Order and Flexibility in the Motion of Fish Schools

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The coexistence of order and flexibility in the motion of fish schools was studied by using a simple numerical model and a computer simulation. The numerical model is based on behavioral rules for individuals in the school by considering attraction, repulsion, and parallel-orientation behavior. Each individual follows the same rules and makes school movements. The simulation results show that school order and flexibility are affected by the number of neighbors interacting with an individual in the school and by the randomness of individual motion. Increase in the number of interacting neighbors leads to high order, especially when the number increases from a low value (between one and three). An optimal number of interacting neighbors exists that is relatively low (two or three) for high flexibility, indicating that a fish needs only to pay attention to a few neighbors to realize both order and flexibility. The low randomness of individual motion benefits both order and flexibility. These results indicate that schooling fish have evolved specialized ability for establishing both school order and flexibility.

Introduction

Grouping of organisms in motion is observed in a wide range of animal species; examples of such grouping include insect swarming, fish schooling, bird flocking, and terrestrial mammal herding. The adaptive features of animal grouping have been well understood as anti-predator, foraging, or reproductive benefits (Partridge, 1982; Pitcher & Parrish, 1993; Clark & Ducas, 1994; Parrish & Edelstein-Keshet, 1999). An animal group varies its structure spatio-temporally (Powel, 1989; Gueron & Levin, 1993). Passive and active factors cause this variability, including internal conditions such as group size, homogeneity or heterogeneity of the group, reaction between individuals, and the physiological status (hunger, hormonal or health state), and surrounding conditions such as landscape, temperature, brightness, air or water flow, or the existence or prey or predator (Flierl et al., 1999). Such variability of grouping motion might directly or indirectly benefit the survival of the group.

One typical example of how an organism group benefits from such variability is observed in fish schools. A fish school shows two extreme characteristics of movement, namely, order and flexibility. Certain species of fish, such as sardine and herring, form large schools that sometimes exceed millions of individuals and keep moving for long periods and for long distances without fragmenting (Hara, 1986, 1987). Because they move as a group avoiding frequent collisions between individuals and are not easily fragmented into many sub-groups, such large schools have high order in their motion. A fish school...
also has a high degree of flexibility. When a predator attacks a large school, the school escapes by forming various patterns of motion (Partridge, 1982; Pitcher & Wyche, 1983; Hall et al., 1986; Nøttestad & Axelsen, 1999). Both characteristics (order and flexibility) benefit schooling fish. High order decreases energy loss caused by frequent collision and increases the size of the school, and large schools enhance the efficiency of protection, foraging, reproduction, and migration (Shaw, 1970; Pitcher et al., 1982). High flexibility provides the fish with defense tactics against attacks by predators (Partridge, 1982; Pitcher & Wyche, 1983; Hall et al., 1986; Nøttestad & Axelsen, 1999).

The main goal of our current study was clarification of the factors that affect this variability of schooling motion. We did this by examining the mechanism in which schooling fish adjust these two contradictory extreme characteristics, flexibility and order. We used a numerical model because such models have previously helped clarify both the mechanism that enables grouping motion and the factors that affect macroscopic behavior of a group (Sakai & Suzuki, 1973; Okubo, 1980, 1986; Aoki, 1982; Reynolds, 1987; Huth & Wissel, 1992; Niwa, 1994, 1996; Gueron et al., 1996; Grümbaum, 1998; Flierl et al., 1999; Sannomiya, 1999). Results from those studies provide a physical view of the generation mechanism of grouping motion and reveal mathematical factors of how social interaction between individuals affects macroscopic grouping behaviors. The models in those studies can be classified into two groups, “Eulerian” (grid-based) or “Lagrangian” (individual-based) models (Gueron & Liron, 1989; Gueron & Levin, 1993; Grümbaum & Okubo, 1994; Gueron et al., 1996). In a Eulerian model, the population is represented by a density function and the dynamics of the continuum is described by appropriate differential equations. In a Lagrangian model, a finite number of individuals are considered and the rules that control the group dynamics are based on a finite sequence of decisions made by each individual at each time step (Gueron & Levin, 1993). In our model, we used a fish school of 50 individuals because this size of school exhibits distinct schooling motion patterns. This size of school requires a Lagrangian model. Many individual-based Lagrangian models for schooling motion are based on attraction, repulsion, and parallel-orientation behaviors of individuals (Inagaki et al., 1976; Aoki, 1982; Matsuda & Sannomiya, 1985; Warburton & Lazarus, 1991; Huth & Wissel, 1992; Niwa, 1994, 1996; Gueron et al., 1996; Grümbaum, 1998). We based our model on Aoki’s (1982) model and the Huth & Wissel model because of their simplicity and because they simulated well the observed size, polarity, and fluctuations in the distance between individuals of natural fish schools (Aoki, 1982; Huth & Wissel, 1992). In this study, first we tested the validity of our model and parameter ranges for sufficiently reproducing natural fish school motion. Then, we examined the order of school motion when it is cruising, and examined the flexibility of school motion when it is escaping from a predator that is chasing the school.

**Methods**

**INDIVIDUAL BEHAVIOR MODEL**

We expanded Aoki’s and the Huth & Wissel’s models to create a model for individual behavior. In our model, the motion of an individual in a school is calculated in the two-dimensional X-Y plane. Figure 1 shows the position $x_i(t)$ and velocity $v_i(t)$ of the $i$-th individual, and other
parameters such as the direction of the \( j \)-th individual relative to the moving direction of the \( i \)-th individual, \( \mathbf{p}_{i,j} \). The change in \( \mathbf{x}_i(t) \) of the \( i \)-th individual with time is defined as

\[
\mathbf{x}_i(t+1) = \mathbf{x}_i(t) + \Delta t \cdot \mathbf{v}_i(t),
\]

\[
\mathbf{v}_i(t) = (v_i(t), \theta_i(t)),
\]

\[
\theta_i(t) = \theta_i(t-1) + \phi_i(t),
\]

where \( \Delta t \) denotes the decision step size at which an individual changes its speed and moving direction in response to its neighbors or a predator. The turning angle \( \phi_i(t) \) and the moving speed \( v_i(t) \) of the \( i \)-th individual are calculated to determine the new position of this individual. These parameters and the simulation parameters in our model are described below.

