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Effectiveness of Allelomimesis of Individuals in Dynamical Response of Fish School to Emergent Affairs

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A simulation model of collective motion of a fish group was presented to investigate the role of allelomimesis of fish individual in emergence of dynamically stable schooling behaviors. The present model was formulated based on the individual decision-making approach. Allelomimesis, doing what your neighbors do, was considered as the essential tactic of decision-making by which coherent collective behaviors such as schooling are generated. Besides the allelomimetic actions of individuals, the collision avoidance actions are also another essential tactic. As a measure of the tactic of decision-making, the ratio of contributions of allelomimetic and avoidance actions is adopted. It was investigated changing systematically value of the contribution ratio how and to what extent fish individuals mimic their neighbors so that the fish group shows the schooling behaviors. It was shown that the schooling behaviors generated using the optimal values of the ratio correspond to a self-organized critical state. The main purpose of the present modeling is to investigate whether the tactic of individual decision-making suited to generate good schooling behaviors works well also in maintaining dynamical stability of the fish school under emergent affairs. Emergent splitting of a school into two groups and flash expansion of a school were used as the emergent affairs. The extent of dynamical stability of a school was evaluated using two kinds of measures, the recovery time period and the critical distance of splitting or expansion. It was found that the tactic suitable for schooling generates the dynamically stable response of the school to emergent affairs.

1. Introduction

Groups of some kinds of fish show a characteristic social aggregation, school[1], although the fish group is not controlled by leaders. Schooling behavior of fish is a typical example of self-organized grouping in which numerous fish individuals perform a unified collective movement with parallel orientation.

Many researchers have actively investigated the schooling mechanism by which the fish group maintains collective motions being stable dynamically. The experimental studies[1)~3)] showed that the mutual attraction and parallel orientation between fishes contribute mainly to school formation. It was also shown that the most important senses of schooling are the eyes and the lateral line[4)]. However, it is not clear yet how the diverse collective behaviors are organized under various situations, because observation of the behaviors could be made in only several limiting conditions. Therefore, many theoretical and modeling studies[5)~18)] have been made in order to understand the mechanism by which the schooling behaviors are generated and modified as a function of individual activity. The studies have shown by what interfish interaction the coherent schooling behaviors are generated in the usual homogeneous spaces.

Those models of fish school are classified roughly into two types, Newtonian dynamics model and individual decision-making model. In the Newtonian dynamics models[5)~11)], each fish individual is treated as a solid sphere and various interactions between the spheres are considered so that the essential actions of individuals such as mutual attraction and parallel orientation are generated in the simulation of collective motions. However, the interactions considered in those models are qualitatively different from the interactions between real fishes, because any fish is scarcely affected by neighboring fishes which the fish does not watch.

In the individual decision-making models[12)~16)], each fish decides its new direction of motion based on the information about positions and moving directions of neighboring

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fish which can be known through its eyes. The models [12)~16)] are somewhat different from each other in the method by which each fish decides its moving direction based on the visual information.

We present here a model of fish groups, in which each fish decides its new moving direction based on the information about its surroundings obtained through both its eyes and lateral lines. The visual information is used in the present model only for the allelomimetic action which consists of approaching a neighbor and moving in parallel with a neighbor, while the lateral line information about change in water pressure is used only for the avoidance of collision with neighbors. In the previous models [12)~16)], each fish makes every action based on the visual information.

We investigate for what value of the contribution ratio of visual and lateral line information the collective motion of the fish group becomes a coherent schooling behavior, by changing the ratio systematically.

All of the previous models [5)~16)] have succeeded in reproducing good schooling behaviors in homogeneous water spaces with or without fence. However, it is not yet investigated in detail whether those models work effectively in responses of fish schools to emergent affairs such as appearance of rocks and attack of predators. It has been observed clearly [3),4),17)] that the large populations of fish individuals in a school can change systematically their collective behavior under the emergent affairs, although there is no leader and every fish can know only about local situations around itself. The fish group appears to make a collective decision in a self-organizing manner under emergent situations as if the group has a single intelligence as a single animal does.

In the present paper, the main purpose in presenting our model of fish school is to solve the problem whether the tactic of individuals, which decide their instantaneous actions in their dynamically stable response behaviors under emergent affairs, is the same as the tactic adopted in their schooling behaviors in homogeneous spaces. We consider allelomimesis, that is, doing what your neighbors do, as the essential tactic based on which individuals decide their actions. In the situation where relatedness to, or knowledge of, neighbors may be minimal but the group is maintained through collective individual responses, a simple mechanism such as allelomimesis may play an essential role to prevent structural breakdown of the group [18),19)]. This allelomimetic action is made based on the visual information. The collision avoidance action is considered as the other essential tactic and made based on the lateral line information. As a measure of the tactic to decide the next action of fish individual, we adopt the ratio of contributions of visual and lateral line information to the decision-making.

First, we investigated how fish individuals mimic their neighbor, that is, to what neighbor the fish pays attention and how the fish follows the neighbor's action, so that the fish group generates coherent schooling behaviors. Second, we investigate to what extent the allelomimetic actions suitable for generating the schooling behaviors are effective to generate the collective response being dynamically stable to emergent affairs.

The format of the present paper is as follows. In Section 2, we explain briefly various models of fish school presented so far in order to describe the relation of our model to the previous models. In Section 3, we describe our model. In Section 4, we determine the contribution ratio of the allelomimetic and avoidance actions which is suitable for schooling behaviors, based on the results of various simulations. In Section 5, we investigate how effectively the individual allelomimetic actions work for the group to make the dynamically stable responses to sudden splitting and flash expansion of the school. Section 6 is devoted to concluding remarks on the present model.

2. Previous Models of Fish School

Many researchers have reported simulation models of the collective behaviors of fish group. Each of them has clarified one or two of various important characteristics of the relation between interfish interactions and coherent collective motions, based on the simulation of collective motions using their models. Each model has been formulated by using one of the two types of approaches, Newtonian dynamics approach and individual decision-making approach.

2.1 Newtonian Dynamics Approach

In the models formulated based on Newtonian dynamics approach, each fish is treated as a small solid sphere and the motion of each sphere in a fish group is determined by Newtonian equations of motion. The essential differences among those models come from the differences in the situation which the fish group has. It has been shown in those models what forces are essential for a collective motion to be generated in the relevant situation.

Inagaki, Sakamoto, and Kuroki 5) investigated the change of form of fish school varying the combination of intensity of the forces consisting of mutual attractive or repulsive force, mean swimming force, and random force. They showed that the fish group maintains a schooling behavior when the intensities of the mutual force and the random force are balanced.

Matuda and Sannomiya 6) presented the mathematical model in order to investigate the problems of fish behavior in a water tank in relation to fishing gear. They took account of propulsive, interactive, schooling, repulsive, directional, and random forces. They showed that the moving patterns of fishes obtained by the simulations are similar to actual behaviors of fish school and the model is suitable for investigating fish behavior in relation to fishing gears. Matsuda and Sannomiya 7) modified their model 6) so that model can simulate the fish behaviors in the water tanks including various types of traps. They obtained a good agreement with respect to the rates of entering, escaping, and remaining of a 5 fish group between the water tank experiment and the corresponding computer simulation.

Okubo 8) explained in detail the theoretical studies of animal grouping and presented a model of two-fish school in which frictional, harmonic, and swimming forces are considered. He described the essential dynamical properties of two fish group.

