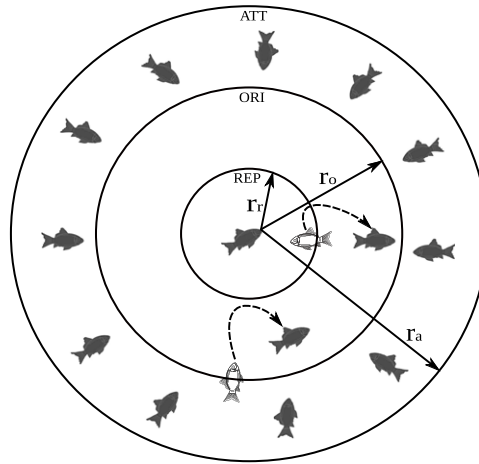


Fig. 1. Illustration of the behavioural zones. Fishes in the repulsion zone (REP) swim apart from each other, in the orientation zone (ORI) align themselves and in the attraction zone (ATT) they move towards each other.

this model have been discussed. For instance, the strength of the noise (due to imperfect interaction or disturbances in the media) was shown to play a fundamental role on the very existence of the swarms [12,21,17,22–24].

For being a simplified model that considers only the directional alignment in self-propelled particle systems, the model proposed in [12] represents, indeed, a particular version of the model proposed previously by Reynolds [2] – a computer model based on certain behavioural rules, namely cohesion, separation and alignment. Other agent based models also simulate the internal dynamics of a group of interacting animals and incorporate sensory regions into their simulations [25–29], discussing aspects of school dynamics and organization, based on the experimental behaviour of fishes. School dynamics emerges from the interactions between individuals within a perception range and the individual movement only depends on the positions of their neighbours [10].

In particular, in the model studied by Couzin et al. [29], each fish can exhibit one of three basic behavioural rules: repulsion, orientation and attraction. Those rules are based on experimentally observed behaviours. Fishes too close to one another will repel themselves in order to avoid collision. In a middle range, fishes tend to swim together in the same direction, while at a larger range they try to get closer. This zonal behaviour is in agreement with the observation of schools of surf scoters on water surface [30]; however for mosquitofishes repulsion is principally mediated by changes in speed [31]. Recently, it has been claimed that three body interaction in fact occur in the schools, but pairwise interactions qualitatively capture the spatial structure of small groups [32]. In this contribution, we show that a slightly modified version of this model (the noise is different, see Section 2) which is able to reproduce experimentally observed behaviours of a school of fish [7]. In such experiments, fishes (tilapia) were placed in an aquarium and their trajectories were recorded with a CCD camera. From the movie, several properties were analysed, such as the nearest neighbour distance distribution and the orientation distribution.

In the next section, we present the model used in this contribution and discuss its computational implementation. In Section 3, we present our results and in Section 4 we discuss their implications.

2. The model

In this paper, we consider a variant of the model proposed by Couzin et al. [29]. The fishes are represented by point particles in a $L \times L$ square lattice (with periodic boundary conditions). Each individual is characterized at time t by its position vector $\mathbf{r}_i(t)$ and its velocity vector $\mathbf{v}_i(t)$. The model assumes discrete time evolution and that the fishes move freely between time steps (τ), hence the new positions are given by

$$\mathbf{r}_i(t + \tau) = \mathbf{r}_i(t) + \mathbf{v}_i(t)\tau. \quad (1)$$

After each time step, the fishes interact with their neighbours according to phenomenological rules discussed below. In all our simulations, the modulus of the velocity is kept constant and the time step is $\tau = 1$.

In order to mimic the fish behaviour, the model is composed of three interaction regions, according to the distance between fishes d_{ij} . If the fishes are too close, $d_{ij} < r_r$, they will repel each other (repulsion zone) to avoid collisions – hereafter, r_r denotes the radius of the repulsion zone, likewise r_a and r_o denote the radii of the attraction and orientation zones, respectively. For distances, $r_r < d_{ij} < r_o$, the fishes will try align and move in a common direction (orientation zone), while for $r_o < d_{ij} < r_a$ the fishes move towards each other, avoiding being isolated. For even larger distances, $d_{ij} > r_a$, the fishes do not feel the presence of the other fishes at all. These behavioural rules are illustrated in Fig. 1.

