Kinetic Theory of Fish Schooling*

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Abstract

Fish schools show a high degree of polarization in absence of a leader or external stimuli. An attempt is made to model the schooling on the basis of dynamics of fish swimming, and to describe the collective motion of schooling kinematically. Mechanics for motion of schooling fish is formulated similarly to gas molecules with locomotion, inbuilt response of organisms to each other, and fluctuation of motion. The question addressed is how polarized patterns or structures arise spontaneously. Transient behavior and onset of the polarized schooling structure are discussed.

1. Introduction

The schooling of fish is one of the most familiar forms of animal social behavior. Many species of ichthyoid including crustacean form either schools, in which the constituent individuals swim with similar orientation, or swarms, in which the individuals, though forming a group, have a lesser degree of uniformity in orientation, depending on their activities or environmental conditions. For examples, herring schools are polarized in the daytime but form nonpolarized and loose aggregation at night (Buerkle, 1983); the anchovy schools increase the inter-fish distance at night compared to daytime, with forming swarms, and the nearest neighbor distance shows very great variation (Aoki & Inagaki, 1988); the threespine sticklebacks form a nonpolarized school which remain stationary as each fish forages, and spacing and orientation among the individuals are variable, however, if alarmed, the same fish quickly move away from the source of disturbance, for instance predator, as a cohesive unit, the individuals closely and parallel to each other, external stimuli force sticklebacks to organize the polarized school (Keenleyside, 1955); mysid shrimps can also exhibit schooling and swarming behavior (Clutter, 1969). Moreover Partridge (1980) made time series analysis with European minnows and showed that correlation between instantaneous velocities of fish increased with school size and as inter-fish distance decreased.

One of most striking quantities of a school of fish is its synchronization: hundreds of small fish glide in unison, more like a single organism than a collection of individuals, and the distance between individuals is uniform (Hunter, 1966; van Olst & Hunter, 1970). Fish do not need a leader or external stimuli to form polarized structure. Each fish, having established its position, uses its eyes and its lateral lines simultaneously to measure the speed of all the other fish in a school (Pitcher, 1979; Partridge, 1982). The correlation between the velocity of a particular fish and those of other fish in a school is not strong (Aoki, 1980; Partridge, 1980). The results show that the school has no leader: speed and direction are not closely related to those of any other single fish. The strong correlations are observed between the velocity of the individual and average velocity of the entire school. It then adjusts its own speed to match an average. Thus in a sense the entire school is the leader and individual is a follower. This leads us to the question of self-organization (Haken, 1983).

In this paper, the question addressed is how patterns or structures of fish school arise spontaneously in a setting of collective motion. An attempt is made to reveal mechanisms underlying self-organization in the fish school. Individual fish are regarded as a particles, with locomotion and inbuilt response of organisms to each other. The inbuilt response is supposed to work as two-body interaction, which is internal force acting on one body due to another body in a group, following Newton's laws of motion (Okubo, 1980, 1986). The total internal force produced on one body by a number of the other bodies placed around it is the vector sum of the individual two-body forces. It should be noted that no implemented command structure exists between individual and a school, i.e. hierarchical levels. Let us assume that the system consists of individuals which have all the same properties and which intend in the same way. Then we wish to show that even such a system can organize itself into a new macroscopic state with a well-defined structure or, in other words, a well-defined organization.

2. Dynamics of Fish Swimming

A fish can swim forward by pushing its environmental water backward; the surrounding in turn reacts to provide thrust to the fish. Performance depends on the balance between thrust and drag. Since unavoidably the temporal behavior of fish swimming appears to be random, the motion is supposed to be deterministic in a statistical sense and the swimming velocity v is regarded as a random variable. Hence the temporal evolution of the probability density $P(v, t)$ of the process $v(t)$ is assumed to be governed by the

Fokker-Planck equation

$$\frac{\partial}{\partial t}P(\boldsymbol{v},t) = -\frac{\partial}{\partial \boldsymbol{v}} \cdot (\boldsymbol{f}P) + \epsilon\frac{\partial^2 P}{\partial \boldsymbol{v}^2}, \tag{1}$$

where $\boldsymbol{f}$ describes the systematic evolution of $\boldsymbol{v}(t)$, and ϵ the fluctuation around it.