Niwa 9) treated individual fishes as gas molecules and took into account locomotor force, attraction force, array force, and random force. He derived a non-linear Langevin equation describing self-organized formation of fish schools with practical approximation methods. Using the model, he studied how polarized patterns of schooling fish group arise spontaneously on the basis of elemental properties of individual fish. He showed that fish schools are governed by synergetic, which represent the principal feature of polarization-no polarization transitions. Niwa 11) derived two equations for the school mean velocity and the variance of swimming velocity based on his model 9). Using these equations, he investigated the transient process in which the fish group approaches the stationary polarized schooling.

Tian and Sannomiya 10) focused their attention on the whole of a fish school rather than the individual motions, and described the school motion using motions of its gravity center and four individuals locating at the boundary of the school. They showed that the model is effective for estimating the behavior of fish school with many individuals.

2.2 Individual Decision-making Approach

In the models 12)~16) formulated by using individual decision-making approach, each fish decides its new direction of motion based on the information about positions and moving directions of neighboring fishes. The main differences among those models arise from how each fish decides its moving direction.

Aoki 12) assumed based on the observed results 1) that the speed and direction of movement are mutually independent and determined for each individual by characteristic probability distributions. The mean and variance of the moving direction are defined in relation to the location and heading of neighbors in the fish's own field of view. The fish avoids, moves in parallel with, and approaches the neighbor to which the fish attends, when the distance between the fish and the neighbor is close, appropriate, and far, respectively. Then, the moving direction is determined from the weighted sum of the influence of each neighbor, where the closer the neighbor is to the fish, the larger the influence becomes. Aoki 12) showed using his model that schooling behaviors could occur despite each individual lacking knowledge of movement of the entire school, and in the absence of a consistent leader.

Huth and Wissel 13),14) improved Aoki's model by modifying the response rule according to which the fish responds to its neighbors. They showed that it is essential for school formation how a fish mixes the influences of its neighbors. If a fish averages arithmetically the influences, the model fish group shows a typical schooling behavior. On the other hand, if a fish responds only to a single neighbor, the model creates a confused fish group.

Reuter and Breckling 15) changed the response rule in Aoki's model for the rule that the influence of all visible neighbors is weighted reciprocal to their distance. They showed that their model performs the main characteristics of real fish school, regardless of how many fish the school consists of.

In all of the previous models [12)~15)], the rule determining the new moving direction of individual is common to every fish. However, Romey [16)] presented the model to address the issue of how individual differences may influence group stratification and group trajectory. They described the model, but the effect of individual differences has not been reported yet.

3. The Present Model of Fish School

3.1 Objective of Our Study of Fish School

Aggregation of fishes has been viewed as an evolutionarily advantageous state [3),18)], in which members derive the benefits of protection, mate choice, and centralized information, balanced by the costs of limiting resources. In order to clarify how fish aggregations generate the benefit of protection, we are concerned with the functional role of schooling of fish groups in response behavior of the groups induced by attacks of predators under various situations. However, attacks of a predator have not been taken into account in all of the previous models [5)~16)].

As a first step towards our purpose, we have made a preliminary model [20)] based on the individual decision making approach. The model [20)] does not include any predator, but may be extended straightforwardly so as to treat predator attacks. In fact, we made the extension in the next model [21)] and investigated the response behaviors of fish school induced by attacking of a single predator. Each fish in these preliminary models decides its new moving direction based on the information about positions and moving directions of neighboring fishes, which may be obtained through its eyes and lateral lines. The method by which each fish determines its moving direction based on the visual information is essentially the same as the methods used by Aoki [12)] and Huth and Wissel [13)]. Each fish in our preliminary models knows the average direction of neighbor's motion through its lateral lines and tends to head in the average direction.

These models [20),21)] reproduced well the schooling behaviors in case of no predator and showed the dynamically stable responses to emergent splitting and flash expansion of the school in the cases where the magnitudes of splitting and expansion are not large. However, we could not obtain any clear result indicating the functional role of fish schooling which is beneficial to evasion of predator's attacks.

Therefore, we modified our preliminary models [20),21)] as follows. The visual information about the position and moving direction of neighbors is used only for the allelomimetic action of the relevant fish and the lateral line information [4)] about the variation in water pressure around the relevant fish is used only for the collision avoidance. The contribution ratio of the visual and lateral line information is changed systematically. In our preliminary models, the visual information was used also for the collision avoidance, and the contribution ratio was fixed to a value determined somewhat arbitrarily.

The preliminary form [22)] of the present model has been presented in International Conference on Neural Information Processing in 2000. In the present paper, we describe in detail the final form of the model in case of no predator. In order to investigate whether the model school maintains collective motions under attacking of predator, we investigate using the model to what extent the allelomimetic actions suitable for generating the schooling behaviors are effective to generate the collective response being dynamically stable to emergent affairs such as emergent splitting and flash expansion of the school. We applied preliminarily the present model to the case where a single predator attacks the school [22)] and obtained some positive results. In a forthcoming paper, we will describe in detail the extension of the model to the case where multiple predators as well as a single one attack the school.

The present model is described in detail in Sections 3.2–3.7.

3.2 Tactics of Individual Decision-making in the Present Model

Individual fishes have to decide their moving direction at every moment so as to prevent structural breakdown of the group, although they do not know the movement of entire group and there exists no consistent leader. We consider allelomimesis [18),19)] as the essential tactic of decision-making for individuals to generate collective movements on the condition that every individual knows only about a local situation around itself.

It has been shown based on the experimental observations [1)~3)] and the simulations of fish schools [5)~16)] that the essential action of individual fish for generation of schooling behavior consists of avoiding collision with neighbors, moving in parallel with neighbors, and approaching neighbors.

We consider that the parallel movement and the approach are allelomimetic actions, because the fish moving in parallel with a neighbor is mimicking the motion of the neighbor and the fish approaching a neighbor is going to mimic the neighbor. Besides the allelomimetic actions, we need to consider the collision avoidance as one of the essential decision-making.

In the present model, we assumed that the allelomimetic actions are made based on the visual information about the local situation and the avoidance actions are made based on the information about the variation in water pressure around the relevant fish. Each fish uses its eyes and its lateral lines simultaneously to make its decision of moving direction [3),4)], where the lateral lines sense broadly the approaching of neighbors through the increase of water pressure around the relevant fish. Therefore, the allelomimetic action and the avoidance actions may be made simultaneously.

We described how the moving directions of individuals are determined by the allelomimetic actions and the avoidance actions, respectively, in Sections 3.3 and 3.4.

3.3 Role of Allelomimesis in Decision-making

3.3.1 Areas for Classification of Influence of Neighbors

The influence of a neighbor on the fish's action changes depending on neighbor's position relative to the fish. According to Aoki's model [12)], we classified the space into four kinds of areas as shown in **Fig. 1**, where we consider fish's motions in a two dimensional space without boundary. The four areas are named avoidance area, parallel orientation area, attraction area, and invisible area [12),13)], respectively. The ranges of the areas are defined following Aoki [12)] as

avoidance area:

$0.0\,\mathrm{BL} < r_{ij} \leq 0.5\,\mathrm{BL}$,

parallel orientation area:

$0.5\,\mathrm{BL} < r_{ij} \leq 2.0\,\mathrm{BL}$, and not in the dead angle area,

attraction area:

$2.0\,\mathrm{BL} < r_{ij} \leq 5.0\,\mathrm{BL}$, and not in the dead angle area,

invisible area:

$r_{ij} > 5.0\,\mathrm{BL}$,

where r_{ij} is the distance from the relevant fish i to its neighbor fish j, BL is the length of fish's body, and the dead angle is 60°.