Originally, the model proposed by Couzin and collaborators [29] admitted a possible “blind volume”, defined as a cone of angle $360 - \alpha$, behind each self-propelled particle, where neighbours cannot be detected. Hence, the angle α represents the

field of perception of the particles. In [29], the role of this field of perception was discussed and it was shown that smaller values of α favour group formation (angles in the range $200^\circ \leq \alpha \leq 360^\circ$ were considered). For fishes, however, this blind region is probably not relevant because the lateral lines (sensitive organs) allow the perception of the region behind the fishes [33]. Therefore, we consider the particular case of $\alpha = 360^\circ$, that is, there is no blind volume at all.

In the repulsion zone, the fishes tend to swim apart from each other to avoid collisions. This behaviour is modelled by changing the direction of the i -th fish to

$$\mathbf{d}_i^{(REP)} = - \sum_{j \neq i}^{N_r} \mathbf{r}_{ij} / \left| \sum_{j \neq i}^{N_r} \mathbf{r}_{ij} \right|, \quad (2)$$

where the sum is performed over all the N_r fishes in the repulsion zone of the i -th fish and $\mathbf{r}_{ij} = (\mathbf{r}_j - \mathbf{r}_i)/|\mathbf{r}_j - \mathbf{r}_i|$. Since the avoidance of collisions with other fishes involves the integrity of the animals, the repulsion rule has a higher priority and the orientation and attraction rules will be applied only in the absence of fishes in the repulsion zone.

If the fishes are far away from each other, but not too far, so they can still feel the presence of their neighbours, they will try to get together. This is the behaviour of the fishes in the attraction zone, which is given by

$$\mathbf{d}_i^{(ATT)} = \sum_{j \neq i}^{N_a} \mathbf{r}_{ij} / \left| \sum_{j \neq i}^{N_a} \mathbf{r}_{ij} \right|. \quad (3)$$

Here, the sum runs over all the N_a fishes in the attraction zone of fish i .

In a middle range lies the orientation zone, where the fishes tend to align to the average direction of all neighbours (including itself) in this region, that is,

$$\mathbf{d}_i^{(ORI)} = \sum_{j=1}^{N_o} \mathbf{v}_j / \left| \sum_{j=1}^{N_o} \mathbf{v}_j \right|. \quad (4)$$

In the absence of biological reasons for the choice of orientation or attraction, the average direction is assumed when there are fishes in both zones of a given fish

$$\mathbf{d}_i = \frac{1}{2} [\mathbf{d}_i^{(ATT)} + \mathbf{d}_i^{(ORI)}]. \quad (5)$$

Furthermore, considering possible “measurement errors” of the position or direction of movement of the other fishes, we add a noise term $\delta \varepsilon$ to the direction of movement. This is the main difference of the model used in this contribution and the model introduced in [29] (the other difference is the spatial dimension, bidimensional here, against tridimensional there). While, following [12], we use a white noise term [ε is a uniform random variable ($\varepsilon \in [-\pi, \pi]$) and $0 \leq \delta \leq 1$ is the strength of noise], whereas in [29] the noise follows a spherically wrapped Gaussian distribution. This modification was introduced in order to simplify the model and show that the behavioural zones are the missing ingredient of the model proposed by Vicsek and collaborators, while still being able to reproduce the experimental results.

Finally, if there is no fish in any of the three zones at all, the fish follows its route. In this case $\mathbf{d}_i = \mathbf{v}_i(t)$.