The faster fish swims, the greater the resistance. Thus in the steady state fish moves at the most probable speed v_s such that this propulsion just equals resistance. Hence the steady state distribution of the velocity $P_s(\boldsymbol{v})$ has maxima at $|\boldsymbol{v}| = v_s$, and a minimum at $|\boldsymbol{v}| = 0$. Let us express the stationary solution as the following form

$$P_s(\boldsymbol{v}) = \mathcal{N}\exp\{-U(\boldsymbol{v})/\epsilon\}, \tag{2}$$

where the function $U(\boldsymbol{v})$ is defined by $\boldsymbol{f} = -\dfrac{\partial U}{\partial \boldsymbol{v}}$, and $\mathcal{N}$ is normalization constant. Then the function $U(\boldsymbol{v})$ has minima at $|\boldsymbol{v}| = v_s$, and a local maximum at $|\boldsymbol{v}| = 0$. In order to facilitate our investigation we will formulate a cumulant expansion around $\boldsymbol{v} = 0$. Supposing the symmetry of the space, the first and third order terms of a Taylor series vanish. Thus we will represent $U(\boldsymbol{v})$ as

$$U(\boldsymbol{v}) = -\frac{\kappa}{2}\boldsymbol{v}^2 + \frac{\kappa\beta}{4}\boldsymbol{v}^4, \tag{3}$$

where $v_s = \beta^{-\frac{1}{2}}$, and κ is a positive constant. This functional form of $U(\boldsymbol{v})$ represents that $P_s(\boldsymbol{v})$ is the non-Gaussian distribution, which arise from the finite steady swimming speed.

If the stochastic process $\boldsymbol{v}(t)$ is regarded as the Gaussian process, we have the Langevin equation corresponding to the Fokker-Planck equation (1);

$$\frac{d\boldsymbol{v}}{dt} = \boldsymbol{f} + \boldsymbol{\eta}(t) = \kappa(1 - \beta\boldsymbol{v}^2)\boldsymbol{v} + \boldsymbol{\eta}(t), \tag{4}$$

where $\boldsymbol{\eta}(t)$ is a fluctuating force, and a parameter κ represents the rapidity attaining equilibrium. This equation corresponds to the Newton's second law of motion. The first term on the right is the vector sum of the exerted forces; locomotory force or forward thrust, and hydrodynamic drag.

3. Dynamical Model for Fish Schooling

Consider a school composed of N fish individuals. Shaw (1969) suggested that schooling should be considered as a two order system: the first order is mutual attraction which is an elementary factor in schooling; the second order is polarization which is different in

its degree depending on activities of fish, environmental conditions, or among schooling species. So the interaction between individuals can be divided into two components; $f_{ij}^{(g)}$ for the grouping force, and $f_{ij}^{(p)}$ for the arrayal force, where f_{ij} stands for an internal force acting on ith body due to jth body in a school. Hence, for a free system (no external forces), the kinetic equation for the ith individual fish in the school is expressed as

$$\frac{dv_i}{dt} = \kappa(1 - \beta v_i^2)v_i + \sum_{j=1}^{N} f_{ij}^{(g)} + \sum_{j=1}^{N} f_{ij}^{(p)} + \eta_i(t). \tag{5}$$

All fish in the school are considered equivalent and individual differences between members are neglected.

Let us assume that the attractive interaction only works in not so long range of the distance between two individuals. For a large school, $N \gg 1$, the number-density distribution of grouping organisms is supposed to be uniform almost everywhere, so the same surroundings are found almost everywhere in the school. Then $\sum_{j=1}^{N} f_{ij}^{(g)} = 0$ holds. Partly because of a limited number of individuals in a school and partly because of nonuniformity in their spatial distribution, the resultant internal force $\sum_{j=1}^{N} f_{ij}^{(g)}$ on an individual also produces a fluctuating force.

Two neighboring fish tend to swim parallel with each other and to equalize their velocities. Since each individual effectively interacts with a mean field produced by all the other individuals, that is, the average velocity of the entire school, the arrayal interaction is supposed to depend only on the relative velocity between two individuals. We approximately express the arrayal force as the first-order term in a Taylor series;

$$\sum_{j=1}^{N} f_{ij}^{(p)} = \frac{J}{N} \sum_{j=1}^{N} (v_j - v_i), \tag{6}$$

where J is the coefficient of arrayal force.

