

Steering mechanism of fish schools

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Abstract

The steering mechanism of fish schools was analysed by using an analytical model and computer simulation. The analytical model is based on fundamental behavioural rules such as attraction, parallel-orientation, and repulsion. Multiple individuals following the same rules interact with each other and thus realize school movements. The results show that when the school advances, unstable movements by the front individuals cause a change in the moving direction of the individuals that follow that individual. The transmission of the change in moving direction of the front individuals to rear individuals depends on how the individuals react to the motion of their neighbours. When the individuals react mainly to the motion of their front neighbours, the change in direction of the front individuals is transmitted quickly to the rear individuals, resulting in sharp turns by the school. In contrast, when the individuals react mainly to the motion of their side neighbours, the change in direction of the front individuals is slowly, if at all, transmitted to the rear individuals, resulting in only gradual turns by the school. Our results show that the transmission of information among individuals affects the macroscopic behaviour of the school.

1. Introduction

An important question in behavioural biology is how groups of animals coordinate their actions while moving. Simulation studies have proved immensely useful in understanding not only how such coordination is achieved, but also how the behaviour of different groups of animals differs. Previous simulation studies have successfully demonstrated how individual behaviour produces the observed characteristics of motion in several species, such as flocks of birds and swarms of bees (Reynolds, 1987; Sumpter & Bloomhead, 2000). They have also provided insight into how and why these animal groups differ from one another. In this study, we look at the schooling behaviour of fish. In particular, we focus on the steering mechanism of fish schools.

Schools of fish represent a well-known and typical biological group. The main characteristic of fish schools is uniformity. A school is composed of individuals of the same

species, same size, swimming at the same speed and direction. There is no leader or hierarchy in the school (Breder, 1959; Partridge, 1982; Radakov, 1973; Shaw, 1975). When the school advances, its moving direction, therefore, is not determined by the leader, but determined by individuals autonomously interacting with each other. In this study, using an analytical model based on fundamental behavioural rules and computer simulation, we analysed the mechanism that governs the moving direction of a school, namely, the steering mechanism. Aoki's model (Aoki, 1982) and Huth & Wissel's model (Huth & Wissel, 1992) are appropriate as the basis for our model for two reasons. First, their models are simple and include the essential characteristics of fish behaviour, such as gathering or moving in parallel to neighbouring fish. Second, their results on the dynamical movements of school, such as size and polarity of the school, and the fluctuations in the distance between individuals agreed well with the movements of natural fish schools (Aoki, 1982; Huth & Wissel, 1992). The principal difference between our model and those two models is that we add the preferred direction of an individual in terms of its sensing the surroundings. Among neighbouring individuals, the one located near the preferred direction of the sensing individual has high priority in attracting the attention of that individual.

Variation in the preferred direction of an individual might affect the transmission of information in the school, such as transmission of the change in the moving direction of part of the school to others in the school. With this model, we therefore analysed the effect of variation in the preferred direction of an individual on the steering behaviour of schools.

2. Models

We expanded Aoki's model and Huth & Wissel's model to obtain an individual behaviour model. In our model, the position $x_i(t)$ and the velocity $v_i(t)$ of the i -th individual, the direction of the j -th individual with respect to the i -th individual $\beta_{i,j}$, and the turning angle of the i -th individual $\phi_i(t)$ are defined in the two-dimensional X-Y plane (Fig. 1). Four behavioural rules for individuals are used as follows according to the position of other individuals in the reaction field (Fig. 2).