3. Results

In a recent paper, Becco and coworkers [7] studied experimentally the dependence of the collective motion of a school of fish on density. The fishes (tilapia juveniles) were allowed to swim freely inside a thin aquarium and their trajectories were recorded. The small thickness of the aquarium ($40 \text{ cm} \times 30 \text{ cm} \times 2 \text{ cm}$) was purposely chosen to make the dynamics of the school nearly two dimensional. They focused their analysis on two quantities: the distribution of shortest distances between nearest neighbours s and the distribution of the difference in the orientation θ of the velocities of nearest neighbours.

As expected, it was observed that for larger densities the shortest distance distribution is narrower and its average is smaller, that is, the fishes swim closer when the density is larger. Despite the triviality of this result, Becco et al. manage to characterize the shortest distance distribution as well as the orientation distribution. The shortest distance distribution was found to be well fitted by a log-normal while an exponential was able to fit the orientation distribution.

Here we show that the model presented in the previous section is able to reproduce the results from [7]. We carried out extensive numerical simulations in order to determine the set of parameters which lead to good quantitative agreement with the experimental results. While a large range of noise was able to give rise to qualitatively similar distributions, quantitative agreement was obtained for δ around 0.1. Therefore, in all the results presented in this manuscript, we set $\delta = 0.1$. In order to avoid short time correlations we perform our measurements at each 100 time steps. Further, we used as unit of length the average body length of the fishes (bl), and set $r_r = 1bl$ in order to avoid collisions, $r_o = 3bl$ and $r_a = 4bl$. These values are in the same range as the ones used in [28]. We have also set the modulus of the velocity to $4bl$ per unit of time (τ) and the side of the lattice $L = 35bl$. These values are in accordance with the average velocity of the tilapia juveniles and the size of the aquarium given in [7]. Hence the single parameter left to be varied was the density. In the following, we show our results for the nearest neighbour distances and the difference of orientations distributions.

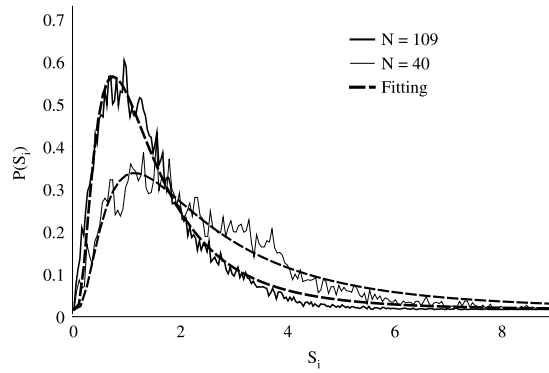


Fig. 2. Distribution nearest neighbour distance for $N = 40$ and $N = 109$.

3.1. Nearest neighbour distances

The nearest neighbour distance s_i for fish i is found by computing the minimum distance between fish i and all other fishes j ,

$$s_i(t) = \min(|\mathbf{r}_j(t) - \mathbf{r}_i(t)|). \quad (6)$$

In Fig. 2, we show the nearest neighbour distance distribution for two different values of the density ρ , compatible with the ones used in [7]. For $N = 40$, the width of the distribution is considerably larger than for $N = 109$, that is, the fishes are more disperse in the former case, while the school becomes more cohesive in the later one. In both cases, the distribution $P(s)$ is well fitted by a log-normal distribution

$$P(s) = \frac{1}{sw\sqrt{2\pi}} \exp\left[-\frac{(\log(s) - \mu)^2}{2w^2}\right], \quad (7)$$

where μ and w are the fitting parameters, as can be seen in Fig. 2. Hence, the visual comparison of Figs. 2 and 3 of Ref. [7] indicates a good agreement between the model and the experimental results (please notice that, since the length of the fishes used in [7] is of the order of 1 cm, the units in the x -axis can be read either as body length or centimetres).