The equation of motion for ith body thus reads

$$\frac{dv_i}{dt} = \kappa(1 - \beta v_i^2)v_i + \frac{J}{N} \sum_{j=1}^{N} (v_j - v_i) + \eta_i(t). \tag{7}$$

Here we can regard a parameter β as nonlinearity of the system, and κ^{-1} as sensitivity of individual behavior to surrounding companions or environment. The fluctuating force $\eta_i(t)$ will of course have a certain influence on the collective motion of fish schooling. Thus the system is considered to be coupled to an environment as a noise source. We assume that the correlation time of the fluctuating force is very short on the typical macroscopic

time scale of the equations of motion. This allows us to pass to the idealization of the Gaussian white noise. So we set mean value and variance matrix

$$\langle \boldsymbol{\eta}_i(t) \rangle = 0, \qquad \langle \boldsymbol{\eta}_i(t) \boldsymbol{\eta}_j^{\mathrm{T}}(t') \rangle = 2\epsilon \delta_{ij} \delta(t - t') \boldsymbol{I} \tag{8}$$

respectively, where ϵ denotes the strength of the fluctuating force, $\boldsymbol{I}$ is the 3×3 unit matrix, and $\langle \ldots \rangle$ describes the ensemble average.

Summing eq.(7) over all individuals in the school and defining the velocity of the center of mass by

$$\boldsymbol{V} \equiv \frac{1}{N} \sum_{j=1}^{N} \boldsymbol{v}_i, \tag{9}$$

we reduce eq.(7) to

$$\frac{d\boldsymbol{V}}{dt} = \kappa \left(1 - \frac{5}{3} \beta \sigma^2(t) \right) \boldsymbol{V} - \kappa \beta V^2 \boldsymbol{V} + \boldsymbol{F}(t), \tag{10}$$

where the variance $\sigma^2(t) \equiv \langle (\boldsymbol{v}_i - \boldsymbol{V})^2 \rangle$, and the Gaussian stochastic force $\boldsymbol{F}(t)$ satisfies the relation

$$\langle \boldsymbol{F}(t) \boldsymbol{F}^{\mathrm{T}}(t') \rangle = \frac{2\epsilon}{N} \delta(t - t') \boldsymbol{I}. \tag{11}$$

In order to analyze the variance, we investigate eq.(7) with a simple dynamical molecular field theory. The simple dynamical molecular field treatment may be to replace the nonlinear term $v^2(t)v(t)$ by $\langle v^2(t) \rangle v(t)$, where the average $\langle v^2(t) \rangle$ is determined self-consistently using the solution of linearized equation. Thus we arrive at the following equation

$$\frac{d\sigma^2}{dt} = -2(J - \kappa + \kappa \beta \langle v^2 \rangle) \sigma^2 + 6\epsilon. \tag{12}$$

In general the microvariables which exhibit the movement of the constituents vary much more rapidly the macrovariables which exhibit the collective property. Hence we can assume that $\langle v^2 \rangle$ attains equilibrium faster than $\langle v \rangle^2$, so supposing $\langle v^2 \rangle \cong \beta^{-1}$, we obtain

$$\frac{d\sigma^2}{dt} = -2J\sigma^2 + 6\epsilon, \tag{13}$$

and the solution is then given by

$$\sigma^2(t) = \frac{3\epsilon}{J}(1 - e^{-2Jt}) + \sigma^2(0)e^{-2Jt}. \tag{14}$$

Aoki (1980) observed this relaxation phenomenon in experiments, using *Gnathopogon elongatus elongatus* school composed of eight individuals. In Fig.1 is shown the comparison between the theory and observation.

Consequently we have the asymptotic form of the equation governing the collective motion of schooling;

$$\frac{dV}{dt} = \kappa\left(1 - 5\frac{\beta\epsilon}{J}\right)V - \kappa\beta V^2 V + F(t). \tag{15}$$

It is seen that for $1 - 5\frac{\beta\epsilon}{J} > 1$, fish as a whole tend to perform a rectilinear movement, thus forming a polarized school structure; on the other hand, for $1 - 5\frac{\beta\epsilon}{J} < 1$, the center of mass of school hardly moves and the unpolarized school performs an amoebic movement due to the fluctuating force. We can see that the fluctuation can deeply modify the collective property of the system, i.e. noise induced transition.

