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Self-organizing Dynamic Model of Fish Schooling

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Fish schools show a high degree of polarization in the absence of a leader or external stimuli. In this paper the problems of the collective motion of fish schooling are analyzed, and the question of how polarized patterns or structures arise spontaneously is addressed. I attempt to show collective properties on the basis of elemental properties. Individual fish are regarded as gas molecules having locomotion, inbuilt responses with respect to each other and fluctuations of motion. A non-linear Langevin equation describing self-organized formation of fish schools is obtained with practical approximation methods. It is shown that fish schools are governed by specific mathematical relations, i.e. synergetics, which represent the principal feature of order–disorder (polarization–non-polarization) transitions. Systems composed of many fish dramatically change their structure when certain parameters are varied. Moreover, transient behavior and the onset of polarized schooling structure are discussed with reference to the non-linear Langevin equation near the instability point. Experimental data on the transient behavior of the formation of schooling structure are shown for comparison with the theoretical result.

1. Introduction

The schooling of fish is one of the most familiar forms of animal social behavior. Hundreds of small fish glide in unison, more like a single organism than a collection of individuals. Fish schools are much more highly organized than insect swarms. Fish do not need a leader or external stimuli to form a polarized structure. For the school to have flourished as a social form over a long evolutionary history it must provide some benefit. It has been thought that the evolutionary advantage of schooling lies in escape from predation (Cushing & Harden Jones, 1968; Treisman, 1975*a*, *b*), energy saving (Weihs, 1973*a*, 1975; Breder, 1976), and reducing error in navigation (Larkin & Walton, 1968).

The schools usually consist of individuals of the same size range within a certain permitted limit (Inoue, 1970; Breder, 1976; Aoki *et al.*, 1986; Aoki & Inagaki, 1988), so that with similar cruising speeds as these depend on body length (Bainbridge, 1958; Brett, 1964, 1965*a*; Blaxter, 1969; Webb, 1971*a*, *b*, 1975, 1977; Wardle, 1977; Weihs, 1977; Wu, 1977; Graham *et al.*, 1990; Kaufmann, 1990; Goolish, 1991). One of the most striking quantities of a school of fish is its polarization, i.e. the parallel arrangement of the members. The distance between individuals is uniform and the motion of individual fish is synchronized (Hunter, 1966; van Olst & Hunter, 1970). The tendency of the fish to remain at the preferred distance serves to maintain the 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: that is, speed and heading 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 velocity to match an average. Thus, in a sense the entire school is the leader and an individual is a follower. This raises the question of self-organization (Haken, 1983).

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Fish are usually spaced regularly when the average distance between nearest neighbors is less than one fish length. However, when the distance is greater, namely, at lower density, spacing between fish is such that the fish are in states of loose aggregations, which hardly move as a whole (Symons, 1971). This suggests that some critical density is necessary for the occurrence of schooling. 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 is polarization which is different in its degree depending on activities of fish, environmental conditions, or among schooling species. In a seminal paper, Sakai (1973) discussed the global behavior of temporal evolution of the formation of fish schooling. She proposed a computer simulation model for schooling based on Newton's equation of motion, and found that no group movement occurred by mutual attraction only, while the additional factor of polarization permitted group movement and produced schooling structure.

In this paper, the question of how patterns or structures of fish school arise spontaneously in a setting of collective motion is addressed. An attempt is made to reveal mechanisms underlying self-organization in the fish school from the standpoint of individual mechanics. Individual fish are regarded as particles having locomotion and inbuilt responses with respect to each other. The inbuilt response is assumed to work as two-body interaction, which is the internal force acting on one body due to another body in a group and follows Newton's laws of motion (Okubo, 1980, 1986). The total internal force produced on one body by a number of other bodies placed around it is the vector sum of the individual two-body forces. Specific emphasis is on the interpretation of the characteristic features on an animal system in term of the *forces*, which are supposed to operate on the animal individuals and to govern their motions in the system. The term "animal system" defines any biologically significant aggregation of animals—here, a fish school. We consider a system in which no implemented command structure exists between individual and a school, i.e. hierarchical levels. We further assume that the system consists of a large number of fish which have all the same properties and which act in the same way. We wish to show that such a system can organize itself into a new macroscopic state with a well-defined structure or, in other words, with a well-defined organization.