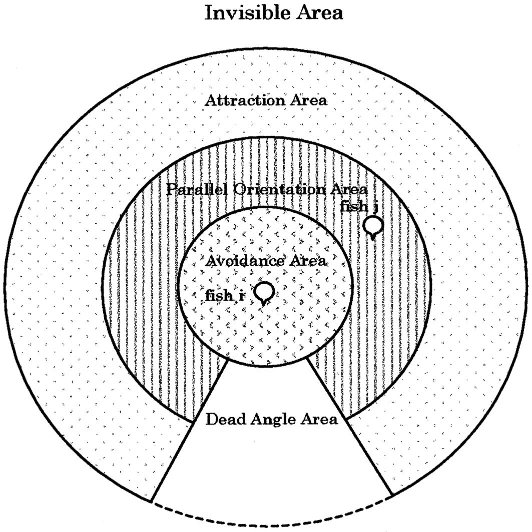

Fig. 1 Four kinds of areas around fish i. The interaction of fish i with neighbor fish j is changed depending on in which area fish j is.

3.3.2 Allelomimetic Actions

When neighboring fishes are in the parallel orientation area and/or in the attraction area, the relevant fish i makes an allelomimetic action as follows.

(1) Fish i pays attention instantaneously to one of the neighbors in both the areas, and the neighbor j is chosen as follows. Fish i chooses one direction θ_0 randomly in its view $-130° \leq \theta_0 \leq 130°$ and looks for the nearest neighbor j in the region of both the areas between $\theta_0 - 20°$ and $\theta_0 + 20°$. If there is no fish in the region, fish i tries to choose another direction between $-130°$ and $130°$.

(2) When the neighbor j is in the parallel orientation area, fish i turns so that it moves in the same direction as fish j. The new moving direction ${\beta_i}^{AL}(t + \Delta t)$ which the fish i decides based on its allelomimetic action at time t is

$$\beta_i^{AL}(t + \Delta t) = \alpha_j(t), \qquad (1)$$

where $\alpha_j(t)$ is the moving direction of fish j at time t. Each direction is represented by an angle between the x-axis and the direction, where the direction of x-axis is fixed in the water space.

(3) When the neighbor j is in the attraction area, fish i moves in the direction of fish j to approach fish j. Then, the moving direction ${\beta_i}^{AL}(t + \Delta t)$ of fish i is given by

$$\cos {\beta_i}^{AL}(t+\Delta t) = \frac{x_j(t)-x_i(t)}{\sqrt{(x_j(t)-x_i(t))^2+(y_j(t)-y_i(t))^2}}, \quad (2)$$

where $x_k(t)$ and $y_k(t)(k = i, j)$ are x and y coordinates, respectively, of the position of fish k at time t.

(4) When there is no fish in both the areas, fish i needs to search fishes whose action fish i mimics. Then, the moving direction ${\beta_i}^{AL}(t + \Delta t)$ of fish i is given by

$${\beta_i}^{AL}(t+\Delta t) = \alpha_i(t) + \theta_{SR}(t), \quad (3)$$

where $\theta_{SR}(t)$ is a random number between $-45°$ and $45°$. This means that fish i turns its moving direction away randomly from its present moving direction $\alpha_i(t)$.

3.4 Role of Collision Avoidance in Decision-making

Each fish needs to decide its new moving direction so as to avoid colliding with fishes in the avoidance area based on the information about the relative position and movement of the neighbors, which is obtained through its own lateral lines.

The new moving direction ${\beta_i}^{AV}(t + \Delta t)$ of fish i is given by

$${\beta_i}^{AV}(t+\Delta t) = \frac{1}{N_{av}} \sum_{j=1}^{N_{av}} \theta_{ij}(t) + 180°, \quad (4)$$

where N_{av} is the number of neighbors in the avoidance area and $\theta_{ij}(t)$ is the relative direction of fish j at the position of fish i at time t. We assumed that every fish can know the average relative position of fishes in its avoidance area through its lateral lines.

When there is no neighbor in the avoidance area, that is, $N_{av} = 0$, the fish does not need to change its moving direction. Therefore, the new moving direction ${\beta_i}^{AV}(t+\Delta t)$ decided based on the lateral line information is

$${\beta_i}^{AV}(t+\Delta t) = \alpha_i(t). \quad (5)$$

3.5 Determination of the New Position of Individual Fish

The new position $(x_i(t + \Delta t), y_i(t + \Delta t))$ of fish i being on $(x_i(t), y_i(t))$ at time t after one time step Δt is determined by

$$x_i(t+\Delta t) = x_i(t) + \Delta t \cdot v_i(t+\Delta t) \cos\alpha_i(t+\Delta t), \quad (6)$$

$$y_i(t+\Delta t) = y_i(t) + \Delta t \cdot v_i(t+\Delta t) \sin\alpha_i(t+\Delta t), \quad (7)$$

where $v_i(t + \Delta t)$ and $\alpha_i(t + \Delta t)$ are the magnitude(speed) and direction of the velocity, respectively, of fish i at time $t + \Delta t$.

Following Aoki[12)], the speed $v_i(t + \Delta t)$ and the direction $\alpha_i(t + \Delta t)$ are determined mutually independently. The rule of determination of $\alpha_i(t+\Delta t)$ based on the local situation around fish i at time t is described in Section 3.6. The rule of determination of $v_i(t + \Delta t)$ is described in Section 3.7.

In the present model, every individual makes a decision for its new heading at each time step. We estimated that one time step corresponds to 0.1 sec. Aoki[12)] used 0.5 sec for one time step in his model. However, this value seems to be rather too large to describe the detailed motions of individuals in a group because of the following observed results. Shaw[23)] reported that every individual in a group of herrings finishes changing its moving direction within 0.5 sec. Aoki[1)] reported that although there is a lag time of 0.5 ∼ 1.0 sec between the initiator of the turning action in the Trachurus school and the followers at the rear of school, it is less than 0.5 sec between the initiator and its neighbor. Because every individual can affect directly only its neighbors in the present model, it seems reasonable that the individual decision-making is made every 0.1 sec.

3.6 Determination Rule of Moving Direction

Fish i determines its direction $\alpha_i(t + \Delta t)$ of new movement taking simultaneously account of both the directions ${\beta_i}^{AL}(t + \Delta t)$ and ${\beta_i}^{AV}(t+\Delta t)$ convenient for allelomimetic action and collision avoidance, respectively. Then, $\alpha_i(t + \Delta t)$ is represented as

$$\begin{aligned} \alpha_i(t+\Delta t) &= \alpha_i(t) \\ &+ \gamma_{AL} \cdot D_{ev}(\beta_i^{AL}(t+\Delta t) - \alpha_i(t)) \\ &+ \gamma_{AV} \cdot D_{ev}(\beta_i^{AV}(t+\Delta t) - \alpha_i(t)), \end{aligned} \quad (8)$$

where the function $D_{ev}(\beta - \alpha_i(t))$ indicates the deviation of direction β from the original moving direction $\alpha_i(t)$ of fish i and $D_{ev}(x)$ takes x for $|\ x\ | \leq 180°$ and $x \pm 360°$ for $|\ x\ | \geq 180°$. In Eq. (8), γ_{AL} and γ_{AV} are constant values and represent the degree of contribution of allelomimetic action and collision avoidance, respectively, to the decision of new moving direction, and $\gamma_{AL} + \gamma_{AV} = 1$.