We now consider the transient behavior of fish schooling. In the initial region of the schooling process, since $V \approx 0$, we can linearize the governing equation (10);

$$\frac{dV}{dt} = \kappa\left(1 - \frac{5}{3}\beta\langle v^2\rangle\right)V + F(t). \tag{16}$$

Supposing $\langle v^2\rangle \approx \frac{1}{\beta}\left(1 + \frac{5}{4}\frac{\beta\epsilon}{\kappa}\right)$, which is the equilibrium solution of eq.(4), we obtain

$$\langle V^2(0)\rangle = \frac{\dfrac{9}{2}\dfrac{\epsilon}{\kappa N}}{1 + \dfrac{25}{8}\dfrac{\beta\epsilon}{\kappa}}. \tag{17}$$

Since the variance is written as $\sigma^2(t) = \langle v^2(t)\rangle - \langle V^2(t)\rangle$ by using the dynamical molecular field $\langle V^2(t)\rangle$, we can estimate the variance for small t,

$$\sigma^2(0) = \frac{1}{\beta}\left(1 + \frac{5}{4}\frac{\beta\epsilon}{\kappa}\right) - \frac{\dfrac{9}{2}\dfrac{\epsilon}{\kappa N}}{1 + \dfrac{25}{8}\dfrac{\beta\epsilon}{\kappa}}. \tag{18}$$

This means that the growing rate of the system, $\kappa\left(1 - \frac{5}{3}\beta\sigma^2\right)$, is negative in the initial time region, $t \approx 0$. Hence it can be said that $\langle V^2(t)\rangle$ expresses the fluctuation of the velocity of the center of school, $V(t)$, for rather small t, but that when the fluctuation grows in amplitude and the order of magnitude of $\langle V^2(t)\rangle$ becomes quite different from initial value of the order of ϵ/N, symmetry of the system then spontaneously breaks down at time t_1 such that $1 - \frac{5}{3}\beta\sigma^2(t_1) = 0$, namely the transition from initial nonpolarized form to polarized schooling structure occurs.

Thus the enhancement of the fluctuation is regarded as the essential mechanism of the formation of polarized schooling structure. The time for this onset of schooling structure

is given by t_1, then we have

$$
\begin{aligned}
t_1 &= \frac{1}{2J} \ln \left(\frac{\frac{5}{3}}{1 - 5\frac{\beta\epsilon}{J}} \left[1 - 3\frac{\beta\epsilon}{J} + \frac{5}{4}\frac{\beta\epsilon}{\kappa} - \beta\langle V^2(0)\rangle \right] \right) \\
&= \frac{1}{2J} \ln \left(\frac{\frac{5}{3}}{1 - 5\frac{\beta\epsilon}{J}} \left[1 - 3\frac{\beta\epsilon}{J} \left\{ 1 - \frac{5}{12}\frac{J}{\kappa} \left(1 - \frac{\frac{18}{5}\frac{1}{N}}{1 + \frac{25}{8}\frac{\beta\epsilon}{\kappa}} \right) \right\} \right] \right) .
\end{aligned}
\tag{19}
$$

The onset time t_1 has a qualitative meaning around which the nature of fluctuation changes from microscopic order to macroscopic one. It gives a characteristic time for the formation process of macroscopic order or structure. It should be noted that the mechanism for fluctuation enhancement is found to be synergism (or cooperative effect) of initial fluctuation, random force and nonlinearity of the system. The onset time t_1 becomes larger, as the initial fluctuation $\langle V^2(0)\rangle$ becomes small, or as the strength of the random force ϵ and the nonlinearity β become large. In addition this time becomes larger, as the interaction coefficient J becomes small, or the sensitivity κ^{-1} and the school size N become large.

The asymptotical form (15) for the governing equation qualitatively describes a global feature of the transient behavior of the system. We can systematically investigate the transient phenomena in the non-equilibrium system near the asymptotically unstable point on the basis of eq.(15) with the Suzuki's theory (Suzuki, 1978, 1981; Niwa, 1991a), and the solution takes the following asymptotic form;

$$
\langle V^2(t)\rangle = \langle V^2\rangle_{st} \frac{\tau}{1 + \tau},
\tag{20}
$$

where the scaling variable

$$
\tau = \frac{\beta}{1 - 5\frac{\beta\epsilon}{J}} \left\{ \langle V^2(0)\rangle + \frac{\frac{3\epsilon}{N}}{\kappa\left(1 - 5\frac{\beta\epsilon}{J}\right)} \right\} \exp \left[2\kappa\left(1 - 5\frac{\beta\epsilon}{J}\right)t \right],
\tag{21}
$$

and the mean square of the velocity in the stationary state

$$
\langle V^2\rangle_{st} \approx \frac{1}{\beta}\left(1 - 5\frac{\beta\epsilon}{J}\right) + \frac{\frac{5}{4}\frac{\epsilon}{N}}{\kappa\left(1 - 5\frac{\beta\epsilon}{J}\right)}.
\tag{22}
$$