Experience from physics or chemistry shows that even if the rules governing the behavior of individual particles are well known, an understanding of the collective properties of systems of particles may be quite difficult or intractable (for example, in ferromagnetic systems). When the system consists of biological organisms, we also encounter the problem of aggregate properties or collective motion (see the excellent review by Edelstein-Keshet, 1990). For instance, the organization of traffic patterns in ants (Aron *et al.*, 1990). It is an important phenomenon that a collection of interacting units, even very simple ones, can exhibit complex behavior.

A mode of fish swimming in response to stimuli is taxis. However, investigation of the motion in response to stimuli is almost entirely at the qualitative stage, in contrast with classical mechanics. The motion does not necessarily follow set rules, but response is not entirely random. The motion appears to be deterministic in a statistical sense (Okubo, 1980, 1986). Since the temporal behavior of swimming fish appears to be random, a number of processes can be described by the application of Newton's laws of motion:

$$\frac{\mathrm{d}\boldsymbol{v}}{\mathrm{d}t} = \tilde{\boldsymbol{F}}(\boldsymbol{x}, \boldsymbol{v}, \epsilon), \tag{1}$$

where $\boldsymbol{v}$ is the individual's velocity, which is the time rate of change of position $\boldsymbol{x}$ (the three-dimensional co-ordinates denoted by x, y, z), i.e. $\boldsymbol{v} = \mathrm{d}\boldsymbol{x}/\mathrm{d}t = (\mathrm{d}x/\mathrm{d}t, \mathrm{d}y/\mathrm{d}t, \mathrm{d}z/\mathrm{d}t)^{\mathrm{T}}$, and $\tilde{\boldsymbol{F}}$ the vector sum of the exerted forces, which may be of physical, physiological, behavioral or ecological origin. ϵ represents a parameter determined by the internal or external fluctuation. The equation of motion (1) expresses Newton's Second Law, that is, a time change of the velocity of an organism occurs in the direction of the total force, and the rate of change of momentum, the product of mass and acceleration of the organism, is equal to the total force. If we consider times that are small compared with those required for noticeable loss or gain in weight of the organism, the change in mass can be ignored. Assume that $\tilde{\boldsymbol{F}}$ can be decomposed according to

$$\tilde{\boldsymbol{F}} = \boldsymbol{F} + \boldsymbol{\eta} \tag{2}$$

into a deterministic part $\boldsymbol{F}$, and a stochastic force $\boldsymbol{\eta}$, which is treated as a random variable. The exact origin of the stochastic force will not be considered here.

The fluctuating force $\boldsymbol{\eta}$ will of course have a certain influence on the collective motion of the fish school. This situation, which is equivalent to systems that are coupled to an environment as a noise source, motivates the following question: Do systems always adjust their macroscopic behavior to the average properties of the individuals or can one find some drastic modifications of their macroscopic behavior respond-

ing to the fluctuations? In this paper, the following theoretical analysis will establish that the fluctuation can alter the macroscopic behavior of a fish school, namely noise-induced transition phenomena between polarized school with a rectilinear movement, and non-polarized aggregation the center of which hardly moves, such as the order–disorder transitions of ferromagnetic systems. We will see that random motion of individuals plays an important role in self-organization of schooling structure.

2. Dynamical Model for Fish Schooling

We start with the kinetic equation (1) for the i-th individual fish in a school ($i = 1, 2, \ldots, N$), for the case that the deterministic part $\boldsymbol{F}$ is supposed to consist of the following three characteristic forces: (i) locomotory force $\boldsymbol{F}^{(l)}$ composed of forward thrust and hydrodynamic drag, which is approximately proportional to the velocity squared for the Reynolds number much greater than 1; (ii) attraction $\boldsymbol{F}^{(g)}$ from other individuals in a school; (iii) arrayal force $\boldsymbol{F}^{(p)}$ to equalize velocities of two neighboring fish:

$$\frac{\mathrm{d}\boldsymbol{v}_i}{\mathrm{d}t} = \boldsymbol{F}_i^{(l)} + \boldsymbol{F}_i^{(g)} + \boldsymbol{F}_i^{(p)} + \boldsymbol{\eta}_i. \tag{3}$$