**Turning Angle**

The turning angle of the \( i \)-th individual, \( \phi_i(t) \), can be determined stochastically from the deterministic turning angle, \( \alpha_i \), by using the following equation:

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

\[
\phi_i(t) = \text{random} \ (p(\phi_i)),
\]

where \( \sigma \) specifies the randomness of individual motion and is the standard deviation of a normal probability distribution.

The deterministic turning angle \( \alpha_i \) denotes the angle between the moving direction of the \( i \)-th individual at the current time step and the moving direction at the new time step determined by the interaction of this individual with its neighbors or the predator as follows:

\[
\alpha_i = \hat{\alpha}_i(\mathbf{a}_i, \mathbf{v}_i(t)),
\]

\[
\mathbf{a}_i = c \mathbf{a}_{i,\text{school}} + (1-c) \mathbf{a}_{i,\text{predator}} \quad (0 \leq c \leq 1),
\]

where \( \mathbf{a}_i \) is the vector whose direction is the deterministic moving direction of the \( i \)-th individual at the new time step, the function \( \hat{\alpha}_i(\mathbf{a}_i, \mathbf{v}_i(t)) \) is the angle of \( \mathbf{a}_i \) measured from \( \mathbf{v}_i(t) \), which is positive when measured counter-clockwise, the vectors \( \mathbf{a}_{i,\text{school}} \) and \( \mathbf{a}_{i,\text{predator}} \) are the unit vectors determined by the interaction with other individuals in the school and with the predator, respectively, and the coefficient \( c \) represents the obedience level defined as the tendency of an individual to follow the motion of its neighbors. Each individual has its own reaction field that consists of the three different fields shown in Fig. 2. The effects of multiple neighbors in the reaction field are averaged by summing vectors determined by each neighbor:

\[
\mathbf{a}_{i,\text{school}} = \sum_{j \neq i}^{N_i} \mathbf{a}_{i,j} / \sum_{j \neq i}^{N_i} |\mathbf{a}_{i,j}| \quad (0 \leq N_b \leq N_{b,\text{max}}),
\]

where \( \mathbf{a}_{i,j} \) is the unit vector determined by the interaction of the \( i \)-th individual with the \( j \)-th individual in the reaction field. The angle of \( \mathbf{a}_{i,j} \) measured from \( \mathbf{v}_i(t) \) is \( \alpha_{i,j} \), which is distance-dependent on the position of the \( j \)-th individual as explained in the behavioral rules in the following paragraph. The value of \( N_b \) is the number of neighbors in the reaction field, and \( N_{b,\text{max}} \) is the maximum number of neighbors that can be involved in mutual interactions. When \( N_b \) exceeds \( N_{b,\text{max}} \), \( N_{b,\text{max}} \) individuals that are located in front of the \( i \)-th individual are selected as interacting neighbors, because “front priority” is frequently

![Fig. 2. Reaction field around an individual, consisting of repulsive-orientation, parallel-orientation, and attractive-orientation fields whose radii are \( R_c \), \( R_p \), and \( R_s \), respectively. The region beyond the attractive-orientation field is outside the detection region of an individual, and a blind region exists behind an individual because of its body. (\( \theta \)) Attractive-orientation field; (\( \theta \)) parallel-orientation field; (\( \theta \)) repulsive-orientation field.](image)
observed in natural fish schools (van Olst & Hunter, 1970; Aoki, 1980; Partridge, 1980; Partidge & Pitcher, 1980), where a fish pays more attention to fish in front of it than to ones to the side or rear.

In our model, the obedience level $c$ is used to simulate the change in the attention of an individual depending on its behavioral or environmental conditions. Partridge (1980) reported that a minnow school changes from a non-polarized state to a highly polarized state when the fish in the school notices a predator. This indicates that a fish changes its attention to its neighbors, namely, changes its tendency towards obedience, according to the existence of a predator. Therefore, in our model we assumed that an individual pays part of its attention ($c$) to other individuals and pays the rest ($1 - c$) to a predator, and that $c$ can change according to the situation.

The vector $a_{i,\text{predator}}$ in eqn (3) is a unit vector and has an angle $a_{i,\text{predator}}$ measured from $v_i(t)$. Both $a_{i,j}$ and $a_{i,\text{predator}}$ are determined by the following five behavioral rules.

**Rule 1: Approach.** When the $j$-th individual of a school is in the attractive-orientation field of the $i$-th individual, the $i$-th individual moves toward the $j$-th individual [Fig. 3(a)], so that

$$a_{i,j} = b_{i,j}. \quad (5)$$

**Rule 2: Parallel orientation.** When the $j$-th individual of a school is in the parallel-orientation field of the $i$-th individual, the $i$-th individual moves in the same direction as the $j$-th individual [Fig. 3(b)], so that

$$a_{i,j} = \theta_j(t) - \theta_i(t). \quad (6)$$

**Rule 3: Repulsion.** When the $j$-th individual of a school is in the repulsive-orientation field of the $i$-th individual, the $i$-th individual moves away from the $j$-th individual to avoid a collision [Fig. 3(c)]. The moving direction of the $i$-th individual is then set perpendicular to the direction of the $j$-th individual, $\beta_{i,j}$. The turning angle $a_{i,j}$ is defined as

$$a_{i,j} = \min(\beta_{i,j} + 90^\circ, \beta_{i,j} - 90^\circ), \quad (7)$$

where $\min(\xi, \zeta)$ yields $\xi$ or $\zeta$, in which the absolute values $|\xi|$ and $|\zeta|$ are compared and then the smaller value is selected (e.g. $\min(-30^\circ, 20^\circ) = 20^\circ$, $\min(50^\circ, -10^\circ) = -10^\circ$).