The characteristic time for this onset of schooling structure is then given by $\tau = 1$, thus

we have the scaling time of the system;

$$
t_0 = -\frac{1}{2\kappa\left(1 - 5\frac{\beta\epsilon}{J}\right)} \ln\left[\frac{\beta}{1 - 5\frac{\beta\epsilon}{J}}\left\{\langle V^2(0)\rangle + \frac{\frac{3\epsilon}{N}}{\kappa\left(1 - 5\frac{\beta\epsilon}{J}\right)}\right\}\right]. \tag{23}
$$

The mechanism of school organization is found again to be synergism of initial fluctuation, random force and nonlinearity of the system.

Fig.2 shows the comparison between the theory and observation for transient behavior of self-organizing the polarized school structure.

4. Discussion

In this paper we have discussed collective properties of the fish school, where the constituent individuals are treated similarly to gas molecules following Newton's laws of motion. We extracted the dynamic features of self-organization of schooling formation, namely structural transition and transient behavior of the onset of schooling, by using nonlinear Langevin equation near the asymptotically instability point. The transient process from initial nonpolarized aggregation to polarized school is shown as follows (Sakai, 1973; Aoki, 1980): First, individuals do not yet move as a whole but gather; accidentally removed individuals from companions are appeared; then the other individuals are quickly attracted toward and follow them, and fish as a whole gradually perform a rectilinear movement; thus forming a polarized structure. These agree with what we have discussed here; the essential mechanism of the onset of polarized schooling structure is the macroscopic enhancement of fluctuation from the initial microscopic one, where synergism or cooperative effect of initial fluctuation, random force and nonlinearity of the system plays an important role.

Instead of the mutual attractive interaction of short range supposed here, when considering the long range interaction of a type of Newtonian gravitational attraction, the resultant internal attraction $\sum_{j=1}^{N} f_{ij}^{(g)}$ produces, as the average, a centrally attractive force acting on an individual dependent only on the distance from the center. The dynamical features of collective motion of fish school with the long range grouping force corresponding to Parr-Breader's model (Breader, 1954) is, however, equivalent to those of school with the short range interaction, and the same governing equation is also obtained (Niwa, 1991a). Moreover, it can be shown that in the equilibrium the inter-fish distance in a school depends on the school size N, and the number-density is deeply affected by the fluctuating force.

So far we have assumed the similarity in the swimming ability of schooling members which depends on body length (Wu, 1977), so that there were not differences between individuals. This simplified procedure was convenient to extract a basic mechanism of fish schooling. However, the schools usually consist of individuals within a certain size range (Aoki & Inagaki 1988), hence a certain permitted limit of the swimming ability. Thus we are interested in quantitatively determining this permitted limit of swimming ability, with which individuals adjust their cruising speeds to each other, and form a stable schooling structure.

In this investigation on schooling, we also supposed that each individual efficiently interacts with an average velocity of the entire school. However the average which is most strongly correlated is not the simple arithmetic mean of the speeds and headings of the members of the school. A fish is much more strongly influenced by the nearest neighbors than the distant members of the school. The contribution of each fish to the average is inversely proportional to either the square due to vision, or the cube due to the lateral line's sensitivity to water displacement, of the distance (Partridge,1980,1982).

These are another important character of fish schooling. The general theory on their behavior must take into consideration this situation.