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

We assume that the correlation time of the fluctuating force is very short on the typical macroscopic timescale of eqn (3). This allows us to pass to the idealization of the so-called Gaussian white noise. We set the mean value and variance matrix

$$\langle \boldsymbol{\eta}_i(t) \rangle = 0, \quad \langle \boldsymbol{\eta}_i(t) \boldsymbol{\eta}_j^{\mathrm{T}}(t') \rangle = 2\epsilon\delta_{ij}\delta(t - t')\mathbf{I} \tag{4}$$

respectively, with the Kronecker's symbol δ_{ij}, and the Dirac delta function $\delta(t)$; where $\langle \ldots \rangle$ describes the ensemble average; ϵ denotes the strength of the random force $\boldsymbol{\eta}$; $\mathbf{I}$ is the 3×3 unit matrix.

Let us first consider the locomotory force. From a purely mechanical standpoint a fish can swim forward by pushing its environmental water backward; the surrounding in turn reacts to provide thrust to the fish. Performance (speed and acceleration) depends on the balance between thrust and drag. From the hydromechanical and physiological standpoint, the energy expenditure E to transport a unit weight of fish body a unit distance, which is called the specific energy cost of transport, can be written as (Weihs, 1973*b*, 1974; Webb, 1975; Wu, 1977)

$$E = \alpha\left(\frac{1}{v} + \beta v\right), \tag{5}$$

where α, β are constants. When an individual is moving in steady swimming, its speed v_{m} is given by $\beta^{-1/2}$, at which the specific energy cost E has a minimum. Actual speed that can be maintained almost indefinitely, for example the ocean migrant speed of sockeye salmon, is very close to the minimum energy cost (Brett, 1965*b*; Webb, 1971*a*, *b*), where v_{m} is approximately 1 fish-length sec^{-1} (see also Graham *et al.*, 1990; Kaufmann, 1990; Goolish, 1991). The tendency of the specific energy cost E to seek a minimum value provides the locomotory force which impels the swimming velocity toward the minimum energy cost of transport. We assume that the acceleration of fish swimming is proportional to the gradient of specific energy cost with respect to swimming velocity, i.e. $\partial E/\partial v$, thus the locomotory force is expressed as

$$F^{(l)} = -\tilde{\kappa}\frac{\partial E}{\partial v}, \tag{6}$$

where $\tilde{\kappa}$ is a parameter which may depend on the swimming speed v. At rest fish consume energy at a minimal metabolic rate, accordingly we require that $v = 0$ is the other solution of equation of motion (3), though unstable. Hence we express the locomotory force $\boldsymbol{F}^{(l)}$ as

$$\boldsymbol{F}_i^{(l)} = \kappa(1 - \beta \boldsymbol{v}_i^2)\boldsymbol{v}_i, \tag{7}$$

where κ is constant.

Second, we consider the attractive interaction. For aggregate fish the internal forces are generally attractive in nature except for being repulsive in the very vicinity of individuals. Like the Parr–Breader model (Breder, 1954), using the analogy of intermolecular forces, an individual is subject to attraction and repulsion from other individuals in a school. This mutual interaction force acting on one body located at $\boldsymbol{x}_i$ due to another body located at $\boldsymbol{x}_j$ is assumed to be directed along the line joining the individuals, and to be dependent only upon the distance between two individuals, and is expressed as

$$\boldsymbol{F}_{ij}^{(g)} = a\frac{\boldsymbol{x}_j - \boldsymbol{x}_i}{|\boldsymbol{x}_j - \boldsymbol{x}_i|} - b\frac{\boldsymbol{x}_j - \boldsymbol{x}_i}{|\boldsymbol{x}_j - \boldsymbol{x}_i|^3}, \tag{8}$$

where a and b are constant. Here, it is supposed that the attractive part of $\boldsymbol{F}_{ij}^{(g)}$ is independent of the inter-fish distance, and that the action–reaction law holds, i.e. $\boldsymbol{F}_{ij}^{(g)} = -\boldsymbol{F}_{ji}^{(g)}$. The preferred distance between individuals r_{e}, at which the attractive and repulsive forces balance exactly and the net force vanishes, is given as

$$r_{\mathrm{e}} = \sqrt{\frac{b}{a}}. \tag{9}$$

Observations of various fish schools reveal that r_{e} is

16–25% of the mean body length, and the preferred distance is a statistical quantity found by averaging the actual distance over a long period (Pitcher, 1973; Breder, 1976; Partridge & Pitcher, 1979; Dill *et al.*, 1981; Yarvik & Murav'yev, 1982; Serebrov, 1984).