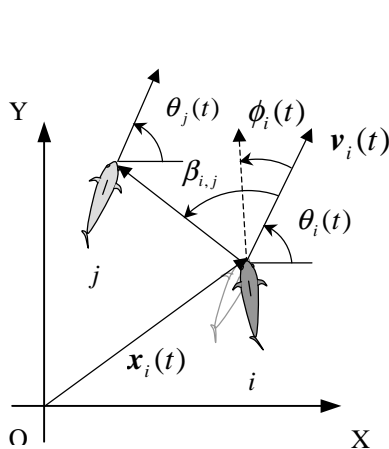


Figure 1. Definition of values

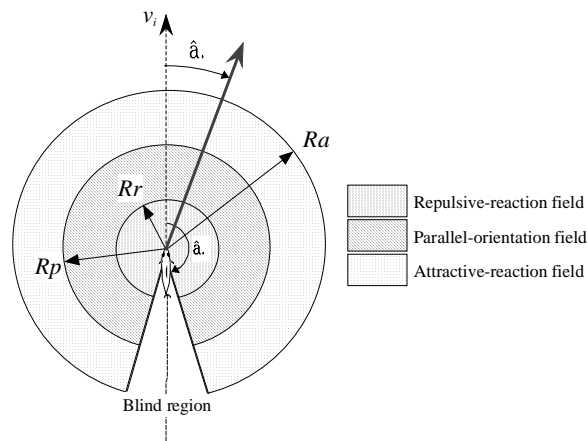


Figure 2. Reaction field

Rule-1 Attraction: Move toward the j -th individual when it is in the attractive-reaction field of the i -th individual (see Fig. 3a).

Rule-2 Parallel Orientation: Move in parallel with the j -th individual when it is in the parallel-orientation field of the i -th individual (see Fig. 3b).

Rule-3 Repulsion: Move away from the j -th individual to avoid collision when it is in the repulsive-reaction field of the i -th individual (see Fig. 3c).

Rule-4 Search: Move in a random direction to search for other individuals when no other individuals are found in the reaction field.

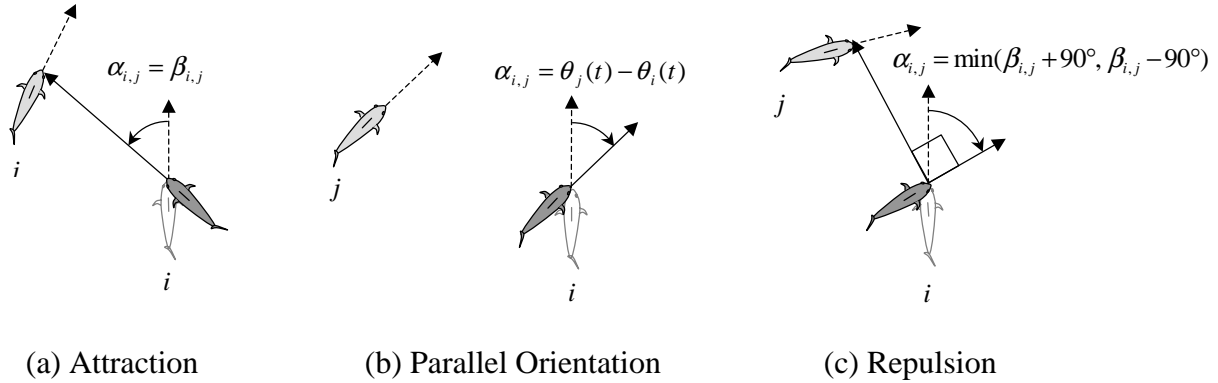


Figure 3. Behavioural rules. The value of $\alpha_{i,j}$ is the deterministic turning angle of the i -th individual determined by the j -th individual. The function $\min(a,b)$ in Repulsion represents the minimum value of a or b , both of which are compared as absolute values $|a|$ and $|b|$.

The effect of multiple individuals in the reaction field are averaged as follows:

$$\mathbf{a}_i = \sum_{j \neq i}^{N_b} \mathbf{a}_{i,j} / \left| \sum_{j \neq i}^{N_b} \mathbf{a}_{i,j} \right| \quad (0 \leq N_b \leq N_{b,\max}) \quad (1)$$

\mathbf{a}_i : unit vector whose angle between $\mathbf{v}_i(t)$ is the deterministic turning angle of the i -th individual α_i .

$\mathbf{a}_{i,j}$: unit vector whose angle between $\mathbf{v}_i(t)$ is $\alpha_{i,j}$ determined in Fig. 3.

N_b individuals in the reaction field are selected based on the direction priority. Individuals near the direction of $\pm\delta$ degrees are selected with high priority (Fig. 2).

The actual turning angle of the i -th individual $\phi_i(t)$ is determined stochastically based on the deterministic turning angle α_i using a normal probability distribution of moving direction as follows:

$$p(\phi_i) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(\phi_i - \alpha_i)^2}{2\sigma^2}\right) \quad (2)$$

$$\phi_i(t) = \text{chance}(p(\phi_i))$$

where the function $\text{chance}(p(x))$ represents the creation of random values by using a probability distribution function $p(x)$.