Another interesting result obtained in [7] is the so-called interdistance. The interdistance s_{int} , defined as the most probable minimum distance between the fishes, can be readily obtained from Eq. (7) as

$$s_{\text{int}} = \exp(\mu - w^2). \quad (8)$$

In order to obtain a statistically relevant result, we averaged s_{int} over different samples. Thereby, from Eq. (8) we have

$$\bar{s}_{\text{int}} = \frac{1}{N_\beta} \sum_{\beta=1}^{N_\beta} \exp(\mu_\beta - w_\beta^2), \quad (9)$$

where $N_\beta = 10$ is the number of samples. The average interdistance \bar{s}_{int} , presented in Fig. 3, was calculated for all pairs of neighbouring fish in function of the density ρ , and, following Ref. [7], fitted by

$$a_1(\rho_c - \rho)^\alpha + b_1. \quad (10)$$

An inherent characteristic to s_{int} is its behaviour depending on the density in such a way that for low densities it decays and for high densities it reaches a plateau. This behaviour was characterized in [7] by the saturation constant $b_1 \approx 1.21$ and the decay constant $\alpha = 0.7 \pm 0.3$. From our simulations, we obtained $b_1 = 1.4 \pm 0.5$ and $\alpha = 0.7 \pm 0.4$, in accordance with the experimental results. It is worth mentioning, that, not only the units of the interdistance can be read either as body length or centimetre, as stated before, but the density has a simple conversion factor: fishes/bl = 10^4 fishes/m². Hence the parameter b_1 can be compared directly and the x -axis of Fig. 3 should be multiplied by 10^4 to be compared with Fig. 4 of Ref. [7].

3.2. Difference of orientations between the velocities

Another quantity of interest is the distribution of the angles between the velocity of nearest neighbours. As will be discussed shortly, this quantity measures the degree of alignment of the school of fish. For each pair of nearest neighbours i and j , determined by the condition given in Eq. (6), we calculate the angle θ as

$$\theta = \arccos \left[\frac{\mathbf{v}_i \cdot \mathbf{v}_j}{|\mathbf{v}_i| |\mathbf{v}_j|} \right]. \quad (11)$$

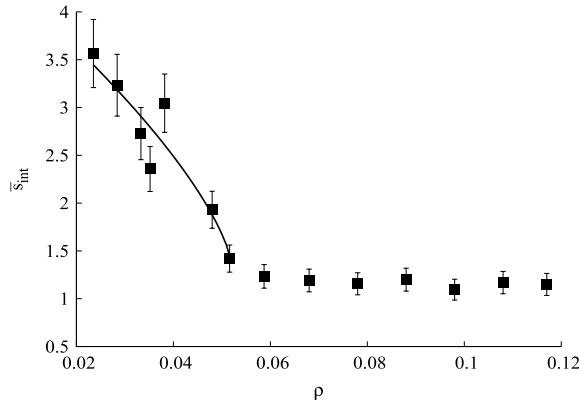


Fig. 3. Interdistance s_{int} (in units of bl) as a function of the density ρ (in units of number of fishes/ bl^2). Symbols with errorbars represent the simulation data and the line is the fitting curve of Eq. (10).

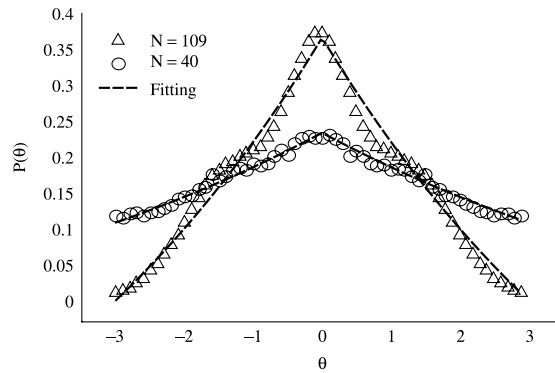


Fig. 4. Distribution of angles between the velocities of nearest neighbouring fishes for $N = 40$ and $N = 109$.