Furthermore, let us suppose that the total 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. Thus, the attractive interaction force acting on one body owing to a system of bodies is written as

$$\boldsymbol{F}_i^{(g)} = \frac{1}{N-1} \sum_{\substack{j=1 \\ j \neq i}}^{N} \boldsymbol{F}_{ij}^{(g)}. \tag{10}$$

Here, the vector sum of $\boldsymbol{F}_{ij}^{(g)}$ is reduced by the school size N, because the range of influence in $\boldsymbol{F}_{ij}^{(g)}$ must be finite. The summation is performed for all bodies j except i. We shall call $\boldsymbol{F}_i^{(g)}$ the grouping force. Summing $\boldsymbol{F}_i^{(g)}$ over all individuals in a school, the resultant internal grouping force vanishes, i.e. $\Sigma_{i=1}^{N} \boldsymbol{F}_i^{(g)} = 0$, as a result of the action–reaction law.

The grouping forces acting on one body in a school depends on the configuration of the other bodies determined by solving the complex many-body problem (3). As eqn (10) is intractable, we assume that the composite individuals of a school are uniformly distributed over a sphere of radius R. We may write the normalized distribution $\rho(\boldsymbol{x})$ as the first-order approximation:

$$\rho(\boldsymbol{x} - \boldsymbol{X}) = \begin{cases} \left(\dfrac{4\pi}{3} R^3\right)^{-1} & |\boldsymbol{x} - \boldsymbol{X}| \leqslant R, \\ 0 & |\boldsymbol{x} - \boldsymbol{X}| > R, \end{cases} \tag{11}$$

where $\boldsymbol{X}$ is the center of the school defined by $\boldsymbol{X} = \Sigma_{j=1}^{N} \boldsymbol{x}_j / N$. Accordingly, the attractive force, acting on one body located at $\boldsymbol{x}_i$ in the uniformly distributed spherical school of radius R, can be expressed as

$$\boldsymbol{F}_i^{(g)} = \frac{\omega^2}{N} \left[1 - \frac{\gamma^2}{N^2} \left\{ \sum_{j=1}^{N} (\boldsymbol{x}_j - \boldsymbol{x}_i) \right\}^2 \right] \sum_{j=1}^{N} (\boldsymbol{x}_j - \boldsymbol{x}_i), \tag{12}$$

where $\omega^2 = (a/R)(1 - r_c^2/R^2)$, $\omega^2\gamma^2 = a/5R^3$, and $|\boldsymbol{x}_i - \boldsymbol{X}| \leqslant R$. We regard eqn (12) as the first-order approximation of the grouping force produced on one body owing to the other bodies surrounding it. The detail of derivation is given in Appendix A. Equation (12) is rewritten in the following form:

$$F^{(g)}(r) = -\omega^2(1 - \gamma^2 r^2) r, \tag{13}$$

where $r = |\boldsymbol{x} - \boldsymbol{X}| \leqslant R$. This means that the force $F^{(g)}$ is attractive toward the center of the school, and ω is the frequency of harmonic component, and γ represents the inharmonicity of the grouping force. Using the analogy of intermolecular interaction, we speculate that the resultant internal attraction of grouping fish produces, on average, a centrally attractive force acting on an individual. Partly because of a limited number of individuals in the school and partly because of non-uniformity in their spatial distribution, the resultant internal force acting on an individual also produces a fluctuating force which arises chiefly from chance encounters with individuals who happen to be in the neighborhood of the individual in question.