**Rule 4: Escape.** When a predator is in any region of the reaction field of the $i$-th individual, the $i$-th individual moves in the direction opposite to that of the predator to escape. Then,

$$a_{i,\text{predator}} = \beta_{i,\text{predator}} + 180^\circ, \quad (8)$$

where $\beta_{i,\text{predator}}$ is the direction of the predator relative to the moving direction of the $i$-th individual.

**Rule 5: Search.** When no other individuals are found in the reaction field, the individual moves in a random direction until other individuals are found in the reaction field:

$$a_i = \text{random}(-180^\circ, 180^\circ). \quad (9)$$

![Fig. 3. Behavioral rules for interaction with other individuals; (a) approach, (b) parallel-orientation, (c) repulsion. These rules were first proposed by Aoki (1982) and Huth & Wissel (1992), together with the random direction at which an individual turns to search for other individuals.](image)
ORDER AND FLEXIBILITY IN THE MOTION OF FISH SCHOOLS

In our model, the predator moves only to find and catch prey. The predator then follows Rule 1 when it finds prey in its reaction field and the obedience level $c$ is set to 1.0, because in this study we did not include any other predators. When the predator finds no prey in its reaction field, it follows Rule 5. The size of its reaction field ($R_{a,predator}$) is set larger than that for individuals in the school. The maximum number of individuals interacting with the predator is limited to $N_{b,max,predator}$. Then, the turning angle of the predator $\theta_{predator}(t)$ is determined by using eqns (2)-(5) and eqn (9), with standard deviation $\sigma_{predator}$.

**Speed of an Individual**

The speed of each individual in a school can be determined stochastically by a gamma distribution, that is, a probability distribution of speed of an individual in observed biological groups (Siniff & Jessen, 1968; Aoki, 1980, 1982; Okubo, 1980, 1986; Huth & Wissel, 1992);

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

$$v_i(t) = \text{random}(p(v)),$$  \hspace{1cm} (10)

where $\Gamma(K)$ is a gamma function and $v_i(t)$ is the speed of the $i$-th individual at time $t$. The speed of a predator, $v_{predator}(t)$, is determined by multiplying the speed of the individuals in the school by the speed ratio $S_p(\geq 1)$:

$$v_{predator}(t) = S_p \times \text{random}(p(v)).$$  \hspace{1cm} (11)

**OTHER MODEL PARAMETERS AND SIMULATION PARAMETERS**

To evaluate the order of a cruising school, the model uses the average angular deviation of school, $\delta$, that is, the time average of standard deviation of the moving direction of an individual from the moving direction of the school, and the average turning angle of the school, $\tau$, defined, respectively, as follows:

$$\delta = \frac{1}{T} \sum_{t=1}^{T} \sqrt{\frac{1}{N} \sum_{i=1}^{N} [\Delta \cdot (q_i(t), \bar{q}(t))]^2},$$  \hspace{1cm} (12)

$$\tau = \sqrt{\frac{1}{T} \sum_{t=1}^{T-1} \sum_{i=1}^{N} [\Delta \cdot (q_i(t), \bar{q}(t))]^2},$$  \hspace{1cm} (13)

where $T$ is the total time of the calculation and $q_i(t)$ and $\bar{q}(t)$ are the unit vectors whose direction is the moving direction of the individual and the school, respectively, as follows:

$$q_i(t) = v_i(t)/|v_i(t)|,$$

$$\bar{q}(t) = \sum_{i=1}^{N} q_i(t)/\left|\sum_{i=1}^{N} q_i(t)\right|.$$  \hspace{1cm} (14)

The value of $\delta$ increases as each individual in the school moves in a random direction and decreases as the individuals move in the same direction, and $\tau$ increases when the school frequently changes direction and decreases when the school moves in a straight line. Our model uses $\delta$ and $\tau$ to evaluate the order of school motion; the school order increases when either $\delta$ or $\tau$ decreases.

Initially, in our simulations, all individuals were distributed randomly in a square area with sides of length $L$, and all individuals faced the same direction. We made ten simulations for each set of parameters and for each initial position and then averaged the results. In the simulations involving a predator, the predator was placed at a distance $D$ from the center of the square starting area of the school in the initial step. Parameters for the configuration of a fish body and parameters that are assumed constant in this simulation are shown in Table 1. The patterns of escaping behavior observed in this simulation were classified according to the classification of sand-eel behavior reported by Pitcher & Wyche (1983). The use of numerical analysis prevents subjective classification and decreases the time required to classify the patterns. However, recognition of dynamical changes in the outline of the school shape required for pattern classification is too complex to develop into a numerical method. Furthermore, the simultaneous occurrences of multiple patterns at different parts of a school made it difficult to distinguish them numerically. Therefore, we defined geometric criteria for pattern classification (Fig. 4) to significantly decrease the human errors involved.
To ensure that our model corresponds to the behavior of a natural fish school, we needed to determine the range of model parameters. In our model, we used the following five parameters for individual motion: the randomness of individual motion $s$, the maximum number of interacting neighbors $N_{b,max}$, and the sizes of the attractive-orientation, parallel-orientation, and repulsive-orientation fields $R_r$, $R_p$, and $R_a$, respectively. We chose the parameter ranges (Table 2) so that the average distance to the nearest neighbor ($NVD$) was from 0.3 to 3 body lengths and that the average angular deviation of an individual's moving direction from the school's moving direction

$$AD = \left( \frac{1}{TN} \sum_{i=1}^{T} \sum_{i=1}^{N} \left| q_{i}(t), \bar{q}(t) \right| \right)^{1/2}$$

was from 8 to 42° degrees as observed in natural fish schools (van Olst & Hunter, 1970; Aoki, 1980; Huth & Wissel, 1992). This $AD$ is defined differently from $\delta$, see Huth & Wissel (1992).

