Mathematical model of fish schooling behaviour in a set-net

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We investigated the validity of a mathematical model to describe fish schooling behaviour towards a simple set-net model. We apply a model considered to be "an autonomous decentralized system" and based on Newton's equation of motion. It includes the parameter M, which indicates "the quantity of information exchange" (i.e. the number of neighbours that affect an individual's behaviour) and strongly affects fish school size and schooling behaviour in an enclosed space. To evaluate the model, simulations of fish schooling behaviour in a set-net model consisting of a leading fence and a box-shaped trap similar to a primitive type of set-net were compared with experimentally observed behaviour of bitterling and mackerel, with a focus on M. A small M induces improper behaviour because there is low cooperation among fish in a school. On the other hand, if M is too large, improper simulation results of individuals in deadlock states in the trap are obtained as a result of excessive information exchange among the fish. The results suggest that the mathematical model can describe the behaviour in a set-net model adequately when M is greater than 2 and less than 10.

Keywords: fish schooling behaviour, mathematical model, quantity of information exchange, set-net.

Introduction

The behaviour of an individual fish swimming alone can be described as not well ordered, whereas a school of fish consists of individuals that move in concert. Models that simulate the behaviour of a school of fish are useful for exploring how individuals affect overall school behaviour and what cooperative behaviour is involved. Aoki (1982) developed a stochastic model of a school of fish that was based on an individual fish model, and the behaviour of each individual affected that of its neighbours. In the model, the orientation and velocity of individuals were defined by the probability density function of a normal distribution and Gamma distributions, respectively. Simulations using the model showed that attraction to neighbours and parallel orientation behaviour are important factors in the organization of a fish school. Aoki's model was the basis for other stochastic models proposed subsequently (Huth and Wissel, 1992, 1994; Reuter and Breckling, 1994; Inada and Kawachi, 2002). Huth and Wissel (1992) developed a stochastic fish school behaviour model that could simulate the response to a predator, and demonstrated that the order and flexibility of a fish school are affected by the number of fish considered neighbours and the randomness of each individual.

These simulations of fish school behaviour have provided a better understanding of the basis of the behaviour mechanism in fish schooling and valuable information for fisheries science. The simulation results of Huse et al. (2002), using boids model (individual-based) (Reynolds, 1987), demonstrated that the migration patterns of Norwegian spring-spawning herring change in accordance with the number of individuals with an assigned location. This is interesting because it suggests that differences in recruitment numbers may affect herring migration patterns.

Fish school behaviour can be simulated not just by these stochastic models but also by physical mathematical models that can simulate fish school behaviour deterministically.
Sannomiya et al. (1990, 1993) and Nakamine and Sannomiya (1995, 1998) developed an individual-based model in which individuals’ behaviour is decided by certain external forces that have a defined function. Since there are no stochastic processes in this model, the effect of each external force on the behaviour of a school of fish can be quantitatively evaluated in more detail. In the model, the behaviour of a school of fish is treated as being that of “an autonomous decentralized system”, through a systems engineering approach. This means that overall order emerges from each autonomous subsystem that constitutes the whole system, and consequently the system achieves its objectives. This is similar to the concept of individual-based models. Since such a model can include the behaviour of individuals in response to obstacles such as walls and if such a model of fish school behaviour can describe actual fish schooling behaviour in various situations, it could be applied to problems in the field of fishing technology, such as estimating the capture process, or deciding the best type of fishing gear to use. Simulation results derived from the model could thus provide suggestions for fishing operations or fishing gear design, allowing the catch to be controlled more effectively.

Using the most recent mathematical model Nakamine and Sannomiya (1995, 1998) in the present study, we simulated fish schooling behaviour in a simple set-net similar to a primitive type of set-net. Simulation results were evaluated by comparison with the behaviour of an actual school of fish under experimental settings. In this model, there are certain parameters that need to be quantified before running simulations. The parameter representing the quantity of information exchange (M), i.e. the number of individuals that influence the behaviour of each individual, is one of the most important. The quantity of information exchange has a strong effect on the size of a school of fish and on its behaviour, especially in enclosed spaces. Therefore, to accurately represent the behaviour of an actual school of fish, the optimum value for M must be decided.