For a fish located at $\boldsymbol{x}_i$ outside the school, i.e. $r = |\boldsymbol{x}_i - \boldsymbol{X}| > R$, the force acting on it can be expressed as

$$F^{(g)}(r) = -a\left(1 - \frac{R^2/5 + r_c^2}{r^2}\right). \tag{14}$$

The force $F^{(g)}(r)$ is also attractive toward the center of the school. If a fish is too far away from the school, it swims toward the school (Keenleyside, 1955).

Third, we investigate the arrayal force. Two neighboring fish tend to swim parallel with each other and to equalize their velocities. Weihs (1973*a*, 1975) suggested that hydrodynamic interactions between fish swimming close to each other cause synchronized motion in tight formation. Hydrodynamics tells us that neighboring fish can make use of the energy shed by each other to ease their own motion through the water, and polarized formations can bring large economies in the energy required for swimming at a given speed. Hence we assume that the arrayal interaction takes place only when an individual finds the neighbors within a sphere of influence, and the arrayal force acting on the i-th body is expressed as the following (Sakai, 1973; Aoki, 1982; Huth & Wissel, 1990, 1992):

$$\boldsymbol{F}_i^{(p)} = \frac{J}{N_i} \sum_{\boldsymbol{x}_j \in S_i^{(p)}} \left(\frac{d\boldsymbol{x}_j}{dt} - \frac{d\boldsymbol{x}_i}{dt} \right), \tag{15}$$

where J is the coefficient of arrayal force; $S_i^{(p)}$ represents the sphere of influence around the i-th body; the summation is performed only for the bodies within the sphere of influence $S_i^{(p)}$ around the i-th body, and N_i is the number of fish within the sphere. Here, the action–reaction law is also supposed to hold. Let us suppose that the range of interaction is very long, so that each individual effectively interacts with a mean field, $\bar{\boldsymbol{v}} \equiv \Sigma_{j(\neq i)} \boldsymbol{v}_j/(N-1)$, produced by all the other individuals. Therefore we have

$$\boldsymbol{F}_i^{(p)} = J(\bar{\boldsymbol{v}} - \boldsymbol{v}_i) = \frac{J}{N} \sum_{j=1}^{N} (\boldsymbol{v}_j - \boldsymbol{v}_i). \tag{16}$$

This means that each individual has an effective constant interaction with all the other individuals (Stanley, 1980).

In summary, the equation of motion for i-th individual in the school ($i = 1, 2, \ldots, N$) can be written as

$$\ddot{x}_i = \kappa(1 - \beta\dot{x}_i^2)\dot{x}_i + \frac{J}{N}\sum_{j=1}^{N}(\dot{x}_j - \dot{x}_i)$$

$$+\frac{\omega^2}{N}\left[1 - \frac{\gamma^2}{N^2}\left\{\sum_{j=1}^{N}(x_j - x_i)\right\}^2\right]\sum_{j=1}^{N}(x_j - x_i) + \eta_i(t), \tag{17}$$

where dot represents time derivative, i.e. $\dot{x} = \mathrm{d}x/\mathrm{d}t$, $\ddot{x} = \mathrm{d}^2x/\mathrm{d}t^2$. Here we may regard parameter β as the non-linearity of the system; parameter κ^{-1} as the sensitivity of individual behavior to surrounding individuals or environment. Movements of individual fish with small κ are easily affected by environment.

3. Analysis

A general solution of these non-linear stochastic equations (17) is probably hopeless. However, there are classes of interesting phenomena in which these equations can be considerably simplified and reduced. In order to investigate global properties of the system which consists of a great number of individuals, we separate $\dot{x}_i$, into the following two terms

$$\dot{x}_i = \dot{X} + \dot{\xi}_i, \tag{18}$$

where $\dot{X}$ is the velocity of the center of the school defined by $\dot{X} \equiv \Sigma_{i=1}^{N}\dot{x}_i/N$, and the remaining part denotes fluctuation around it. By inserting (18) into (17), and averaging over all individuals in the school, we have the equation for macrovariable $\dot{X}$ describing the collective properties of the movement of the school:

$$\ddot{X} - \kappa\left(1 - \frac{5}{3}\beta\sigma_v^2\right)\dot{X} + \kappa\beta\dot{X}^2\dot{X} = \bar{\eta}(t), \tag{19}$$

where $\sigma_v^2 \equiv \Sigma_{i=1}^{N}\dot{\xi}_i^2/N$, and stochastic force $\bar{\eta}(t) \equiv \Sigma_{i=1}^{N}\eta_i(t)/N$. $\bar{\eta}(t)$ denotes a Gaussian random force satisfying the relation

$$\langle\bar{\eta}(t)\bar{\eta}^{\mathrm{T}}(t')\rangle = \frac{2\epsilon}{N}\delta(t - t')\mathbf{I}. \tag{20}$$