The moving speed is determined stochastically based on the following Gamma distribution, which is a probability distribution of the speed of individuals in observed biological groups (Aoki, 1980; Okubo, 1980, 1986; Siniff & Jessen, 1968):

$$p(v) = \frac{A^K}{\Gamma(K)} \exp(-Av) \cdot v^{K-1} \quad (3)$$

$$v_i(t) = \text{chance}(p(v))$$

The change of position $\mathbf{x}_i(t)$ is defined as

$$\begin{aligned} \mathbf{x}_i(t+1) &= \mathbf{x}_i(t) + \Delta t \cdot \mathbf{v}_i(t) \\ \mathbf{v}_i(t) &= (v_i(t), \theta_i(t)) \\ \theta_i(t) &= \theta_i(t-1) + \phi_i(t) \end{aligned} \quad (4)$$

3. Results

The cruising motion of a school was calculated, where N individuals interact with each other, by using the specified parameters as shown in Table 1. Gamma distribution parameters are biologically based (Aoki, 1980). Parameters that are not biologically based are angle of blind region, size of each reaction field, maximum number of interacting neighbours, and standard deviation of normal distribution of an individual's moving direction. However, we chose their values so that the simulated values of the average nearest neighbour distance and school polarity agree with those observed for natural fish schools (details of these verification are omitted due to the limited space here). The resulting cruising motion simulated by our model using those parameters is shown in Fig. 4

3.1 Number of neighbours in the reaction field

The number of neighbours in the different fields within the reaction field varies depending on the position of the individual as shown in Fig. 5. The number of neighbours in the parallel-orientation field is dominant for individuals in the front and middle regions of the school. The number of neighbours in the attractive-reaction field of individuals in the front region is larger than that of individuals in the middle region. The individuals in the rear region of the school have the largest number of neighbours in the attractive-reaction field compared with the individuals in the front and middle regions of the school.

Table 1. Parameters

Parameters	Abbr.	Values
Angle of the blind region in the reaction field	Greek omega	150 deg
Radius of attractive-reaction field	Ra	10.0 BL
Radius of parallel-orientation field	Rp	5.0 BL
Radius of repulsive-reaction field	Rr	1.0 BL
Parameters of the Gamma distribution	K	4
	A	3.3
Time interval of a step in the simulation	Greek delta t	0.5sec
Number of individuals in the school	N	50
Maximum number of neighbours that can be	Nb,max	8
Standard deviation of normal distribution of an	Greek sigma	1 deg

Greek omega, Greek delta, and Greek sigma are the Greek symbols ω , Δ , and σ , respectively. BL means body length of fish.



Figure 4. Cruising school. Each filled circle is the head of a fish, and the short line is its body. The long curve shows the trajectory of the centre of gravity of the school ($\delta = 0^\circ$).

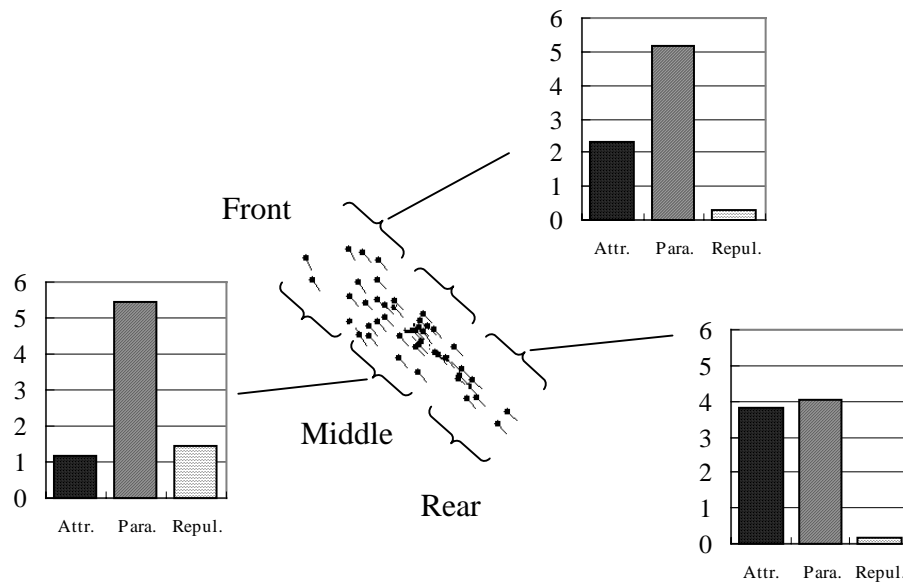


Figure 5. Number of neighbours in the reaction field of an individual ($\delta = 0^\circ$). Vertical axis is the number of neighbours in the three fields within the reaction field. Five individuals are selected in each region; front, middle, and rear regions. Numbers are an average of these five individuals. When δ is large ($\delta = 70^\circ$), the number of neighbours in each field varies from this result, but the large and small relations of the values are the same.