### Table 1

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abbreviation</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angle from the moving direction of an individual to the border of its blind region</td>
<td>$\omega$</td>
<td>150°</td>
</tr>
<tr>
<td>Parameters of the gamma distribution</td>
<td>$K$</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>$A$</td>
<td>3.3</td>
</tr>
<tr>
<td>Decision step size in the simulation</td>
<td>$\Delta t$</td>
<td>0.5 s</td>
</tr>
<tr>
<td>Number of individuals in the school</td>
<td>$N$</td>
<td>50</td>
</tr>
<tr>
<td>Final time-step</td>
<td>$T$</td>
<td>500</td>
</tr>
<tr>
<td>Side length of the square starting area</td>
<td>$L$</td>
<td>5$BL$</td>
</tr>
<tr>
<td>Initial distance of the predator from the center of the square starting area</td>
<td>$D$</td>
<td>30$BL$</td>
</tr>
<tr>
<td>Speed ratio of the predator to an individual in the school</td>
<td>$S_p$</td>
<td>1.5</td>
</tr>
<tr>
<td>Maximum number of individuals in the school that can be perceived by a predator</td>
<td>$N_{b,max,\text{predator}}$</td>
<td>4</td>
</tr>
<tr>
<td>Radius of attractive-reaction field of the predator</td>
<td>$R_{a,\text{predator}}$</td>
<td>50$BL$</td>
</tr>
<tr>
<td>Standard deviation of the normal distribution of the predator’s moving direction</td>
<td>$\sigma_{\text{predator}}$</td>
<td>5°</td>
</tr>
</tbody>
</table>

Fig. 4. (a–g): Patterns of escaping behavior. (a) **Herd:** When a predator gradually approaches from behind the school, the closest individuals to the predator form a depression, directing their heads radially from the head position of the predator. Depression often grows from slightly concave to lunar-shaped as the predator comes closer to the school (i → ii → iii), usually leading to split or hourglass. (b) **Split:** When the individuals on either side of a concaved or lunar-shaped school that is in herd pattern turn to the opposite direction from each other, the school splits into two sub-groups, and those sub-groups flee in different directions. (c) **Hourglass:** When the individuals on either side of school that is in a herd pattern turn in the same direction, the school does not split, and then the constricted part of the school connects two clusters by making a “bridge” between them. Usually, the predator moves along this bridge (i). When the predator comes close to part of a cluster, this part of the cluster develops into a herd pattern (ii). This means hourglass and herd appear simultaneously in one school. (d) **Vacuole:** When a predator invades a school, the individuals do not flee but surround the predator. This is conspicuous when the tendency of an individual to obey its neighbors, motion is strong. Three distinct patterns are possible: (i) the school does not create a clear gap and the predator passes among the individuals, (ii) the school creates a clear gap and surrounds the predator, (iii) the individuals surrounding the predator rotate around it, like a mill pattern reported by Breder (1965). The first pattern tends to appear frequently because the predator swims faster than individuals and remains a relatively short time in the school, thus not giving enough time for the second or third pattern to develop in the school. (e) **Flash expansion and (f) Flash turn:** Flash expansion and flash turn are distinguished according to which group of individuals move radially from the predator when it invades the school. Flash expansion occurs when all of the individuals move radially from the predator, whereas flash turn occurs when some individuals move radially from the predator and the rest of the school continues to move forward. Flash expansion rarely occurs in a large school because not all individuals can perceive the predator invasion. Two patterns of flash turn are possible: (i) the predator goes around a school for several seconds, and then invades the periphery of the school; (ii) the predator invades the center of the school directly. The first pattern of flash turn tends to occur more frequently than the second pattern when $c$ or $N_{b,max}$ is large. (g) **Fountain effect:** When a predator approaches the center of the school, the school splits to both sides of the predator, and then rejoins at the rear of the predator. When the rear edge of a split school is attacked by the predator again, it develops into a herd pattern. This is another example of simultaneous occurrence of multiple patterns. These criteria are based on patterns, except flash turn, reported by Pitcher & Wyche (1983). Flash turn was reported only in our study. Filled circles show the heads of fish, and the short lines show their bodies.
In this study, we made simulations of two types of schooling motion: cruising motion with 50 individuals without a predator and escaping motion with 50 individuals and one predator. In each calculation in the simulations, all 50 individuals had the same motion parameters, and thus the school was homogeneous.