The strength of the random force, ϵ/N, is inversely proportional to the system size N. It should be noted that σ_v^2 arises from the interplay between the individual fluctuating behavior and the non-linearity of the system. Subtracting eqn (19) from eqn (17), we obtain

$$\ddot{\xi}_i - \kappa(1 - \beta\dot{X}^2)\dot{\xi}_i + 2\kappa\beta(\dot{X}\cdot\dot{\xi}_i)\dot{X}$$

$$= -J\dot{\xi}_i - \omega^2(1 - \gamma^2\xi_i^2)\xi_i + \mathcal{O}(\dot{\xi}_i^2) + \tilde{\eta}_i(t), \tag{21}$$

where $\tilde{\eta}_i(t) \equiv \eta_i(t) - \bar{\eta}(t)$ satisfies the relation

$$\langle\tilde{\eta}_i(t)\tilde{\eta}_j^{\mathrm{T}}(t')\rangle \approx 2\epsilon\delta_{ij}\delta(t - t')\mathbf{I} \tag{22}$$

for a large system, $N \gg 1$. We can estimate the magnitude of $\dot{\xi}_i^2$ at the order of the strength of the random force, ϵ/J. The third term of the left-hand side of eqn (21) acts to decay the fluctuation $\dot{\xi}_i$, strictly speaking the component of the fluctuating correction term of the individual velocity $\dot{x}_i$, parallel to the velocity $\dot{X}$ with which the school moves as a whole, i.e. $\dot{\xi}_{i\parallel}$. This dumping force is proportional to the velocity square, $|\dot{X}|^2$. For simplicity we assume

$$2\kappa\beta(\dot{X}\cdot\dot{\xi}_i)\dot{X} = \frac{2}{3}\kappa\beta|\dot{X}|^2\dot{\xi}_i, \tag{23}$$

where the denominator "3" is the dimensionality of space where the fish swim.

The non-linear term $\xi_i^2\xi_i$ in eqn (21) may be replaced by $\langle\xi_i^2\rangle\xi_i$. As we have the approximate distribution (11) of individuals in the school, the average $\langle\xi_i^2\rangle$ is determined using $\rho(\xi_i)$:

$$\langle\xi_i^2\rangle = \int\xi_i^2\rho(\xi_i)\mathrm{d}^3\xi_i = \frac{3}{5}R^2, \tag{24}$$

where $\mathrm{d}^3\xi\,(\equiv \mathrm{d}\xi_x\mathrm{d}\xi_y\mathrm{d}\xi_z)$ is a three-dimensional volume element at ξ_i. From eqn (9), the space occupied by one body in a school is roughly estimated at volume $4\pi r_e^3/3$, hence we have

$$R^3 = r_e^3 N. \tag{25}$$

Then we obtain

$$\langle\xi_i^2\rangle = \frac{3}{5}r_e^2 N^{\frac{2}{3}}. \tag{26}$$

Consequently, neglecting $\mathcal{O}(\dot{\xi}_i^2)$, we have the linearized equation for microvariable $\dot{\xi}_i$ describing the fluctuating behavior of an individual in the school:

$$\ddot{\xi} - \kappa\left(1 - \frac{J}{\kappa} - \frac{5}{3}\beta\dot{X}^2\right)\dot{\xi}$$

$$+\omega^2\left(1 - \frac{3}{5}\gamma^2 r_e^2 N^{\frac{2}{3}}\right)\xi = \tilde{\eta}(t), \tag{27}$$

where subscript i is omitted.