The values of γ_{AL} and γ_{AV} seem to be determined based on the fish's evaluation about how much important the allelomimetic action and the collision avoidance are for its own future action in the present situation. Therefore, the values may be generally different for different individuals and in different situations. However, we assumed in the present paper as most previous models did that all fishes have identical behavioral characteristics, that is, the single values of γ_{AL} and γ_{AV} are used for all fishes. Then, in order to investigate the dependence of allelomimesis rate γ_{AL} on the situations, we investigated how the dynamical properties of a fish group are changed with the values of γ_{AL} and γ_{AV} in various situations. Based on the results, we consider about whether the values appropriate for a fish group to generate coherent schooling behaviors produce dynamically stable responses of the group to emergent affairs.

3.7 Determination Rule of Swimming Speed

According to Aoki's model[12], the new speed $v_i(t+\Delta t)$ of fish i is chosen independently of the other fish. The value of $v_i(t+\Delta t)$ is calculated by chance with the typical distribution given by the experiments[1], the Gamma distribution[12], which is given by

$$P_{sp}(V) = \frac{A^K}{\Gamma(K)} \exp(-AV) V^{k-1}, \qquad (9)$$

where V is the speed measured in the unit of BL/sec, $K = 4$, $A = 3.3$, and $\Gamma(K)$ is the Gamma function. When the distance moved is expressed in the unit of body length BL, the average speed V_{av} of each fish becomes 1.2 BL/sec.

4. Role of Allelomimesis in Emergence of Schooling Behaviors

4.1 Purpose and Way of Achieving It

In order to investigate how individual decisions, which are made based on allelomimesis and avoidance, influence the collective behaviors and dynamics of the group of individuals, we made simulations of schooling behaviors using the present model in cases of various rates of allelomimesis contribution.

How individuals make their decisions is determined in the present model by giving the value of γ_{AL} in Eq. (8), where $\gamma_{AV} = 1 - \gamma_{AL}$.

In Section 4.2, we describe characteristic quantities by which the properties of collective motions of fish groups are represented. In Sections 4.3 and 4.4, we present the calculated results showing how the characteristic quantities are changed with the value of γ_{AL} in the various situations.

4.2 Characteristic Quantities Indicating Properties of Schooling Behaviors

4.2.1 Polarization $\eta_P(t)$

Schools are groups of fish engaging in cohesive movements with parallel orientation[1)~3)]. One of the most conspicuous properties of schools is the polarization of collective motion, that is, the parallel heading of individuals. The instantaneous polarization $\eta_P(t)$ is defined according to Huth and Wissel[13] as

$$\eta_P(t) = \frac{1}{N_{fish}} \sum_{i=1}^{N_{fish}} \angle(\boldsymbol{v_i^o}(t), \boldsymbol{v_{av}}(t)), \qquad (10)$$

$$\boldsymbol{v_{av}}(t) = \sum_{i=1}^{N_{fish}} \boldsymbol{v_i^o}(t), \qquad (11)$$

where N_{fish} is the number of fish in the school, $\boldsymbol{v_i^o}(\mathrm{t})$ is the orientation unit vector of fish i at time t, $\boldsymbol{v_{av}}(\mathrm{t})$ is the mean swimming direction of the fish group, and $\angle(\mathbf{a}, \mathbf{b})$ means the angle between $\mathbf{a}$ and $\mathbf{b}$.

We use the average of $\eta_P(t)$ over a certain time range T as a measure of the parallel orientation in the school.

Furthermore, the temporal fluctuation of $\eta_P(t)$ includes valuable information on the internal dynamics of the school. In order to analyze the fluctuation[24] we use the power spectrum $S_P(\omega)$ of $\eta_P(t)$ obtained by

$$S_P(\omega) = \frac{1}{T} \left| \int_0^T e^{i\omega t} \eta_P(t) dt \right|^2, \qquad (12)$$

where ω is an angular frequency.

4.2.2 Nearest Neighbor Distance $\eta_{NND}(t)$

While individuals approach and follow members in the school, they maintain a certain personal space around themselves[1)~3)]. This nature of fish generates a regular spatial arrangement within the school. In order to measure the personal space, we use the average nearest neighbor distance $\eta_{NND}(t)$ defined as

$$\eta_{NND}(t) = \frac{1}{N_{fish}} \sum_{i=1}^{N_{fish}} r_{i,nn}(t), \qquad (13)$$

where $r_{i,nn}(t)$ is the distance from fish i to its nearest neighbor at time t.

4.2.3 Expanse of Fish School $\eta_{EX}(t)$

The spatial expanse of whole fish school is one of the essential quantities required for the analysis of spatial arrangement of individuals in an infinitely spreading water space. The expanse $\eta_{EX}(t)$ is defined following Huth and Wissel[13] as the average of the distances quadratic from every fish to the fish group's center of mass,

$$\eta_{EX}(t) = \frac{1}{N_{fish}} \sum_{i=1}^{N_{fish}} \sqrt{(x_i(t)-x_{av}(t))^2+(y_i(t)-y_{av}(t))^2}, \quad (14)$$

where $x_{av}(t)$ and $y_{av}(t)$ are the averages of $x_i(t)$ and $y_i(t)$ $(i = 1 \sim N_{fish})$, respectively. This quantity is used as a measure of the compactness of the school.

We use the time average of $\eta_{EX}(t)$ to evaluate the properties of schooling behaviors.

4.2.4 Frequency of Collision η_{CF}

The number of collisions of fish with neighbors during a certain time period is a good measure to evaluate how successfully fish makes its avoidance in the school. We treat each fish as a circle of which diameter is 0.3 BL.When the distance between two fishes becomes less than 0.3 BL, the two fishes are considered to collide with each other.

We use the average, η_{CF}, of $N_{coll}(i,t)$ over fish and time as a measure of collision frequency in the schooling behavior,

$$\eta_{CF} = \frac{1}{N_{fish}} \sum_{i=1}^{N_{fish}} \frac{1}{T} \int_0^T N_{coll}(i,t)dt, \quad (15)$$

where $N_{coll}(i,t)$ is the number of neighbors of which distance from fish i is less than 0.3 BL at time t.

4.3 Effect of Allelomimesis on Collective Motion

In order to investigate the effect of allelomimesis on collective motions of a fish group, we calculated the characteristic quantities described in Section 4.2 with various values of γ_{AL}.

4.3.1 Values of γ_{AL} Generating Collective Motions

First, we investigated the role of allelomimetic action of individuals in forming an aggregate of individuals. We made the following simulations using the present model. We changed the value of γ_{AL} in the range between 0.0 and 1.0, and observed whether the fish group splits into more than two subgroups or not.

The result is shown in **Fig. 2**, where the probability that the fish group gathered at $t = 0$ is not split until $t = 5,000$ time step, is represented as a function of γ_{AL} for groups with different number of individuals. The every group maintains schooling behaviors in the probability more than 90% when the allelomimesis rate γ_{AL} of individual becomes more than 0.3. As the value of γ_{AL} becomes smaller, the fish groups become easy to split.