Fish schools, such as Pacific mackerel migrating over enormous distances, are much more highly organized than those of tropical fishes that inhabit a coral reef. In spatial heterogeneous environmental condition (for example, the temperature, the concentration of chemical substance such as salinity), how do such migrant fish organizing a school swim to find out comfortable place, and then what distribution pattern of the assembly of schools does resultantly arise in the sea? It is desirable to connect the individual properties and the stationary distribution of the assembly of schools under a gradient of the marine environmental condition. Rising temperature causes the chemical machinery of a cold-blooded vertebrate to turn fast. Thus the environment influences the swimming activity of a fish via its metabolism (Brett,1964). Whereas the behavior of fish is deterministic in a statistical sense, so that the environment has also influences on the strength of its fluctuating movement. If fish swim in a bad environment with stress factor, the fluctuating movement of the constituents of a school may be enhanced. Hence not only the swimming activity but also the fluctuation of the individual behavior determines the features of migration in heterogeneous environment. Furthermore the fluctuation is important to randomly search the comfortable environment. We are interested in the influences of the fluctuating movement on the resultant distribution of the assembly of migratory fish schools in the sea. It can be shown that the fluctuating movement of the member of a school determines the features of the migrating behavior and the pattern of resultant distribution of schools in a spatial gradient of the environment, on the basis of

the nonlinear Langevin equation (15) describing the motion of fish school (Niwa,1991b).

It is interesting that this model is regarded as a metaphor of the self-organization of public opinion. Then the parameters may be supposed as follows: J represents the communicability in a group, κ the rapidity with which a person forms his own idea, and β^{-1} the stubborn nature or tenacity for his own opinion. Thus the conditions for self-organization and global features of forming public opinion are similarly considered.