Equations (19) and (27) show the dynamics of formation of the fish school, and hierarchical structure (e.g. Nicolis, 1986) of the system, which means that the school receives selective information (i.e. σ_r^2) *from below*, namely composite elements, and in turn it exercises efferent feed-forward control commands (i.e. $\dot{X}^2$) on the dynamics of the individual level. We can see that this hierarchical structure is constructed by the non-linearities of the system.

Since, in general, microvariables vary much more rapidly than macrovariables, eqn (27) is solved first for fixed $\dot{X}^2$. The collective property $\dot{X}^2$ is determined self-consistently using the solution of eqn (27). The solution of the Langevin equation (27) for a harmonic oscillator with the frictional force proportional to the velocity takes the following asymptotic forms (e.g. Hori, 1977):

$$\langle \xi^2 \rangle \approx \frac{3\epsilon}{\omega^2\left(1-\frac{3}{5}\gamma^2 r_e^2 N^{\frac{2}{3}}\right)\left(\frac{5}{3}\kappa\beta\dot{X}^2+J-\kappa\right)} \approx \frac{3r_e N^{\frac{1}{3}}\epsilon}{a\left(\frac{5}{3}\kappa\beta\dot{X}^2+J-\kappa\right)}, \tag{28}$$

$$\langle \dot{\xi}^2 \rangle \approx \frac{3\epsilon}{(5/3)\kappa\beta\dot{X}^2+J-\kappa}, \tag{29}$$

for large t. These show the approximate relations between the variances of microvariables and the collective property. The spatial size of the fish school, defined by the variance $\langle \xi^2 \rangle$ of the distribution of fish in the school, is proportional to the one-third power of the population size of school, N. The fluctuation of the individual velocity in the school, $\langle \dot{\xi}^2 \rangle$, is independent of the grouping cohesiveness, ω^2, and hence is explicitly independent of the population size N. The spatial school size (28) was obtained from the linearized Langevin equation (27) by using the variance of the uniformly distributed spherical school [eqn (11)] as stated above. We should note that the variance (26) of the supposed distribution is proportional to $N^{2/3}$. A more precise distribution of the composite individual may be self-consistently obtained by iterating the above procedure. Namely, we replace the many-body problem (3) by the problem of solving the motion of one fish on which a certain self-consistent force acts; from this solution we then go back and calculate the self-consistent force itself; we iterate this procedure until the solution converges. However, as we are here interested in the temporal behavior of the school, we analyze the dynamical equation of motion (3) by using eqns (28) and (29) as the first-order approximation. We will discuss the self-consistent determination of the spatial size of the school later on.

As a result of the above first-order approximation, the number of degrees of freedom of the system (17) is greatly reduced. Substituting $\sigma_r^2 = \langle \dot{\xi}^2 \rangle$ in eqn (19), which holds for a large school, $N \gg 1$, leads to the self-contained equation describing the collective motion of individuals in the school. If individuals are sufficiently sensitive to behavior of other individuals, i.e. the parameter κ is small compared with the arrayal interaction, J:

$$\frac{\kappa}{J} \ll 1, \quad \frac{\kappa\beta\dot{X}^2}{J} \ll 1, \tag{30}$$

collecting the terms of the order of κ, we obtain the following non-linear Langevin equation to first order:

$$\frac{\mathrm{d}V}{\mathrm{d}t} - \kappa\left(1-5\frac{\beta\epsilon}{J}\right)V + \kappa\beta V^2 V = \ddot{\eta}(t), \tag{31}$$

where V is the centroid velocity of the school, i.e. $V \equiv \dot{X}$. Here the coefficient $\kappa(1-5\beta\epsilon/J)$ is a growth rate of the system.