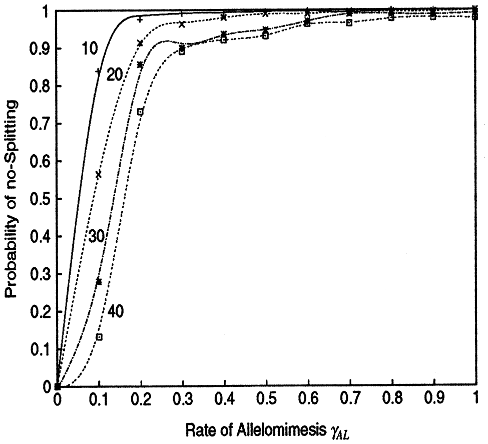

Fig. 2 Dependence of the probability of making a unified fish group on the allelomimesis rate γ_{AL}. The probability was obtained by making 100 simulations and counting the number of event that a fish group gathered at $t = 0$ is not split until $t = 5,000$. Figures attached to the curves denote the number of fish in the group.

The probability of no splitting decreases with increasing the number N_{fish} of individuals, but the dependence of the probability on N_{fish} becomes weaker as N_{fish} is increased as seen in Fig. 2.

4.3.2 Temporal Variation of the Characteristic Quantities in a Typical Schooling Behavior

In order to see the schooling behaviors generated by the present model, we showed a snapshot of schooling behavior in **Fig. 3**, and temporal variations of polarization $\eta_P(t)$, nearest neighbor distance $\eta_{NND}(t)$ and expanse $\eta_{EX}(t)$ of the school in **Fig. 4**, where the number of fish $N_{fish} = 30$ and the value of γ_{AL} is 0.7. It will be shown later that the model generates a good schooling behavior for this value of γ_{AL}.

It is seen in Fig. 4 that three quantities, $\eta_P(t)$, $\eta_{NND}(t)$, and $\eta_{EX}(t)$, fluctuate almost randomly as time proceeds. This fluctuation comes mainly from the fact that fishes in a temporal top group change their headings capriciously and the fishes following the top group need some time lag to adjust their headings to a new moving direction.

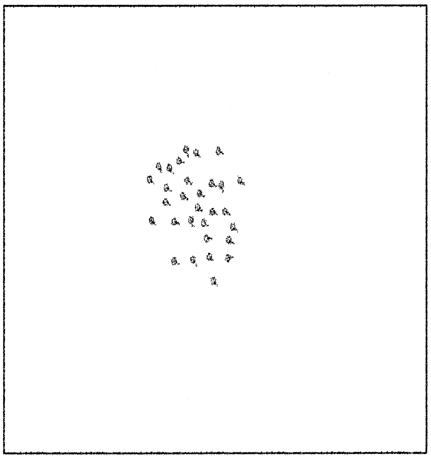

Fig. 3 A snapshot of schooling behavior in case of $N_{fish} = 30$ and $\gamma_{AL} = 0.7$.

4.3.3 Dependence of Time Average of $\eta_P(t)$, $\eta_{NND}(t)$ and $\eta_{EX}(t)$, and of η_{CF} on γ_{AL}

In order to investigate the effects of allelomimesis on collective motion of a fish group, we calculated the time averages of $\eta_P(t)$, $\eta_{NND}(t)$, and $\eta_{EX}(t)$ and η_{CF} for various values of γ_{AL}. Changing the value of γ_{AL} between 0.1 and 1.0, we obtained the time averages of η_P, η_{NND}, and η_{EX}, and η_{CF}. We showed in **Fig. 5** the dependences of those quantities on γ_{AL} as a function of number N_{fish} of fish in the group.

Figure 5 (a) shows that the average polarization $\overline{\eta_P}$ becomes small as the allelomimesis rate γ_{AL} is increased. This is quite reasonable, because the probability that each fish makes the parallel moving is increased with γ_{AL} and as a result the collective parallel swimming is easy to be generated. The magnitudes of the polarizations are quite similar to the values obtained by Huth and Wissel[13]. The large polarization for $\gamma_{AL} \leq 0.2$ comes from that the fish group is easy to split as seen in Fig. 2. The average polarization becomes large as the number of fish is increased. This comes mainly from the fact that the fish in a temporal top group change their headings capriciously and it takes the fish following the top group longer time to adjust their headings to a new moving direction as the number of fish is increased. The dependence of $\overline{\eta_P}$ on N_{fish} becomes weaker as N_{fish} is increased.

Figure 5 (b) shows that the average nearest neighbor distance $\overline{\eta_{NND}}$ decreases with increasing γ_{AL}. This is because fishes make scarcely avoiding action for large γ_{AL}. It is noted that the value of $\overline{\eta_{NND}}$ is within the parallel orientation area (0.5 BL to 2.0 BL) for a value of γ_{AL} between 0.1 and 0.9. In order to generate good schooling behaviors, the value of γ_{AL} should be less than 0.9. The dependence of $\overline{\eta_{NND}}$ on N_{fish} becomes weaker as N_{fish} is increased.

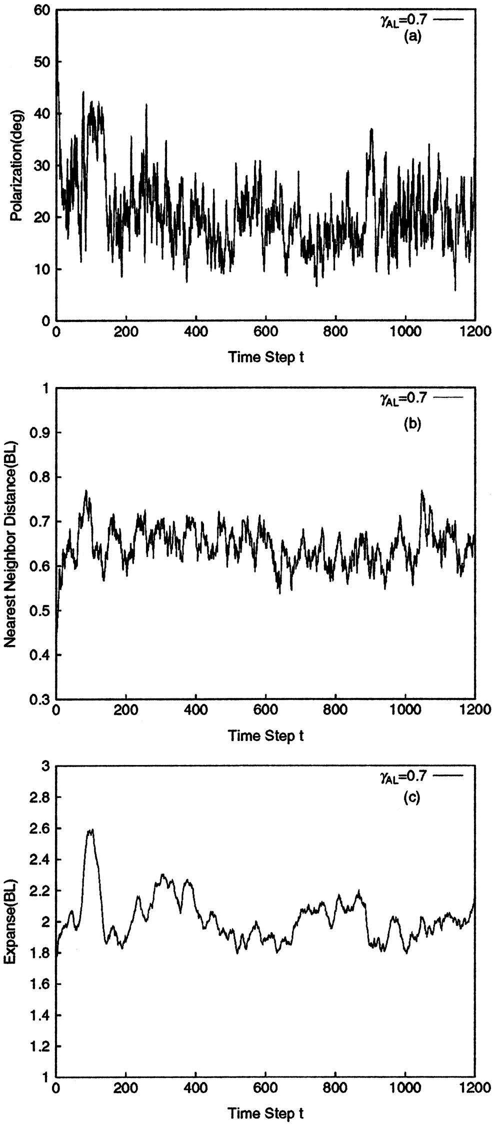

Fig. 4 Temporal variations of (a) polarization $\eta_P(t)$, (b) nearest neighbor distance $\eta_{NND}(t)$, and (c) expanse $\eta_{EX}(t)$ in case of $N_{fish} = 30$ and $\gamma_{AL} = 0.7$

Figure 5 (c) shows that the average expanse $\overline{\eta_{EX}}$ is decreased with increasing γ_{AL}. The small expanse is convenient for every fish to find easily neighbors whose behaviors it mimics. The value of average expanse increases with N_{fish}.