We examined the schooling behaviour of two species of fish — a freshwater fish, bitterling (Rhodeus ocellatus ocellatus), and a saltwater fish, chub mackerel (Scomber japonicus) — to compare experimental data with the results of simulation. The aim of the study was to develop a suitable mathematical model that could realistically describe the behaviour of a school of fish in a set-net, with particular focus on the information exchange parameter.

Methods

Mathematical model of fish schooling behaviour

The motion of individuals is assumed to be restricted to within a two-dimensional space, and is expressed by using Newton’s equation of motion. The position and the velocity of an individual \( i \) are \( x_i = (x_i^1, x_i^2) \) and \( v_i = (v_i^1, v_i^2) \), respectively. The motions of \( N_f \) fish in a school are then described by the following equations:

\[
x_i = v_i, \quad \text{mv}_i = F_{i1} + F_{i2} + F_{i3}, \quad i = 1, 2, \ldots, N_f
\]

where \( \text{mv}_i \) is the inertial force of an individual \( i \). \( F_{i1}, F_{i2}, \) and \( F_{i3} \) are the forces defining the motion of an individual, \( i \), defined as the propulsive force, the force exerted by the walls and nets, and the force of interactions among individuals, respectively. These forces are explained as follows.

The propulsive force, \( F_{i1} \), is used to express the fact that an individual fish swims forward at its own preferred speed:

\[
F_{i1} = -a_i^1(||v_i|| - a_i^2)(||v_i|| - a_i^3)v_i
\]

where \( a_i^2 < a_i^3 \), \( v_i \) is swimming speed and \( v_i \) is the acceleration. When there are no other forces acting on the motion of the fish, Equation (2) describes the swimming speed of an individual, \( i \), and converges on a stable equilibrium point (Figure 1). The swimming speed of an individual, \( i \), converges on \( a_i^2 \) or \( a_i^3 \) or 0, depending on the initial condition. Since \( v_i \) is the differential coefficient of first order with respect to time, \( v_i \) increases when \( v_i \) is positive and decreases when \( v_i \) is negative. The parameters \( a_i^1, a_i^2, \) and \( a_i^3 \) are unknown, and are unique to each individual.

\( F_{i2} \) expresses the environmental effects of the force exerted by walls and netting screens. As fish swim, they do not collide with obstacles, such as walls or netting, but

![Figure 1. Solution trajectory of Equation (2) in the \( v_i-v_i \) plane. \( v_i \) is swimming speed and \( v_i \) is the acceleration.](https://academic.oup.com/icesjms/article-abstract/61/7/1214/882212)
instead swim along the obstacles, following them closely. Consequently, the model assumes that these obstacles act as repulsive and attractive forces on individuals. These forces are represented by:

\[ F_{i2} = k_{wi}^+ \sum_{l=1}^{L} f_{wil}^+ + k_{wi}^- \sum_{l=1}^{L} f_{wil}^- \]  

(3)

\[ f_{wil}^+ = \begin{cases} v_{il} e^{-d^+ / \sigma} & \text{for } v_{il} > 0 \text{ and } d_{il} < d^+ \\ 0 & \text{otherwise} \end{cases} \]  

(4)

\[ f_{wil}^- = \begin{cases} v_{il} e^{-d^- / \sigma} & \text{for } v_{il} < 0 \text{ and } d_{il} < d^- \\ 0 & \text{otherwise} \end{cases} \]  

(5)

where \( L \) is the number of sides to the wall. The unit vector \( \mathbf{e}_l \) refers to wall \( l \) and \( v_{il} \) is the velocity component normal to wall \( l \), given by \( v_{il} = -\mathbf{e}_lv_i \). The quantity \( d_{il} \) describes the distance between an individual, \( i \), and the wall, \( l \). \( d^+ \) and \( d^- \) are the certain distance that repulsive and propulsive forces influence, respectively. \( k_{wi}^+ \) and \( k_{wi}^- \) are unknown parameters that are unique to each individual.