Results
Cruising Motion Without a Predator
Our first simulation involved cruising motion without a predator. Figure 5(a) indicates that $\sigma$ and $N_{b,max}$ strongly affect the average angular deviation of school $\delta$ and the average turning
Table 2
Desirable ranges for the simulation parameters*

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Ranges</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma$ (deg)</td>
<td>1–45 (1–90)</td>
</tr>
<tr>
<td>$N_{b,\text{max}}$</td>
<td>4</td>
</tr>
<tr>
<td>$R_r$ (BL)</td>
<td>1.0</td>
</tr>
<tr>
<td>$R_p$ (BL)</td>
<td>5.0</td>
</tr>
<tr>
<td>$R_a$ (BL)</td>
<td>10.0</td>
</tr>
<tr>
<td>$NND$ (BL)</td>
<td>0.65–0.73</td>
</tr>
<tr>
<td>$AD$ (deg)</td>
<td>6.8–53.9 (6.8–80.0)</td>
</tr>
<tr>
<td>Split range</td>
<td>None</td>
</tr>
</tbody>
</table>

*Simulations were done by changing one parameter, while keeping constant the other parameters listed in the same column. The values of $NND$ or $AD$ are the min–max values and do not necessarily correspond to the min–max values of each parameter range. The lowest row indicates whether a split occurs under the given conditions.

†For showing the phase transition of school motion caused by the large $\sigma$ as shown in Fig. 5(a), $\sigma$ ranged from 1 to 90°, exceeding the desirable range of 1 to 45°. The range of $NND$ and $AD$ corresponding to the range 1° ≤ $\sigma$ ≤ 90° is shown in parentheses.

angle of the school $\tau$; when $\sigma$ decreases or $N_{b,\text{max}}$ increases, both $\delta$ and $\tau$ decrease, thus increasing the school order. Figure 5(b) indicates that in contrast to $\sigma$ and $N_{b,\text{max}}$, the parameters $R_r$, $R_p$, and $R_a$ only slightly influence the school order. However, large $R_r$ or small $R_p$, which indicates a decrease in the parallel-orientation field, causes the slight increase in $\delta$, thus slightly
FIG. 5. (a) Effect of the maximum number of interacting neighbors $N_{b,\text{max}}$ and the randomness of individual motion $\sigma$ on the school order, average angular deviation of the school $\delta$ and average turning angle of school $\tau$. Regression line is for $\delta$ vs. $\sigma$ up to $\sigma = 45^\circ$, above which the school motion becomes disorderly. For all simulations, $R_r = 1.0$ BL, $R_p = 5.0$ BL, and $R_a = 10.0$ BL. $\bullet$ $N_{b,\text{max}}$ vs. $\delta$ ($\sigma = 15^\circ$); $\bullet$ $N_{b,\text{max}}$ vs. $\tau$ ($\sigma = 15^\circ$); $\bullet$ $\sigma$ vs. $\delta$ ($N_{b,\text{max}} = 4$); $\bullet$ $\sigma$ vs. $\tau$ ($N_{b,\text{max}} = 4$); (---) linear fit of $\delta$ vs. $\sigma$. (b) Effect of reaction-field radii ($R_r$, $R_p$, $R_a$) on school order $\delta$ and $\tau$. For all simulations, $\sigma = 15^\circ$ and $N_{b,\text{max}} = 4$. $\bullet$ $R_r$ vs. $\delta$ ($R_p = 5.0$ BL, $R_a = 10.0$ BL); $\bullet$ $R_r$ vs. $\tau$ ($R_p = 5.0$ BL, $R_a = 10.0$ BL); $\bullet$ $R_p$ vs. $\delta$ ($R_r = 1.0$ BL, $R_a = 10.0$ BL); $\bullet$ $R_p$ vs. $\tau$ ($R_r = 1.0$ BL, $R_a = 10.0$ BL); $\bullet$ $R_a$ vs. $\delta$ ($R_r = 1.0$ BL, $R_p = 5.0$ BL); $\bullet$ $R_a$ vs. $\tau$ ($R_r = 1.0$ BL, $R_p = 5.0$ BL).

FIG. 6. Differences in motion for a (a) high-order school ($N_{b,\text{max}} = 10$, $\sigma = 15^\circ$), (b) low-order school ($N_{b,\text{max}} = 2$, $\sigma = 15^\circ$). Both simulations involved 65 steps and $R_r = 1.0$ BL, $R_p = 5.0$ BL, and $R_a = 10.0$ BL. The school orders $\delta$ and $\tau$ are shown in Fig. 5(a). Filled circles show the heads of fish, and the short lines show their bodies. Long curves and zigzags represented by solid lines show the tracks of each individual from the initial step.

decreasing the school order. Linearity exists between $\sigma$ and $\delta$ until $\sigma = 45^\circ$ [Fig. 5(a)], where the linearity disappears and the rate of increase in $\delta$ is more gradual, indicating a phase transition in school motion as $\sigma$ increases. The school does not split except when $N_{b,\text{max}} \leq 2$ or $R_r \geq 1.5$ (Table 2).

Figure 6 clearly shows the difference in the motion between schools with polarized individuals that move in a straight line (high order) and schools with individuals that frequently change their direction in a zigzagged pattern (low order).

**ESCAPING MOTION WITH A PREDATOR**

Our second simulation involved escaping motion with a predator. When a predator was added to the simulations, the simulated school exhibited seven different behavioral patterns as
shown in Fig. 7 (herd, split, hourglass, vacuole, flash expansion, flash turn, fountain effect). Our simulations show that both the variety of patterns and the frequency of occurrence of these patterns are affected by $\sigma$, $N_{b,max}$, and $c$. When we calculated the frequency, we did not include the transient interval at the beginning of the simulation, namely, the time the predator starts foraging to the time the school perceives the approaching predator and starts its escaping behavior, because this interval reflects the arbitrary initial conditions for the moving direction and position. We also did not include the interval in which the predator transfers from one split subgroup to another one, because this interval involves no escaping motion.