In Fig. 4, we plot the distributions of angles $P(\theta)$ for the same densities used in Fig. 2. It is evident in the figure that $P(\theta)$ is well fitted by an exponential

$$P(\theta) = -k_1 \exp\left[\frac{-|\theta|}{\gamma}\right] + k_2, \quad (12)$$

where k_1 , k_2 and γ are free fitting parameters. This exponential dependence has also been observed experimentally [7]. Further, the maximum of the distribution $P(\theta)$, shown in Fig. 4, has a peak centred at zero, indicating a high group polarization, this means that fishes preferably swim in the same direction, which characterize the formation of a school. The more pronounced peak for the denser case indicates the more coherent motion.

From Eq. (12), once again, following [7], we define the cooperativeness $C = \frac{1}{\gamma}$. For calculation purposes, we define also the average cooperativeness

$$\bar{C} = \frac{1}{N_\beta} \sum_{\beta=1}^{N_\beta} \gamma_\beta^{-1}. \quad (13)$$

In Fig. 5 we present our results for the average cooperativeness together with the fitting curve proposed in [7]

$$a_2 (\rho - \rho_c)^\phi + b_2. \quad (14)$$

The average cooperativeness \bar{C} is directly related to the school polarization, that is, the directional alignment between fishes, which characterize the formation of the school. In this sense, it is expected that \bar{C} increases with the density, indicating a stronger alignment. For low enough densities, there is only local alignment, without school formation, and the average cooperativeness saturates. As observed experimentally [7], the increase in the cooperativeness is well described by Eq. (14). Furthermore, the exponent $\phi = 0.9 \pm 0.1$, which characterize the growth of the cooperativeness, is within the error of the experimentally observed exponent $\phi = 0.6 \pm 0.3$.

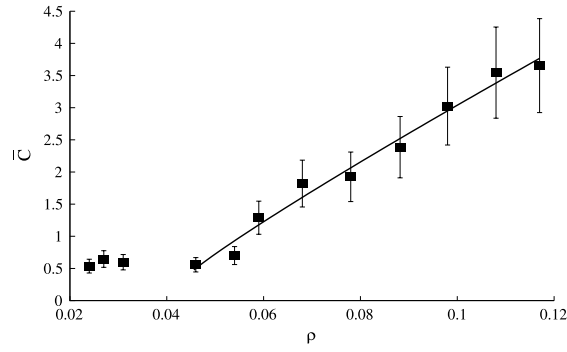


Fig. 5. Average cooperativeness \bar{C} (rad) as a function of the density ρ (in units of number of fishes/ bl^2). Symbols with errorbars represent the simulation data and the line is the fitting curve of Eq. (14).