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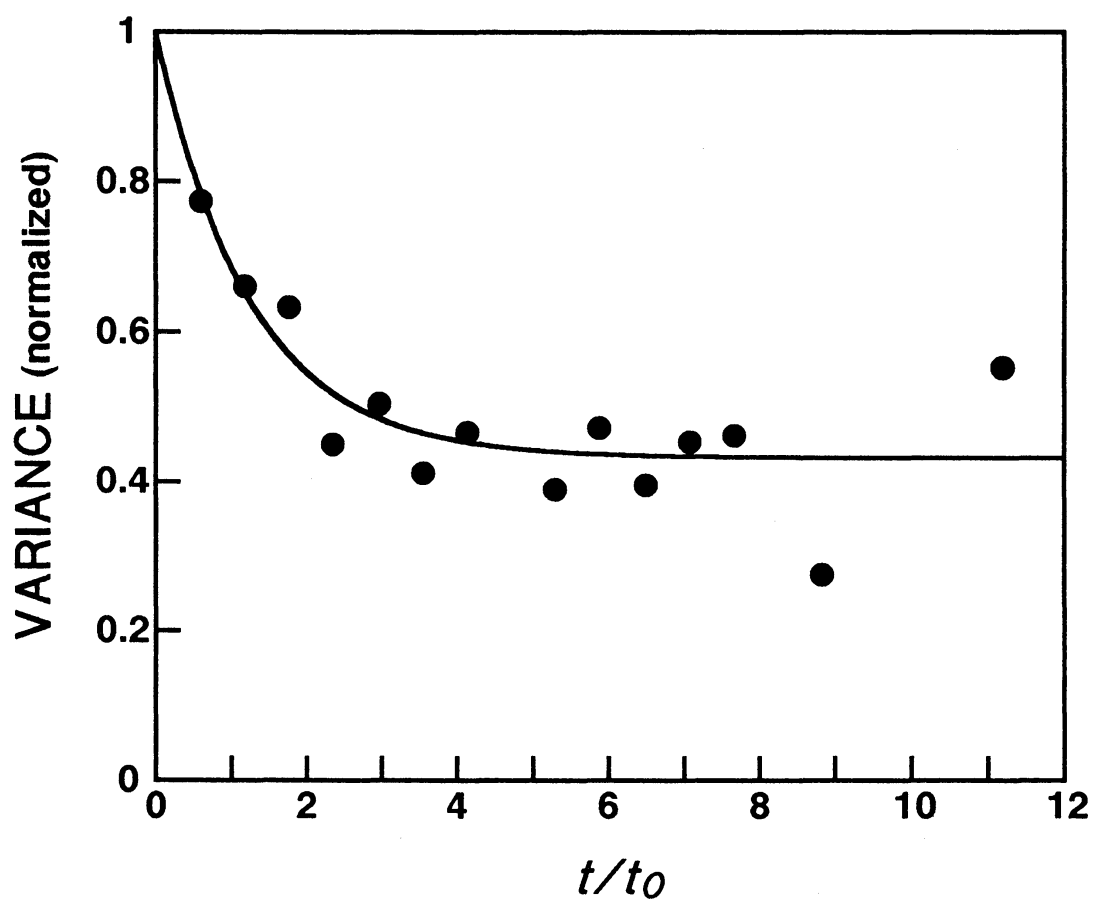
Fig.1   Shown is the time dependence of variance of individual velocity in the *Gnatho-pogon* school. The curve is based on eq.(14), and points are data from Aoki (1980). Time t and variance $\sigma^2(t)$ are normalized with the scaling time of onset of the schooling structure, $t_0 = 0.85$sec, and the initial variance, $\sigma^2(0) = 49.7$cm^{2}sec^{-2}.
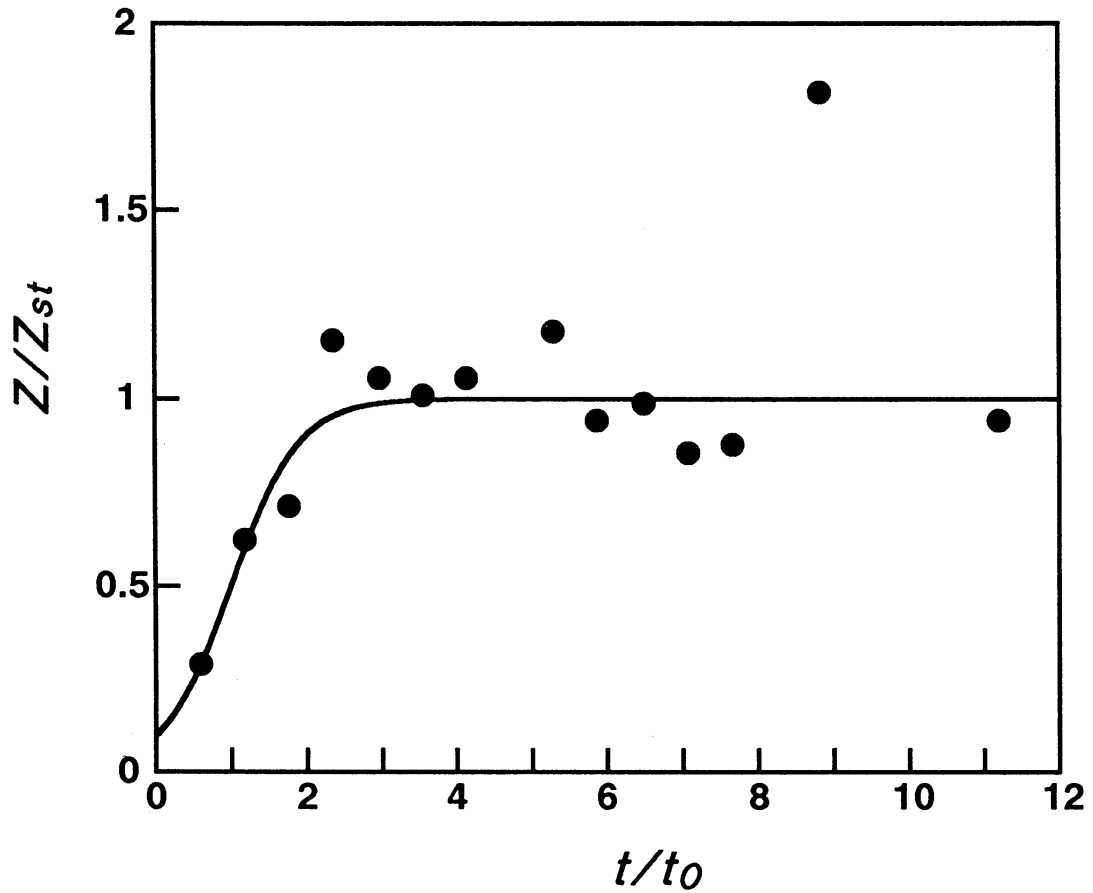
Fig.2 Transient behavior of formation of polarized school structure. Shown is the mean squared velocity of the center of *Gnathopogon* school based on eq.(20), $Z(t) \equiv \langle V^2(t) \rangle$. The experimental points are data from Aoki (1980). Time t and mean squared velocity $Z(t)$ are normalized with the scaling time of onset of the schooling structure, $t_0 = 0.85\mathrm{sec}$, and the steady swimming speed squared, $Z_{st} = 22.0\mathrm{cm}^2\mathrm{sec}^{-2}$.