\( F_{i3} \) expresses the force exerted on each individual \( i \) by its neighbours. The force \( F_{i3} \) is given by

\[ F_{i3} = \sum_{j \in N(i)} b(r_{ij}) \frac{x_j - x_i}{r_{ij}} + \sum_{j \in N(i)} c(r_{ij}) \frac{v_j - v_i}{M_i} \]  

(6)

\[ b(r_{ij}) = \begin{cases} k_{bi} \frac{x_j - x_i}{r_{ij}^3} + k_{bi}^3 & 0 < r_{ij} < \alpha_1 \\ k_{bi} & \alpha_1 < r_{ij} < \alpha_2 \\ k_{bi}^- & r_{ij} > \alpha_2 \end{cases} \]  

(7)

\[ c(r_{ij}) = \begin{cases} k_{ci} & 0 < r_{ij} \leq \delta \\ k_{ci}^- & r_{ij} > \delta \end{cases} \]  

(8)

where \( r_{ij} \) is the distance between individual \( i \) and individual \( j \), given by \( r_{ij} = \| x_j - x_i \| \). The first term on the right-hand side of Equation (6) is the interactive force that maintains a suitable distance between neighboring individuals. The second term is the schooling force that makes the velocity of each individual uniform. Figure 2 shows these functions for \( b(r_{ij}) \) and \( c(r_{ij}) \). The graph of \( b(r_{ij}) \) indicates that when the distance between individuals is small, the force acts on individuals repulsively, whereas when \( r_{ij} \) is large, it acts attractively. \( k_{bi} \), \( k_{bi}^3 \), \( k_{ci} \), \( \alpha_1 \), and \( \alpha_2 \) and \( \delta \) are the unknown parameters.

\( N(i) \) is the subset whose elements consist of the individuals existing in the vicinity of individual \( i \). Let \( M \) be the number of elements in \( N(i) \), where \( M \) is the quantity of information exchange and indicates the number of individuals that have an effect on individual \( i \) when the interactive and schooling forces are estimated. Therefore, the simulation results for schooling behaviour differ as the quantity of information exchange is varied. For instance, if \( M \) is three, the elements of the subset \( N(i) \) consist of three nearer neighbours around \( i \) within the distance \( \alpha_2 \).

The present study sought to estimate an appropriate value for \( M \) in order to develop a model that reflected the behaviour seen in an actual set-net trap. The model equations can be found by substituting unique parameters that are defined for each individual by Equation (1), which is a second-order simultaneous ordinary differential equations system. We can therefore conjecture the swimming trajectory of each individual from the initial position of the individual and its velocity, and by using computational numerical calculations performed on a PC. In the present study, we used the fifth or sixth order of the Runge–Kutta method to solve these differential equations.

Model parameters

To simulate behaviour, we need to estimate the unknown parameters included in the model. We used the parameters estimated for bitterling using the time-series data obtained from experiments performed in previous studies (Sannomiya et al., 1993; Nakamine and Sannomiya, 1995). Five bitterling were placed in a 150 × 100 cm rectangular water tank, and time-series data were acquired for the trajectories of the individuals. If \( d^+ \), \( d^- \), \( \alpha_2 \), \( \delta \), \( x_i \), and \( v_i \) can be defined, linear equations can be obtained for the other parameters \( a_1^+ \), \( a_1^- \), \( a_2^+ \), \( k_{bi} \), \( k_{bi}^- \), \( k_{ci} \), \( \alpha_1 \), and \( \alpha_2 \). Thus, these parameters can be identified by using a least-squares method from the time-series data. The parameters for bitterling are listed in Table 1.

In order to estimate the unknown parameters for mackerel, five individuals were placed in a water tank 90 cm in diameter without the trap. The motion of each fish...
was limited by the shallow water depth (10 cm) because the motion is in the two-dimensional space. Video images of fish school behaviour were taken using a digital video camera 2.5 m above the tank, and time-series data for their trajectories were acquired using digital image analysis. The x–y position of each individual was recorded at 0.1-s intervals over a period of 200 s. The position of each individual was used as time-series data in the fish school behaviour model (Nakamine and Sannomiya, 1995). The unknown parameters were identified by a least-squares method, and are listed in Table 2.

For both bitterling and mackerel, \( d^+, d^-, \alpha_2, \) and \( \delta \) were defined from the observation data as 5 cm, 20 cm, 50 cm, and 50 cm.

### Water tank experiments

To evaluate the behavioural model, we compared actual fish schooling behaviour in a water tank with that of numerical simulations. A set-net is a complicated structure that consists of leader fence nets, a playground, bag nets, and other parts. In this study, however, a simple model of a set net, consisting of a box-shaped trap and a leading fence, was used to obtain the basic characteristics of fish schooling behaviour in a set-net. To compare the behaviour of a school of fish as determined by simulation with that derived from experimental data, two experiments were carried out, using bitterling and mackerel, as follows.