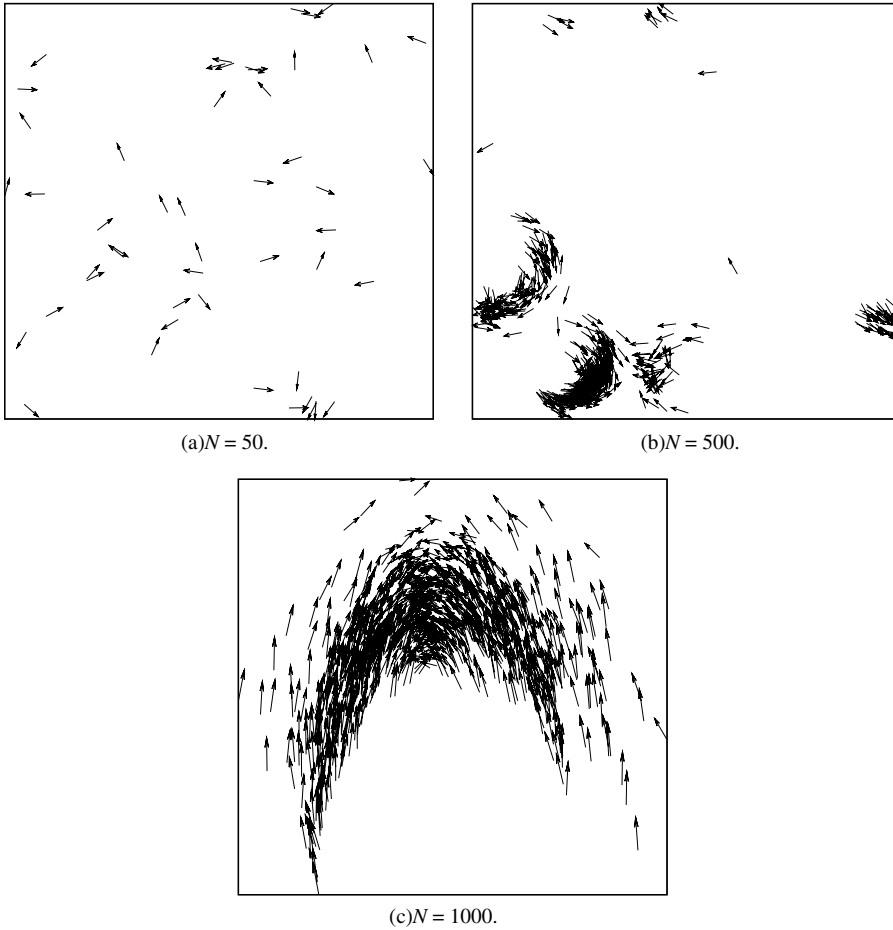


Fig. 6. 6(a) Due to very low density the fishes are dispersed. 6(b) For intermediate densities, the fishes swim in small groups. 6(c) For high densities, the fishes tend to form a compact group with coherent movement.

3.3. Patterns

In this subsection, we present distinct patterns of movement that appear in the model as the density increases. Contrary to the previous subsections, where the density of fishes remained within the experimental range, here it goes way beyond the ones used in the experiments. In Fig. 6, we let the system evolve for a long time before taking a snapshot of the position of the fishes and their direction of movement, indicated by the arrows.

For low density, Fig. 6(a), the fishes move almost independently and no school is observed. As the density increases, small groups show up (Fig. 6(b)). Each one of these groups moves coherently, but they do not get into a single school yet.

The groups may interact, colliding with one another, exchanging members, but they still break apart, even for long times. For even larger densities, almost all the fishes, finally get together into a single school and move coherently (Fig. 6(c)). This school formation reflects a biological strategy used as protection against predators [9,10].

4. Conclusions

Several studies have reported statistics on real schools of fish making numerical simulation and measuring properties such as group polarity, group velocity and inter-individual spacing [34], nearest neighbour distance [35], difference of orientations between its neighbours [36] and spatial distribution of fish in the school [11]. We considered an individual-based model which includes, for each fish, the following biological inspired rules depending on the relative distance: avoidance of collisions, alignment of movement and agglomeration.

We showed that the model is able to reproduce the patterns of movement observed experimentally for tilapia juveniles [7]. Even though we used units of body length in our simulations, the conversion to the experimental units is straightforward and the results are compatible. In accordance with theoretical and empirical evidence the results of the present work indicate that, in schools, individuals, without any hierarchical structure, spontaneously associate with other individuals of the same species. Such an association may confer protection against predators, reduce the cost of locomotion and promote school integrity. In our simulation, the school formation is more and more pronounced as the density of fishes increase. The quantitative density dependence of the school behaviour of the tilapia predicted by the model has not been experimentally checked yet and would be a good test for the strength of the model.

What is more, the main purpose of this contribution – to show that a simple behavioural model is able to correctly reproduce the experimental data of Ref. [7] – was successfully attained. We have shown that the distributions of the smallest separation distance between nearest neighbours and the distributions of difference of orientations between the velocities of nearest neighbours had the same shape as the ones observed experimentally [7]. Moreover, the average cooperativeness and average interdistance of the school also were shown to agree quantitatively with the experimental observations.

In summary, the relatively simple biologically inspired model discussed here was able to reproduce measurements of the tilapia school observed in a thin aquarium. In principle, other model may be able to also fit the experimental data. However, we applied a biologically inspired model, with parameters within the range of the available experimental knowledge and already used in the literature. Hence, the interplay of repulsion, attraction, orientation and noise was shown to be enough to characterize the school formation.

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