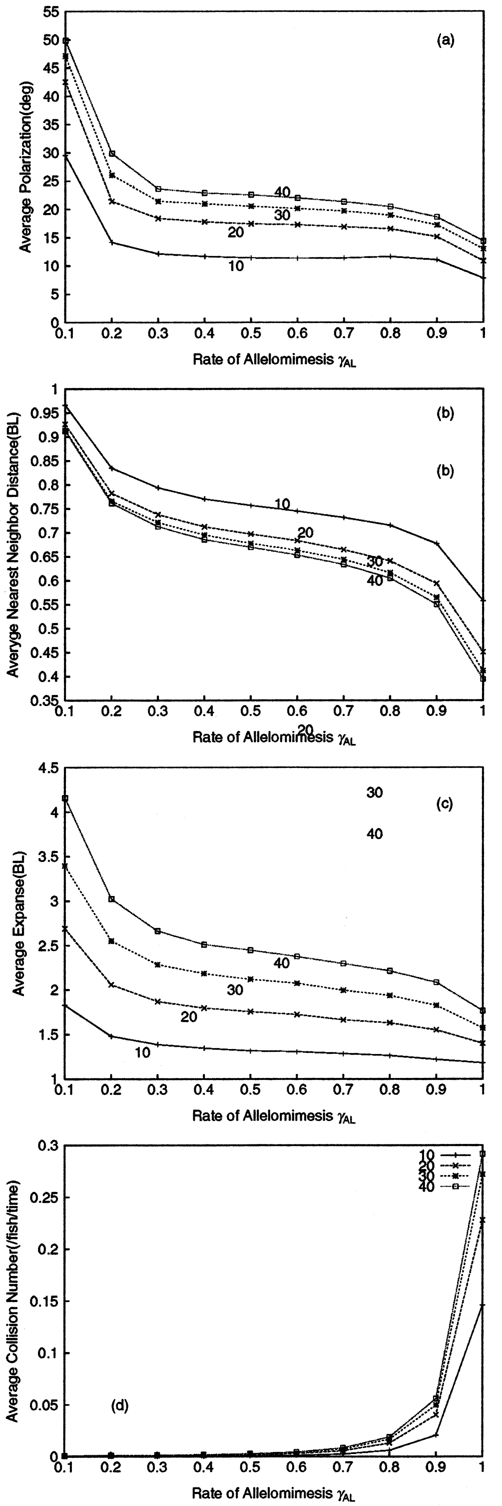

Fig. 5 Dependences of (a) the average polarization $\overline{\eta_P}$, (b) the average nearest neighbor distance $\overline{\eta_{NND}}$, (c) the average expanse $\overline{\eta_{EX}}$, and (d) collision frequency η_{CF}.

Finally, it is seen from Fig. 5 that the collision frequency η_{CF} is increased noticeably as γ_{AL} becomes larger than 0.8, that is, the avoidance rate γ_{AV} bacomes less than 0.2. In order for a fish group to generate collision-free collective behaviors, the allelomimesis rate γ_{AL} should be less than 0.8. The dependence of η_{CF} on N_{fish} becomes weaker as N_{fish} is increased.

On the basis of these results, we found that the values of allelomimesis rate γ_{AL} suitable for good schooling behaviors are within the range from 0.6 to 0.8.

4.4 Self-organized Criticality in Schooling Motion

The self-organized criticality has been established as a useful measure of spatiotemporal property of spatially extended dynamical systems which consist of many elements[25),26)]. The interactions between elements generate a collective order in the system, but the interactions also make the system very susceptible to small disturbances or noise. The system cannot be too sensitive since then it cannot maintain the collective order. When the tendency of a system towards the self-organization is balanced with that towards the high sensibility, the system becomes critical[25)]. The temporal criterion of the self-organized critical state is the presence of f^{-1} noise in dynamical properties of the relevant system[25),26)]. Bak et al.[25)] showed that the frequency spectra with a characteristic power-law f^{-1} included in the spatiotemporal fluctuation of the dynamical properties is not noise but reflects the intrinsic dynamics of self-organized critical systems.

In order to investigate whether the schooling motion generated by the present model corresponds to a self-organized critical state, we calculated the power spectra $S(\omega)$ of the temporal fluctuations of $\eta_P(t)$, $\eta_{NND}(t)$, and $\eta_{EX}(t)$ using Eq.(12), where $\omega = 2\pi f$.

The result of $S(\omega)$ in the case shown in Fig. 3 is shown in **Fig. 6** (a). The three power spectra $S_X(\omega)(X = P,\ NND,\ and\ EX)$ vary approximately as $\omega^{-\lambda}$, as shown by the straight line in Fig. 6. When the fish group shows a schooling behavior, the values of λ for the three power spectra are near unity shown in Fig. 6 (a). Therefore, the fish school is in a dynamically stable state with the self-organized criticality. In order to investigate how the value of exponent λ in the power spectra changes depending on the tactic of fish's decision-making represented by the value of γ_{AL}, we calculated $S_P(\omega)$

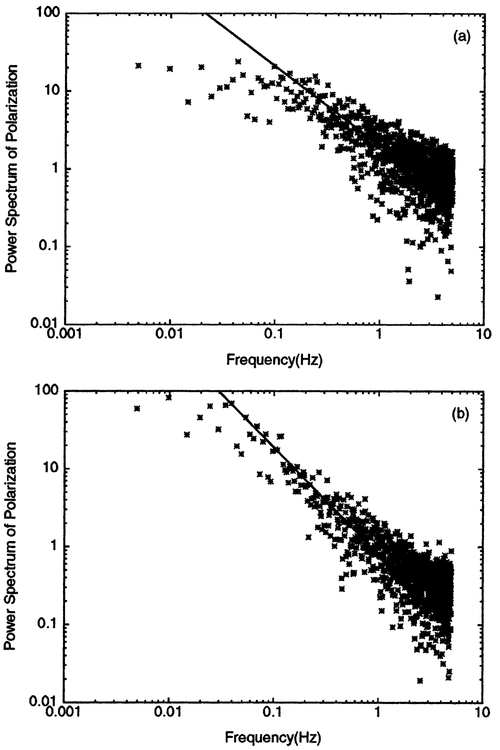

Fig. 6 Power spectrum $S_P(\omega)$ of polarization $\eta_P(t)$ (a) in case of allelomimesis rate $\gamma_{AL} = 0.7$ for which good schooling behaviors are generated, where the straight line is obtained by the least square fitting method and the slope of the line is -1.02, (b) in case of $\gamma_{AL} = 0.1$ for which the fish group split into several subgroups, where the slope of the line is -1.37.

in the two cases where every fish makes scarcely allelomimetic action, that is, $\gamma_{AL} = 0.1$, and no avoidance action, that is, $\gamma_{AL} = 1.0$. Fig. 6 (b) shows the values of $S_P(\omega)$ for $\gamma_{AL} = 0.1$, where every fish moves almost independently of other fishes. The value of exponent is 1.37. This value is noticeably larger than the value 1.02, in case of $\gamma_{AL} = 0.7$ shown in Fig. 6 (a). This comes from the fact that the fish group split into many subgroups in case of $\gamma_{AL} = 0.1$ and there is no interdependence of moving direction between the different subgroups. Then, the temporal fluctuation of fish's heading may be propagated between fishes only in each subgroup. Therefore, the variation of fish's heading becomes rather deterministic as a whole and as a result the value of λ becomes more than unity. The value of exponent λ in case of $\gamma_{AL} = 1.0$ is 1.27 and this is also larger than the value in case of $\gamma_{AL} = 0.7$. This means that the frequency of temporal fluctuation of fish's heading is smaller in case of $\gamma_{AL} = 1.0$ than in case of $\gamma_{AL} = 0.7$. Thus, the values of $S_P(\omega)$ at small frequencies ω become larger in case of $\gamma_{AL} = 1.0$ than in case of $\gamma_{AL} = 0.7$.