Figures 8(a) and (b) show the simulated effect of individual motion randomness $\sigma$ on escape patterns for high ($c = 0.7$) and low ($c = 0.3$) obedience level, respectively. When $c = 0.7$, herd is dominant and vacuole and split are the second- and third-most frequent patterns, respectively. Herd frequency shows a distinct decrease as $\sigma$ increases, and all patterns rarely occur at large $\sigma$ ($\sigma = 40^\circ$). In contrast, when $c = 0.3$, flash turn and herd are equally dominant and flash turn shows maximum occurrence at $\sigma = 40^\circ$. A distinct decrease in frequency is observed in split, but not in other patterns.

Figures 9(a) and (b) show the simulated effect of $N_{b,max}$ on escape patterns for high ($c = 0.7$) and low ($c = 0.3$) obedience level, respectively. When $c = 0.7$, herd is dominant and vacuole, split, and hourglass also appear but are less dominant than herd, similar to the effect of $\sigma$ on the escape patterns (Fig. 8). The frequency of herd peaks at $N_{b,max} = 3$, vacuole at $N_{b,max} = 5$, and hourglass at $N_{b,max} = 4$. In contrast, when $c = 0.7$, flash turn increases as $N_{b,max}$ increases, although the increase fluctuates. The frequency of herd and split peaks at $N_{b,max} = 3$.

Discussion

We used an individual-based model to examine two characteristics of schooling motion,
cruising and escaping. The model includes the three fundamental behavioral components, attraction, repulsion, and parallel-orientation, that are included in other individual-based models, too. The attraction and repulsion components are necessary for retaining the school formation and for keeping a desirable distance between individuals to accurately sense the motion of neighbors with its sensory organs (eyes or lateral line which is an organ sensitive to transitory changes in water displacement) (Partridge & Pitcher, 1980; Pitcher & Parrish, 1993). The parallel-orientation component is necessary for the school to align the moving direction of the individual with that of the school and to migrate to a new place for food or spawning. Natural schools with low polarity do not have much ability for migration (Aoki, 1980). The size of the attractive-orientation field specifies the individual sensing ability, and the sizes of the repulsive and parallel-orientation fields specify the distance between individuals. Those sizes are specified so that the NND and AD used in our model correspond to those of natural fish schools as shown in Table 2.
The use of parameter $N_{p,\text{max}}$ requires that an individual has the ability to count the number of its neighbors. A fish can sense the number of individuals in the school because it changes its relative position in the school and its distance to its neighbors according to the number of individuals in the school (Aoki, 1980; Partridge, 1980; Taneda et al., 1996). Numerous field or laboratory studies have reported that front priority is used as a directional preference of an individual when this individual senses its neighbors (Cullen et al., 1965; van Olst & Hunter, 1970; Aoki, 1980; Partridge, 1980; Partridge & Pitcher, 1980). The front priority implies that followers in the school rely on the early detection of food resources or threat by the front foragers. Distant neighbors might be blinded by near neighbors, and thus, individuals pay more attention to near neighbors than to distant ones, namely, “distance priority”. However, incorporating this priority in our model causes overestimation of the repulsion effect because near neighbors mostly exist in the repulsive-orientation field. We therefore did not include this priority in our model; however, the school size that we used in our model was small enough that an individual was not completely blinded by its near neighbors. The use of front priority seems sufficient for reproducing the motion of natural fish schools.

The decision time step $\Delta t$ is the interval at which an individual changes its speed and moving direction in response to its neighbors or a predator. Change in $\Delta t$ affects the motion of individuals because it affects the traveling distance between each decision. Short $\Delta t$ means that the individual is highly sensitive and changes its speed and moving direction at traveling only a short distance and thus makes frequent changes in school motion, whereas large $\Delta t$ means less sensitivity and thus less frequent changes in school motion. Therefore, the choice of $\Delta t$ in a model should not be subjective but observation-based. The observed $\Delta t$ for a Gnathopogon school when it was cruising without any threat was 0.5 s (Inagaki et al., 1976; Aoki, 1980). Domenici & Batty (1994) reported that response time of a herring school startled by sound stimulus was less than 0.5 s, and Partridge & Pitcher (1980) reported that of a saithe school startled by an object was less than 0.3 s. Therefore, the response time tends to shorten when the school is responding to a threat. However, the reported values by Domenici & Batty (1994) or Partridge & Pitcher (1980) are the initial response to stimulus, and thus successive response times might be delayed somehow because the stimulus is no longer present or because of individual fatigue or experience. In our model, we used the value of $\Delta t$ for a Gnathopogon school and kept it constant throughout the simulation to examine the effect of changes in the other parameters (e.g., $\sigma$, $N_{h,\text{max}}$, $R_e$, $R_p$, and $R_a$) on schooling motion, although a constant $\Delta t$ causes the model to underestimate the response of the school to a predator shortly after the school senses it. The effect of response time on cruising or escaping behavior of school is a topic of future study.

In our model, all individuals are identical, and thus they all have the same behavioral parameters. Natural schools show heterogeneity in characteristics (age, size, sex, physiological condition such as hunger or health), and Romey (1996) developed a numerical model to examine how heterogeneity in a school affects the structure and motion of the school. However, the goal of our study was to clarify the effect of specific parameters, and therefore we chose homogeneity in school. Effect of heterogeneity on cruising or escaping behavior of school is also a topic for future study.

The validity of our model was tested by varying model parameters $\sigma$, $N_{h,\text{max}}$, $R_e$, $R_p$, and $R_a$. The desirable ranges for these parameters that successfully simulate cruising motion of natural fish schools were determined (see Table 2) and thus used in our simulations on order and flexibility study as follows.