3.2 Sharp turns and gradual turns

When the preferred direction δ is small ($\delta < 30^\circ$), sharp turns occur frequently where the school turns abruptly at a relatively sharp angle as shown in Fig. 6a. When δ increases, the frequency of sharp turns decreases, and only gradual turns occur when $\delta \geq 70^\circ$ as shown in Fig. 6b. When δ is small ($\delta = 0^\circ$), the change in moving direction of the front individuals is transmitted immediately to the individuals following the front individuals as shown in Fig. 7. All individuals in the school turn almost simultaneously. In contrast, when δ is large ($\delta = 70^\circ$), the change in moving direction of the front individuals is transmitted only to the individuals in the front or middle regions of school, or if it is transmitted to rear individuals, it transmits slowly as shown in Fig. 8. Transmission of the change to rear individuals when δ is large is slower than that when δ is small, and thus the school turns slowly.

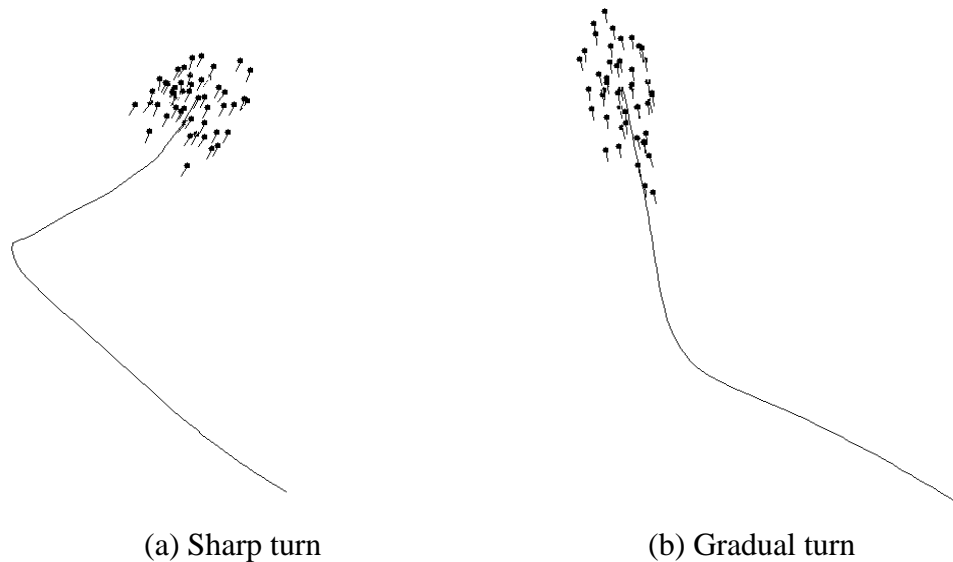


Figure 6. Sharp turns occur when δ is small ($\delta = 0^\circ$) with sharp and rapid change in direction. Sometimes a school turns at an angle larger than 90 degrees. Gradual turns occur when δ is large ($\delta = 70^\circ$) with a gradual change in direction. Long curves show the trajectories.