Thus, the fish school seems to have the best self-organized criticality in case of $\gamma_{AL} = 0.7$, although the difference in λ between different values of γ_{AL} is not very large.

Inagaki, et al.[27] calculated the power spectra of average swimming speed and forms of fish school in the case where 8 fishes are swimming in the water tank. They reported that the spectra in the range of short period (1—0.1 Hz) are represented approximately as the power law with the exponent of -4. Aoki[28] calculated the power spectra of average nearest neighbor distance in some kinds of fish groups of several individuals. The values of exponent λ obtained are between 1 and 2. Niwa[29] showed based on the simulation of collective motion that the temporal fluctuation of average speed of a fish school is represented approximately by the f^{-1} fluctuation. Hattori, et al.[21] calculated the power spectra of $\eta_P(t)$ and $\eta_{EX}(t)$. The value of exponent λ obtained is very close to unity for the expanse $\eta_{EX}(t)$, but somewhat larger than unity for the polarization $\eta_P(t)$.

5. Effectiveness of Allelomimesis in Maintaining Dynamical Stability of Fish School under Emergent Affairs

5.1 Purpose and Way of Achieving It

We investigate here whether the tactic of individual decision-making suited to generate good schooling behaviors works well also in maintaining dynamical stability of the school under emergent affairs. In the present model, the tactic is represented by the value of γ_{AL}.

Therefore, we simulated dynamical response of fish school to emergent affairs for various values of γ_{AL}. We considered two kinds of emergent affairs, emergent splitting of a school into two groups and flash expansion of a school, which are shown in **Fig. 7**. These affairs occur frequently when predators attack fish groups[3),17)]. It is investigated in Sections 5.2 and 5.3 how the allelomimetic actions of individuals work in restoring the fish groups, which are disturbed abruptly by splitting or expansion, to the schooling behavior.

5.2 Dynamical Stability of School Disturbed by Emergent Splitting

In order to evaluate the dynamical stability of fish schools, we used two kinds of measures, re-

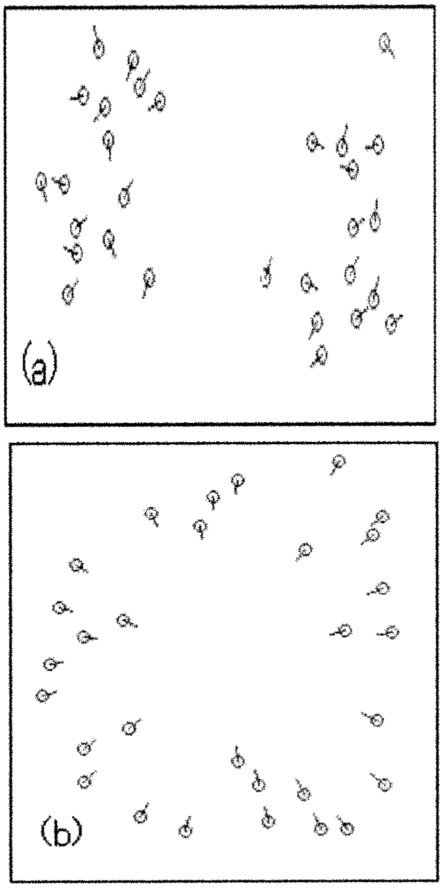

Fig. 7 Spatial distribution of fish individuals generated initially by (a) emergent splitting and (b) flash expansion.

covery time and critical splitting distance. The recovery time means the time period which it takes the fish group split to recover the schooling behavior. The critical splitting distance is defined such that if the splitting distance is larger than the critical one, the fish group split can not return to a single school in a probability of 50%.

5.2.1 Dependence of Recovery Time on the Value of γ_{AL}

We measured the recovery times for a definite splitting distance D_{ES} changing the value of γ_{AL} within the range of 0.4 to 0.9. Because the recovery time becomes different slightly in every simulation even if the value of γ_{AL} and the splitting distance D_{ES} are fixed, we made 10^4 times simulations for each case.

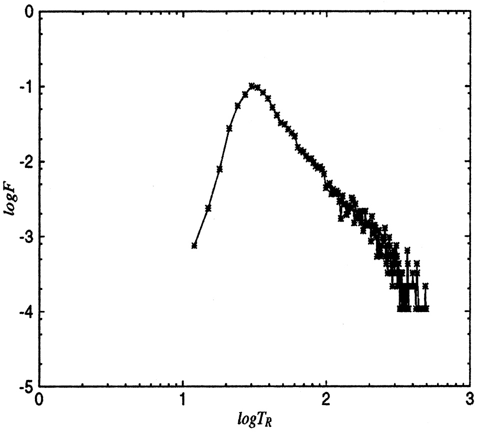

Fig. 8 The frequency F of each recovery time period T_R after the splitting by D_{ES} in case of $N_{fish} = 30$, $\gamma_{AL} = 0.7$, and $D_{ES} = 7.0$ BL. The unit of T_R is 0.1 sec and the simulation was made 10,000 times.

The emergent splitting of a fish school is made by instantaneously moving a half of fishes selected randomly among the school in the right direction by the common distance $D_{ES}/2$ and moving the remaining half of fish in the left direction by $D_{ES}/2$. The splitting distance corresponds to D_{ES}. The initial heading is given randomly in the space. Figure 7 (a) shows the arrangement of fish just after the splitting has been made for $D_{ES} = 7.0$ BL. The definition of the recovery is that at least one neighbor is within the parallel orientation area of every fish. **Figure 8** shows the frequency of each recovery time period in case of $\gamma_{AL} = 0.7, D_{ES} = 7$ BL, and $N_{fish} = 30$, where the value of γ_{AL} used generates a good schooling behavior as shown in the previous section. The frequency becomes maximum at a single value of recovery time T_R which corresponds to the most probable recovery time T_{MPR}. The existence of a single sharp maximum means that the response of the school to the emergent splitting is dynamically stable.

We evaluated the dynamical stability of fish school under emergent splitting using the value of most probable recovery time T_{MPR}. The shorter T_{MPR}, a school is the stable under the splitting with a given distance D_{ES}. In order to investigate the dependence of T_{MPR} on the value of γ_{AL}, we made simulations of school reformation after the splitting with $D_{ES} = 7.0$ BL for various values of γ_{AL}. The results are shown in **Fig. 9**.

The value of T_{MPR} is decreased with increasing γ_{AL}, but the T_{MPR} becomes insensitive for γ_{AL} being larger than 0.7. The minimum value of T_{MPR} was obtained by using the allelomimesis rate in the range of 0.8 to 0.9.

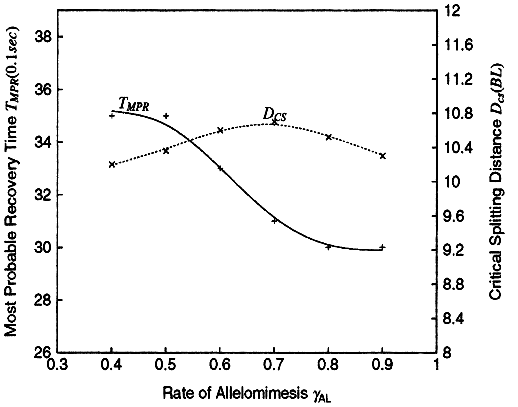

Fig. 9 Dependences of the most probable recovery time period T_{MPR} under the emergent splitting with $D_{ES} = 7.0$ BL and of the critical splitting distance D_{CS} on the value of γ_{AL} in case of $N_{fish} = 30$. The simulation was made 2,000 times for each datum point.