In the experiments with bitterling, a box-shaped trap, 20 cm in length, was used as a bag net. This, together with a leading fence as a leader net, 60 cm in length, was set in a circular water tank with a diameter of 180 cm (Figure 3a). The water depth was 10 cm to restrict the fish to two-dimensional movement. Twenty individual bitterlings, with an average total length of 4.7 cm and an average body weight of 2.5 g, were used for the experiment.

We applied the same methodology as described above in the experiments with mackerel. Five mackerel, with an average total length of 17.7 cm and an average body weight of 61.5 g, were used for the experiment. In this case, a box-shaped trap 50 cm in length was used, and two screen fences were attached at the inlet of the trap to serve as a flapper net (Figure 3b). The screen was 25 cm in length, and the angle between the screen and the entrance line was 60°.

In both experiments, the trajectory of each individual was obtained by video image analysis of digital videos of the schooling behaviours of the fish, using a PC. Time-series data of the x–y coordinates of each individual were recorded every 0.1 s, once the fish had acclimatized to the experimental arenas.

### Results

#### Experiment 1: bitterling

Figure 4 shows the trajectories of the school of bitterling during the process of entering and escaping from the trap. The school of bitterling tended to swim along the wall of the circular tank, and rarely entered the trap. Any temporary irregular behaviour on the part of the leading individuals of the school caused the whole school to change course significantly, as individuals’ movements were coordinated with each other. When the leader of the school encountered the leading fence, the entire school swam along the fence and entered the trap.

As the individual fish entering the trap were slow-moving, they tended to remain in the trap and not escape immediately. Although some individuals were near the exit and had the chance to escape, they did not, because their movements were coordinated with those of the other fish. Although the direction of travel of each individual was similar before entering the trap, once inside no regular

<table>
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<th>( a^1 ) (g cm s(^{-1}))</th>
<th>( a^2 ) (cm s(^{-1}))</th>
<th>( a^3 ) (cm s(^{-1}))</th>
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<th>( k_{a2} ) (g cm s(^{-1}))</th>
<th>( k_{a3} ) (g cm s(^{-1}))</th>
<th>( \alpha_1 ) (cm)</th>
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### Table 1. Model parameters for bitterling.

### Table 2. Model parameters for mackerel.

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behaviour was observed on the part of the school. There were on average 17 s between the first fish entering and the last fish escaping. The majority of the fish in the school did not change swimming speed between entering and escaping, but once 4/5 of the fish had escaped, the remaining fish chased after the leading group by swimming faster.

Simulation results were obtained by reproducing the same conditions as those in the experiments. Five parameter sets, shown in Table 1, were allocated to the model’s equations for 20 individuals. The numerical calculations were thus performed using initial conditions derived from the experimental data for the positions and velocities of the fish. The \( x_e \) coordinates for individuals were estimated from the initial states, every 0.1 s for 150 s. Simulation results for 19 cases were obtained by varying the number of information exchange, \( M \), from 1 to 19. Figure 5 shows the results of simulation when \( M = 7 \). The school of fish swam along the leading fence lengthwise and entered the trap; at this point, individuals encountering the end of the trap could not swim forward, and turned towards the exit of the trap. The school of fish then spread out in the trap. Individuals near the exit escaped and others followed, until finally all individuals escaped. When \( M = 7 \), the simulation results agreed well with those of the experiment; however, the time from entering to escaping was more than 30 s, which was longer than the time taken for the experimental result.

The behaviour was quite different for different values of \( M \). In particular, when \( M \) was a relatively large or small number, the behaviour did not reflect that of the experiment. Using an inappropriate number for \( M \) caused unrealistic simulation results. Figure 6 shows the case when \( M = 1 \), with 19 simulation results after 100 s had elapsed. When \( M = 1 \), a few individuals left the trap slowly, but the school spread out and consequently did not move, i.e. the system attained a state of deadlock. \( M = 19 \) also induced deadlock and high density in the school; as individuals near the exit had to cooperate with those in the slow-moving area near the end of the trap, they could not escape.