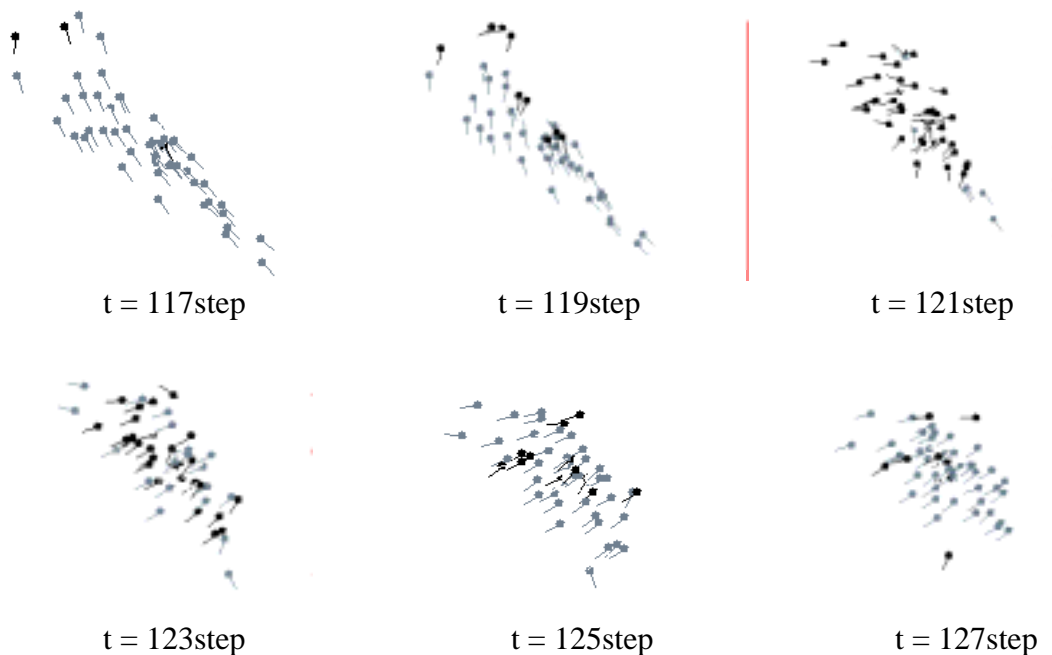


Figure 7. Transmission of the change in direction of the front individuals to the following individuals in a sharp turn ($\delta = 0^\circ$) is shown by the change in individual colour. Individuals in black changed their moving direction more than 15 degrees from the previous step (1step = 0.5 sec). Individuals in gray changed their moving direction less than 15 degrees from the previous step. The change in direction propagates to most individuals after 4 steps from the initial position. Most individuals then change their moving direction almost simultaneously. These figures of turns are from the sharp turn occurring at the halfway point in the trajectory of the school shown in Fig. 6a.

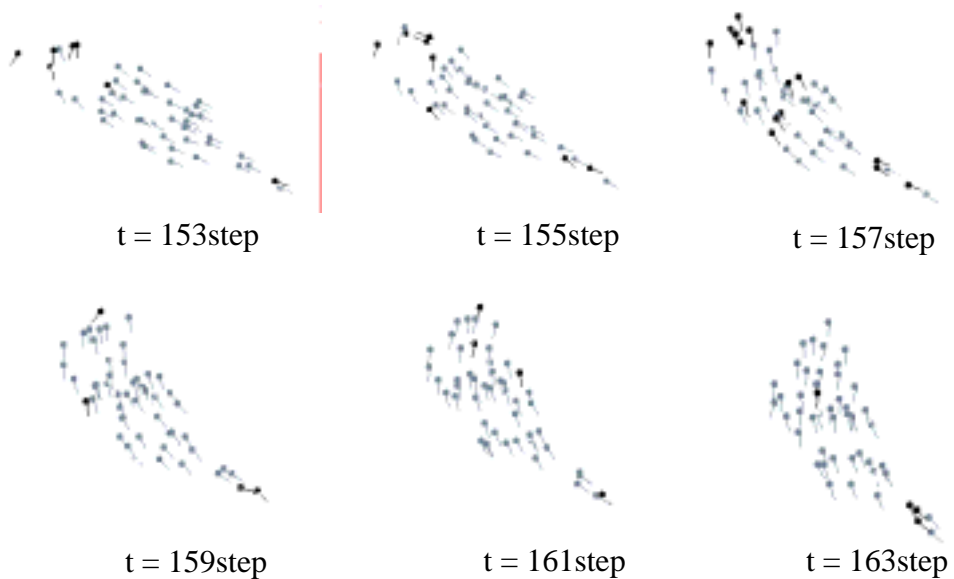


Figure 8. Transmission of the change in direction of the front individuals to the following individuals in a gradual turn ($\delta = 70^\circ$) is shown by the change in individual colour, as described in Fig. 7. The change in direction of the front individuals was difficult to transmit to many of the following individuals. The information is transmitted only to the following individuals in the front or middle regions of school. As a result, the school turns with a gradual change in direction. These figures of turns are from the gradual turn occurring at the halfway point in the trajectory of the school shown in Fig. 6b.