SCHOOL ORDER IN CRUISING MOTION

Using the desirable ranges for model parameters, we identified the order parameters that significantly affect the school order: the maximum number of interacting neighbors $N_{h,\text{max}}$ and the randomness of individual motion $\sigma$. The reason for their effect is that increasing the number of interacting neighbors cancels the effect of neighbors existing in the attractive or repulsive-orientation field because these neighbors are
distributed symmetrically around the individual and because the turning angles determined by these neighbors take symmetrical values that are canceled by the averaging. The effect of neighbors existing in the parallel-orientation field then tends to remain. As $N_{h,\text{max}}$ increases, the averaged value of turning angles determined by these neighbors directs the individual toward the school moving direction. This causes all individuals to align their moving direction to the moving direction of the school, thus increasing school homogeneity and order. Even if the moving direction of the school, thus increasing disorder, this process remains the same. Therefore, their sizes have relatively little effect on the school order. Results in the literature support this averaging effect (Partridge, 1980; Partridge et al., 1980; Aoki, 1980), where the nearest-neighbor distance in a natural fish school decreases when the number of individuals in the school increases. This indicates that the attraction–repulsion system of an individual may be weakened by averaging, and consequently, neighbors are allowed to come closer than the usual distance without disrupting either the aligning motion or the school order.

The randomness of individual motion affects the school order, but its effect is nonlinear. For $\sigma \leq 45^\circ$, the average angular deviation of a school $\delta$ increases linearly [Fig. 5(a)], indicating that $\delta \approx \sigma$ in that range of $\sigma$. Here, $\sigma$ represents the standard deviation in the moving direction of the individual from its deterministic moving direction [see eqn (2)]. This deterministic moving direction is similar to the average moving direction of the neighbors of an individual because of the averaging effect as mentioned above, and $\delta$ represents the standard deviation of the moving direction of the individual from the moving direction of the school. Therefore, $\delta \approx \sigma$ indicates that the average moving direction of neighbors is similar to the moving direction of the school, and thus the local characteristics of the school are relatively consistent with the global characteristics of the school. This consistency helps the school move in a straight line because when $\sigma \leq 45^\circ$, the average turning angle of the school $\tau$ is relatively low [see Fig. 5(a)]. This relation is not linear, however, when $\sigma > 45^\circ$, where the rate of increase in $\delta$ is more gradual and $\tau$ increases rapidly. This nonlinear relation means the school order collapses and randomness overwhelms the school. The value of $\delta$ asymptotically approaches an upper limit when all individuals move in completely random directions. This limit is close to $\delta_{\text{max}}$ as follows, assuming that an infinite number of individuals move in completely random directions:

$$\delta_{\text{max}} = \sqrt{\frac{1}{180} \int_{0}^{180} x^2 \, dx} = \frac{180}{\sqrt{3}} \approx 104 \text{ (deg)}$$

This kind of phase transition is similar to that reported by Niwa (1994, 1996) and Vicsek et al. (1995), and indicates that the order–disorder phase transition in the grouping motion tends to occur by balancing the tendency of an individual towards parallel orientation and that towards motion randomness.

**FLEXIBILITY IN ESCAPING BEHAVIOR**

We examined school flexibility by using simulations to determine the frequency of occurrence of escape patterns when a predator attacks a school. The resemblance of simulated patterns to observed patterns is strong evidence of validity of our model. However, our simulations failed to show the frequently observed increase in compactness that natural fish schools exhibit, where individuals form a tighter and more polarized school as a response to an attacking predator (Hamilton, 1971; Nøttestad & Axelsen, 1999; Domenici et al., 2000). The reaction of compactness is caused by the individuals seeking shelter in the center of the school (Hamilton, 1971; Nøttestad & Axelsen, 1999). The reason our model failed to show this compactness is that the model did not include vigilance or the fear response to seek shelter, but did include reflexive behavior to turn in the direction opposite that of the predator. However, as Domenici et al. (2000) reported, the increasing compactness of a school is a response of a stationary school; a maneuvering school does not show this compaction because each individual needs to have sufficient space for turns and maneuvers without collisions. Our aim is to understand the flexibility or the
maneuverability of a school; our results correspond to the latter.

When individuals in a school have a strong tendency to obey their neighbors’ motion, the frequency of escape patterns tends to decrease as $\sigma$ increases [Fig. 8(a)]. This means that low randomness of individual motion is required for escape patterns to form. The individual motion is interconnected during escaping when randomness of individual motion is low. This interconnection of individual motion is required for the school to form into escape patterns. The increase in randomness of individual motion reduces this interconnection, thus all individuals move differently and then no patterns can be formed. The frequency of pattern occurrence peaks when the maximum number of interacting neighbors $N_{b,\text{max}}$ increases [Fig. 9(a)]. This peak is also related to the interconnection of individual motion. When the number of interacting neighbors is small, interconnection is small because of limited information transmitted between individuals, thus decreasing the frequency of pattern occurrence. In contrast, when the number of interacting neighbors is large, all individuals tend to behave similarly because of high homogenization of the school. This tendency suppresses change in the school shape, thus decreasing the frequency of pattern occurrence. This indicates that an optimal number of interacting neighbors exists.

This optimal number is around $N_{b,\text{max}} = 3$, although it tends to shift to a slightly larger value ($N_{b,\text{max}} = 4$ or 5) for hourglass and vacuole when $c$ is high. In addition, school order is established when $N_{b,\text{max}}$ is relatively small ($= 3$ or 4) because $\delta$ and $\tau$ significantly decrease as $N_{b,\text{max}}$ increases from 1 to 3 or 4, and when $N_{b,\text{max}} \geq 4$, they remain relatively constant [Fig. 5(a)], thus indicating that both school flexibility and order are established when the $N_{b,\text{max}}$ is relatively small ($\geq 3$). This is important because fish in a natural school have larger sensitivity to changes in the number of individuals in a school when the number of individuals in a school is small. Partridge (1980) and Taneda et al. (1996) reported that in a minnow or medaka (Oryzias latipes) school, an individual changes its schooling status, such as relative position in the school or its distance to its neighbors; this change is most conspicuous when the number of individuals in the school increases from two, and becomes barely noticeable when the number of individuals becomes large ($> 3$). This indicates that the characteristic of sensitivity of natural schooling fish corresponds to the result that the small value of number of interacting neighbors establishes both variability and order in schooling motion. If a fish has higher ability of sensing so that it can control the number of interacting neighbors to be large when cruising and relatively small when escaping, it can achieve its optimal performance. However, confirmation that a fish can control its number of interacting neighbors according to the surrounding conditions needs clarification. This is a subject for future research.