To compare the results of simulation with those of the experiment quantitatively, we estimated the centre point of a fish school, \( CP(x_p, y_p) \), and \( d_i(n) \) (\( i = 1, 2, \ldots, N_f \) and \( n \) is time-step), which is the distance between each individual and \( CP \) in each time-step, as well as the time remaining \( T_i \) (\( i = 1, 2, \ldots, N_f \)) for each individual in the trap. We estimated \( \bar{d}(n) \), the average value of \( d_i(n) \) for all individuals in each time-step. For quantitative comparison, based on the size of the school of fish and the remaining time in the trap, we defined two indicators \( D \) and \( T \). These values are given as follows:

\[
D = \frac{1}{N_f} \sum_{n=1}^{N_t} \bar{d}(n) \tag{9}
\]

\[
T = \frac{1}{N_f} \sum_{i=1}^{N_f} T_i \tag{10}
\]

Figure 7 shows \( D \) and \( T \) for the experimental and simulation results for values of \( M \) ranging from 1 to 19.
Note that $\bar{D}$ in Figure 7 indicates the average of a time-series of $\bar{d}(n)$, from the initial position, to the time at which 1 s had elapsed after the centre position of the school had left the trap. The $\bar{T}$ of 150 s in Figure 7 indicates that the school of fish became deadlocked in the trap. In the simulation results, all fish entering the trap became deadlocked when $M = 11, 12, 14, 16, 17, 18$, or 19. When $M = 1$, one individual entered the trap, then others entered, and the system subsequently became deadlocked. When $M = 2, 3,$ and 4, some individuals escaped within 30 to 80 s, but the remaining individuals became deadlocked. Although all individuals could escape when $M \geq 5$, a correlation between the time required to escape and $M$ was not well estimated. When $M = 7$, the time required to escape was the shortest, and was close to the experimental result, $D$; this gave the density of the school of fish as 6.2 cm, and was in agreement with the experimental value of 6.7 cm.

Additionally, we found some interesting behavioural patterns in the simulation results. When $M$ was greater than 10, some individuals in the leading group turned back toward the centre of the school soon after starting the simulation, but this behaviour was not seen in the experiment, suggesting that the school size given as the initial condition was too small to be realistic. Therefore, the appropriate value of $M$ can also be evaluated from the behaviour patterns seen in the simulation results.

Experiment 2: mackerel
Figure 8 shows the trajectories of a school of five mackerel. Their behaviour in the trap with screen fences used as flapper nets was quite different from that of the bitterling in the trap without a flapper screen. When individuals encountered the end of the trap, they turned toward the exit, but their escape was prevented by the flapper screen.
fence. Individuals often remained in the area between the flapper screen fence and the wall of the trap; subsequently, a school would split off, and a few individuals would escape. However, escaping individuals would then approach or enter the trap again because other individuals in or near the trap affected their behaviour. Therefore, these experimental results showed that flapper screens did affect the behaviour of fish that remained in or near the trap.

The parameter sets in Table 2 were allocated for model equations for five individuals, and the numerical simulations were carried out using the initial conditions given by the experimental data. The x–y coordinates for individuals

Figure 7. $\overline{D}$ and $\overline{T}$ for the experimental and simulation results for values of $M$ ranging from 1 to 19. $\overline{D}$ indicates the average of a time-series of $d(n)$ from the initial position to the time at which 1 s had elapsed after the centre position of the school had left the trap.

Figure 8. Trajectories of the school of five mackerel during the process of entering and escaping from the trap with flapper screen fences.
were calculated every 0.1 s for 50 s. Four sets of results were obtained by changing the number of information exchange, $M$, from 1 to 4. In the case of mackerel, individuals moved more actively than bitterling, and split off and joined together fluidly. Entering and escaping from the trap was often seen. Therefore, unlike the case for bitterling, it was difficult to evaluate this quantitatively using $D$ and $T$; to evaluate the model, we therefore compared the simulation results with those of the experiment.

Figure 9 shows the simulation results when $M = 1$. Here, individuals encountered the wall and turned back toward the exit of the trap. The escape of a few individuals, however, was prevented by the flapper screens (Figure 9B). The individuals that could not escape repeatedly came into contact with the wall and the flapper screen, and remained in the area between the two (Figure 9C). These behaviours were similar to the experimental results. After a short time, one individual escaped but the others remained in the trap (Figure 9D); any individuals that escaped did not enter the trap again. When these individuals encountered each other closely, they did not unite to form a school. This behavioural pattern was not seen in the experiment.