4. Discussion

The individuals in the front region of the school have a larger number of neighbours in their attractive-reaction field than do individuals in the middle region as shown in Fig. 5. Neighbours in the attractive-reaction field of the individuals in the front region are mainly in the rear of the individual. This implies that when the distance between individuals in the front region and their rear neighbours increases because of the temporal speed-up of individuals in the front region or speed-down of their rear neighbours, the number of neighbours in the parallel-orientation field of the individuals in the front region decreases and neighbours in the attractive-reaction field become dominant. This causes the individuals in the front region to turn backward to approach their rear neighbours. The change in the moving direction of individuals in the front region, therefore, is unstable. The individuals in the middle region have their largest number of neighbours in their parallel-orientation field. Although they also have neighbours in their attractive-reaction and repulsive-reaction fields causing the individual to turn in the direction defined in rule-1 or rule-3, respectively, the effects of these neighbours tend to be cancelled because of the symmetry of their positions around the individual. Therefore, the effect of neighbours in the parallel-orientation field becomes dominant. The individuals in the middle region of the school, then, tend to adjust their moving direction to that of their neighbours. The individuals in the rear region of the school have the largest number of neighbours in the attractive-reaction field, compared with the individuals in the front or middle regions of the school. Neighbours in the attractive-reaction field of the individuals in the rear region are mainly in front of the individual. The individuals in the rear region, therefore, tend to follow their front neighbours. The behavioural characteristics of individuals, therefore, vary according to their positions in the school. As a result, the individuals in the front region change their moving direction frequently, and thus their

function is to steer the school. The individuals in the middle region adjust their moving direction to be parallel with the direction of individuals in the front region. The individuals in the rear region follow the individuals in front of them.

When the preferred direction δ is small, an individual tends to react mainly to the neighbours in front. Information about the change in direction of the individuals in the front region then is transmitted quickly to the rear region of the school. All of the individuals in the school turn their moving direction almost simultaneously, resulting in sharp turns by the school. In contrast, when δ is large, individuals react mainly to the neighbours to the side. The individuals in the middle or rear regions of the school, therefore, do not or seldom receive information from individuals in the front region. The change in direction, therefore, becomes difficult to transmit to rear individuals. Transmission of the change to rear individuals is slower when δ is large than when δ is small. Therefore, when δ is a large, sharp turn seldom occur and gradual turns become dominant.

As a result, the macroscopic behaviour of a school, such as its steering behaviour, is closely related to the transmission of information within the school as discussed above. In particular, a sharp turn due to the synchronized movements of a majority of individuals in the school is related to the tendency of an individual to receive information about its neighbours mainly in front of it. This kind of synchronized movement is easily observed in natural fish schools such as sardines or herring. Their synchronous behaviour sometimes gives the illusion of a single large organism, which is said to be a defence strategy against attack from predators (Shaw, 1975). Individuals in natural fish schools tend to follow the motion of their front neighbours, a tendency called “front-priority” (van Olst & Hunter, 1970; Partridge & Pitcher, 1980). This front-priority tendency means that individuals in natural fish schools tend to receive information from their front neighbours. In conclusion, “front-priority” is a key factor that enables the synchronous movement of a school. Other factors might also be involved, such as those related to other sensing organs, for example, auditory or pressure-sensitive organs called a “lateral-line”, which is a row of pressure-sensitive cells located on the lateral side of the body of a fish. However, the functions of these organs for the motion synchronicity are not fully understood yet, and these functions then cannot be included in this model and compared with the result here.

Compared with simulations of the grouping behaviour of other animals, such as birds or insects, our model is based on behavioural rules similar to the Reynolds’ “boid” (Reynolds, 1987). Reynolds’ “boid” uses rules such as collision avoidance, velocity matching, and flock centring, which correspond to the repulsive-reaction (rule-3), parallel-orientation (rule-2), attractive-reaction (rule-1) of the model in this study, respectively. Other models of fish schooling include artificial fishes by Terzopoulos (1995) and Sannomiya’s model (Sannomiya, 1999). The reason why we based our model in this study on Aoki’s model and Huth & Wissel’s model is their simplicity. The model in this study is simpler than the boids model, artificial fish model, or Sannomiya’s model because it is based on statistical data of observed individual behaviour such as the moving speed of fish, and does not use physical characteristics based on Newtonian dynamical equations that are the basis for those other models. However, the validity of this model has been discussed and predicted in literature (Aoki, 1982; Huth & Wissel, 1992), and due to its simplicity, this model can clearly determine the principal factor that governs the macroscopic behaviour of fish schools.

Settings of other parameters related to the transmission of information, such as the number of interacting neighbours or the individual sensing area, can be determined by changing other parameters in this model, such as the maximum number of neighbours perceived by the individuals $N_{b,\max}$, the size of the reaction field, and the angle of blind region. This is the subject of our next study.

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