5.2.2 Dependence of Critical Splitting Distance on Value of γ_{AL}

We detected the critical splitting distance D_{CS} changing the value of γ_{AL} within the range of 0.4 to 0.9. Because it is probabilistic whether the fish group split returns to a single school, we defined D_{CS} as the splitting distance for which the fish group split returns to a single school in probability of 50%.

We show in Fig. 9 how the value of D_{CS} is changed with the value of γ_{AL}. The value of D_{CS} is not sensitive to the value of γ_{AL} between 0.4 and 0.9. However, as long as we follow the rule that the larger D_{CS}, the stabler the school, the school becomes the stablest when the allelomimesis rate becomes 0.7.

5.3 Dynamical Stability of School Disturbed by Flash Expansion

5.3.1 Dependence of Recovery Time on the Value of γ_{AL}

We measured the recovery times for a definite magnitude D_{FE} of flash expansion changing the value of γ_{AL} within the range of 0.4 to 0.9. The flash expansion of fishes in a schooling behavior is made by moving each fish along the line from the center of the school to its position by the common distance D_{FE} as shown in Fig. 7 (b). The initial heading of each fish is along the relevant radial line as shown in Fig. 7 (b).

Figure 10 shows the frequency of each recovery time period in case of $\gamma_{AL} = 0.7, D_{FE} = 2.5$ BL, and $N_{fish} = 30$. It is seen in Fig. 10 that there exists a most probable time period. Therefore, the fish group showing a good schooling behavior is dynamically stable also under the flash expansion.

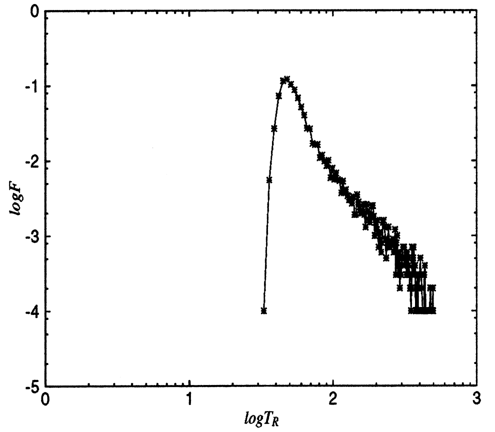

Fig. 10 The frequency F of each recovery time period T_R after the flash expansion by D_{FE} in case of $N_{fish} = 30$, $\gamma_{AL} = 0.7$, and $D_{FE} = 2.5$ BL. The simulation was made 10,000 times.

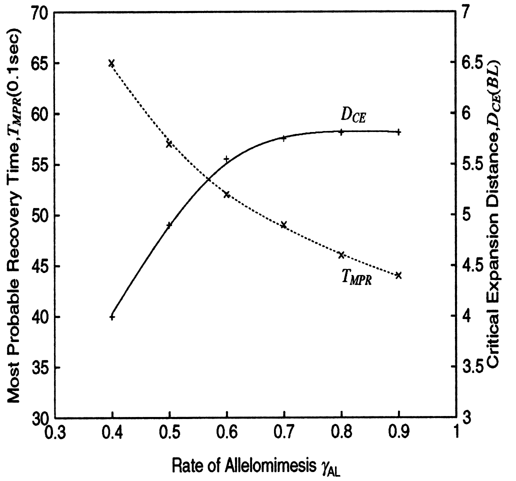

Fig. 11 Dependences of the most probable recovery time period T_{MPR} under the flash expansion with $D_{FE} = 2.5$ BL and of the critical expansion distance D_{CE} on the value of γ_{AL} in case of $N_{fish} = 30$. The simulation was made 2,000 times for each datum point.

In order to investigate how the most probable recovery time T_{MPR} changes with γ_{AL} in the case of flash expansion, we made simulations of school reformation after the flash expansion with $D_{FE} = 2.5$ BL for various values of γ_{AL}. The results are shown in **Fig. 11**. The value of T_{MPR} is decreased with increasing γ_{AL}, and the change rate of T_{MPR} becomes small as γ_{AL} increases. This is similar to the case of emergent splitting. However, the minimum value of

T_{MPR} is obtained at $\gamma_{AL} = 0.9$.

5.3.2 Dependence of Critical Magnitude of Expansion on γ_{AL}

The value of critical magnitude of expanse D_{CE} is shown in Fig. 11 as a function of γ_{Al}. D_{CE} increases with γ_{AL}, but becomes almost constant for γ_{AL} larger than 0.7. This dependence is slightly different from the dependence induced by the emergent splitting. The difference comes from the fact that after application of an emergent disturbance each fish need to make collision avoidance much more frequently in case of emergent splitting than in case of flash expansion, as seen in Fig. 7.

5.4 Effectiveness of Allelomimesis under Emergent Disturbances

We investigated to what extent the allelomimetic actions of individuals generating coherent schooling behaviors work also effectively to generate dynamically stable response to two kinds of emergent disturbances, emergent splitting and flash expansion. The values of allelomimesis rate γ_{AL} suitable to generate good schooling behaviors are around 0.7. It is seen in Fig. 9 that the fish school with γ_{AL} around 0.7 makes the optimal response to the emergent splitting of the school. As seen in Fig. 11, although the response of the school to the flash expansion does not become optimal for γ_{AL} around 0.7, the responses are very similar to the optimal response.

6. Concluding Remarks

The main purpose of the present modeling of fish group is to investigate whether the tactic of individual decision-making suited to generate good schooling behaviors works well also in maintaining the dynamical stability of the fish school under emergent affairs. It has been shown in the previous section that the tactic suitable for schooling generates the dynamically stable response of the school to the two kinds of emergent affairs.

In the present model we assumed that the tactic is formulated based on the allelomimetic actions of fish individual. Visually mediated allelomimesis has been considered as an important factor in the organization of collective behaviors of various animal groups 20),21). Shaw and Tucker 30) showed experimentally that allelomimetic action of fish individuals are essential for fishes to decide their actions. They put several fishes in a cylindrical water tank with a stripped inner wall and rotated the tank with various rates of rotation. Then, they found that the direction of fish's movement becomes the same as that of tank's rotation and the speed of fishes increases with the rotation rate of the tank. It is quite probable that fishes considered the stripe as a neighboring fish group and mimicked the motion of the stripe.

We studied the effectiveness of allelomimetic actions for the dynamical stability of fish school by making simulations of collective motions of fish group. Deneubourg and Goss 19) showed based on the simulation of collective pattern formation in social insects that the mathematical modeling is quite useful to investigate the role of allelomimesis in the formation of collective behaviors. Parrish and Edelstein-Keshet 18) suggested strongly that to solve the question whether all emergent properties of animal aggregations are functional or some simple pattern, the theoretical and modeling studies linked to empirical works are quite useful.

In the present paper, based on several previous experimental and theoretical works, we made a model of fish group that makes dynamically stable responses to various emergent disturbances. In a forth-coming paper, we will extend the model so that we can simulate the response behaviors of the school induced by attack of predators, and investigate the functional roles of fish schooling in evasion of the attacks.

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