The simulation results with $M = 4$ differed considerably from those with $M = 1$ (Figure 10). The school of fish entered the trap, turned back, and escaped after encountering the wall and fence (Figure 10B). However, the fish that escaped first were then again affected by escaping individuals (Figure 10C). These fish then turned back towards the fish near the exit and consequently entered the trap again (Figure 10D). An individual outside the trap, swimming along the wall of the circular tank, was also affected by other individuals, and subsequently swam towards the trap (Figure 10F). These behavioural patterns were also seen in the experiment. These characteristic behaviours were obtained more frequently when $M = 4$ than when $M = 1$, 2, or 3. As individuals affected each other more with increasing $M$, the state of stable equilibrium was not maintained. The simulation results when $M = 4$ were those most like the experimental observations.

**Discussion**

Although the form of the function in our individual-based model is important for fish school behaviour because our model is a physical mathematical model that estimates individuals’ behaviour deterministically, organized fish school behaviour also requires that individuals cooperate with their neighbours. This important fact can be demonstrated by the differences in behaviours that result from changing $M$, the value for the quantity of information exchange. Fish school behaviour in response to a set-net can be quantitatively evaluated by using the indicators $D$ and $T$. The results suggest that the value of $M$ must be optimal to obtain realistic school behaviour. If the value of $M$ is too small, the simulated fish schooling will be unrealistic and can result in a state of deadlock in the trap;

Figure 9. The simulation results for mackerel when $M = 1$. 

![Figure 9](https://academic.oup.com/icesjms/article-abstract/61/7/1214/882212)
cooperation with other fish leads to schooling behaviour, but none of the fish obtains sufficient information to escape. By contrast, if $M$ is too large, each individual has to cooperate with so many neighbours that when the individuals have various orientations, no one individual can move, resulting in deadlock inside the trap. Furthermore, outside the trap, more fish tend to school together than is the case experimentally. Thus, a model using too large or too small a value for $M$ cannot describe the actual behaviour of a school of fish. Our results suggest that $M$ should be set between 5 and 10 in our model.

In the case of bitterling, the behaviour of the simulated school of fish was similar to that seen in the experiment, when $M \approx 7$, and also in accord with quantitative comparisons using the indicators in Figure 7. However, the real school of fish was always able to escape from the trap faster than suggested by the simulation. This difference implies that the quantity of information exchange should not be a constant but rather should be treated as a variable value that depends on the situation. The simulation showed that the school of fish is likely to become deadlocked in the trap if $M$ is too large; this suggests that when fish are packed together, such as in a trap, changing $M$ to a small value can avoid deadlock and may permit prompt escape from the trap.

In the experiment using mackerel, a few individuals often remained by the flapper screens, and we observed that these individuals outside the trap attracted individuals inside the trap and affected their behaviour. This behaviour pattern can also be seen in the simulation, regardless of the value of $M$. The similarity between the simulation and the experiment supports the validity of the model, and confirms that the force of interaction among individuals in our model is important when there is a small number of individuals. However, after escaping from the trap, the individuals will not form a school if $M = 1$, and the behaviour differs from that observed in the experiment or the results of the simulation when $M = 4$. This shows that $M = 1$ is not appropriate. Although the results of the mackerel experiment cannot readily be compared with that conducted with bitterlings, because the former school consisted of only five individuals, they do nevertheless support the suggestion that too small a value of $M$ should not be selected to yield realistic schooling behaviour.

Our model needs to be further refined to address some basic inherent problems, but the experimental results do confirm that the concept of our model is valid. The present study focused on the quantity of information exchange among individuals, but there remain other problems that need to be considered in more detail. For instance, the assumption that the influence area in which neighbours of individual $i$ affect individual $i$ is uniform from $0^\circ$ to $360^\circ$ should be examined and verified because the directions of visual and other sensory stimuli are not uniform.
Further investigation of the relationship between the degree of information exchange in a school and adaptive behaviour in response to environmental variables will improve the performance and accuracy of the model. Simulations and experimental studies should be examined in more detail, and in greater numbers, to provide a basis for further practical use of the model.

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