The randomness of individual motion must be small for both school order and flexibility. A fish in a school can delay its fright response to a threat to enhance either its ability of assessing the nature of the threat to reduce the costly false alarms (Godin & Morgan, 1985) or its directionality to reduce collisions with its neighbors (Domenici & Batty, 1997). In contrast, a solitary fish is not able to do this because of its higher vigilance than that of a fish in a school. This indicates that a fish has the ability to reduce motion errors when it is in a school, thus contributing to a reduction in the randomness of motion.

Both the ability to reduce motion randomness and the high sensitivity to a small number of interacting neighbors are specialized characteristics for fish in a school, and thus, a schooling fish has achieved them in its evolutionary history.

In conclusion, using a simple individual-based model, we examined the sensitivity of school order and flexibility to changes in three individual-motion parameters: the randomness of individual motion, the number of interacting neighbors, and the size of reaction field. The simulation results revealed this sensitivity and the existence of an optimum relation between motion parameters and the school order or flexibility. The probability that a schooling fish utilizes this optimum to achieve high order and flexibility was evident in the simulation results, indicating the evolutionary specialization of schooling fish. Further study is needed on heterogeneity in a school, response time to a neighbor’s motion, and the ability
of a fish to control its number of interacting neighbors.

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REFERENCES


**APPENDIX A**

**Nomenclature**

*A* constant for gamma function

*AD* average angular deviation in the moving direction of an individual from the moving direction of the school based on the Huth & Wissel’s (1992) definition

*a*<sub>i</sub> vector whose direction is the deterministic moving direction of the *i*-th individual at the new time step

*a*<sub>i,j</sub> unit vector determined by the interaction of the *i*-th individual with the *j*-th individual

*a*<sub>i,school</sub> unit vector determined by averaging the values of *a*<sub>i,j</sub>

*a*<sub>i,predator</sub> unit vector determined by the interaction of the *i*-th individual with the predator

*BL* body length of an individual fish in school

*c* obedience level of an individual to its neighbors

*D* initial distance of the predator from the center of the square starting area for the school

*K* constant for gamma function

*L* side length of the square starting area for the school

*min*(a, b) function representing the minimum value of *a* or *b*

*N* number of individuals in a school

*N*<sub>b</sub> number of neighboring individuals found in a reaction field

*N*<sub>b,max</sub> maximum number of neighboring individuals that can be involved in mutual interaction

*N*<sub>b,max,predator</sub> maximum number of individuals that can be perceived by a predator

*NND* average distance to an individual’s nearest neighbor

*p*(v) probability distribution function of speed

*p*(ϕ<sub>i</sub>) probability distribution function of the actual turning angle ϕ<sub>i</sub>(t)

*q*<sub>i</sub>(t) unit vector that has the same direction of *v*<sub>i</sub>(t)

*q*<sub>i</sub>(t) unit vector for the moving direction of the school

*R*<sub>a</sub> radius of the attractive-orientation field of an individual in the school

*R*<sub>a,predator</sub> radius of the attractive-orientation field of a predator

*random*(p(x)), *random*(a, b) function representing the creation of a random number by using a probability distribution function *p*(x), or between *a* and *b*, respectively

*R*<sub>p</sub> radius of parallel-orientation field of individuals in the school

*R*<sub>r</sub> radius of repulsive-orientation field of individuals in the school

*S*<sub>p</sub> speed ratio of the predator to an individual in the school

*T* total time step

*t* time

*v*<sub>i</sub>(t) velocity vector of the *i*-th individual at time *t*

*v*<sub>i</sub>(t) (= |v<sub>i</sub>(t)|) moving speed of the *i*-th individual at time *t*

*v*<sub>predator</sub> (t) moving speed of the predator at time *t*
\( \mathbf{x}_i(t) \) position vector of the \( i \)-th individual at time \( t \)
\( \alpha_i \) deterministic turning angle of the \( i \)-th individual
\( \alpha_{i,j} \) deterministic turning angle of the \( i \)-th individual determined by the \( j \)-th individual
deterministic turning angle of the \( i \)-th individual determined by the predator
\( \beta_{i,j} \) direction of the \( j \)-th individual from the moving direction of the \( i \)-th individual
\( \beta_{i,\text{predator}} \) direction of the predator from the moving direction of the \( i \)-th individual
\( \delta \) average angular deviation of school
\( \Delta t \) decision step size at which an individual changes its speed and moving direction in response to its neighbors or a predator
\( \phi_i(t) \) actual turning angle of the \( i \)-th individual
\( \Gamma(K) \) gamma function
\( \theta_i(t) \) advancing direction of the \( i \)-th individual from the \( X \)-axis at time \( t \)
\( \sigma \) standard deviation of the normal distribution of the probability distribution function of the individuals in the school
\( \sigma_{\text{predator}} \) standard deviation of the normal distribution of the probability distribution function of a predator
\( \tau \) average turning angle of school
\( \omega \) angle from the moving direction of an individual to the border of its blind region
\( \angle (l, m) \) angle of vector \( l \) measured from vector \( m \)