For our purpose it is convenient to switch to the equation governing the temporal evolution of the probability density $P(V, t)$ of the process $V(t)$. This is the so-called Fokker–Planck equation (Haken, 1983):

$$\frac{\partial}{\partial t}P(V,t) = -\frac{\partial}{\partial V}\cdot\left\{\kappa\left(1-5\frac{\beta\epsilon}{J}\right)V + \kappa\beta V^2 V\right\} \times P(V,t) + \frac{\epsilon}{N}\frac{\partial^2}{\partial V^2}P(V,t), \tag{32}$$

where

$$\frac{\partial}{\partial V} \equiv \begin{bmatrix} \frac{\partial}{\partial V_x} \\ \frac{\partial}{\partial V_y} \\ \frac{\partial}{\partial V_z} \end{bmatrix}, \quad \frac{\partial^2}{\partial V^2} \equiv \frac{\partial^2}{\partial V_x^2} + \frac{\partial^2}{\partial V_y^2} + \frac{\partial^2}{\partial V_z^2}. \tag{33}$$

The coefficient of the first derivative, that is, the drift, describes the systematic evolution of $V(t)$, and the coefficient of the second derivative, that is, the diffu-

TABLE 1
Feature of polarization–non-polarization transition of the school structure

State	Non-polarized (disordered)	Polarized (ordered)
Critical relation between parameters	$5\frac{\beta\epsilon}{J} > 1$ $(\theta > 0)$†	$5\frac{\beta\epsilon}{J} < 1$ $(\theta < 0)$
Most probable velocity: $P_{st}(V) = \max$‡ $U(V) = \min$§	$\lvert V\rvert = 0$	$\lvert V\rvert = \sqrt{\frac{1}{\beta}\left(1 - 5\frac{\beta\epsilon}{J}\right)} \propto \lvert\theta\rvert^{1/2}$

† Critical parameter $\theta = 5\beta\epsilon/J - 1$.
‡ Distribution function $P_{st}(V) = \mathcal{N}\exp[-\kappa U(V)/(\epsilon/N)]$, where $\mathcal{N}$ is a normalization factor.
§ Potential function $U(V) = -(\theta/2)V^2 + (\beta/4)V^4$.

sion, the variance around it. The stationary solution of eqn (32) is given by

$$P_{st}(V) \propto \exp\left[\left\{\frac{\kappa}{2}\left(1 - 5\frac{\beta\epsilon}{J}\right)V^2 - \frac{\kappa\beta}{4}V^4\right\}\Big/(\epsilon/N)\right]. \quad (34)$$

The extrema of P_{st} are usually identified with the macroscopic stationary state: The maxima, where the process spends relatively much time, as the stable stationary states, and the minima, which the process leaves rather quickly, as unstable states. The extrema of $P_{st}(V)$ are the roots of

$$\kappa\left(1 - 5\frac{\beta\epsilon}{J}\right)V - \kappa\beta V^2 V = 0. \quad (35)$$

Using this formalism we consider the influence of fluctuation. From eqn (35) we obtain the roots:

$$|V_0| = 0 \quad \text{and} \quad |V_1| = \sqrt{\frac{1}{\beta}\left(1 - 5\frac{\beta\epsilon}{J}\right)}. \quad (36)$$

We have the following situation. For $J < 5\beta\epsilon$, V_0 is a maximum. Thus, in first-order approximation, when the strength of noise dominates the tendency of the polarization, the center of mass of individuals hardly moves, and the non-polarized school performs a Brownian, i.e. amoebic, movement owing to the fluctuating forces. On the other hand, for $J > 5\beta\epsilon$, V_0 becomes a minimum and new maxima appear at $|V_1|$. This time fish as a whole tend to perform a rectilinear movement, thus forming a polarized school. We see that the fluctuation can deeply modify the macroscopic behavior of the system: namely, noise-induced transition (Horsthemke & Lefever, 1983), as exhibited in Table 1. The order of magnitude of school velocity has the characteristic feature of the order parameter (e.g. Stanley, 1980), because it exhibits the degree of polarization (Fig. 1).

We now consider the formation process of macroscopic structure, that is, the polarized schooling, provided that the system is initially inactive and non-polarized: namely, near the instability point, $V = 0$. We analyze the transient phenomena described by the non-linear Langevin equation (31) in the case of $J > 5\beta\epsilon$, with a simple dynamical molecular field theory (Suzuki, 1978*a*, *b*, 1981), where the system has the global stable state at $|V| = \sqrt{(1 - 5\beta\epsilon/J)/\beta}$. The simplest dynamical molecular field treatment may be to replace the non-linear term $V^2(t)V(t)$ in eqn (31) by $\langle V^2(t)\rangle V(t)$, where the average $\langle V^2(t)\rangle$ is deter-

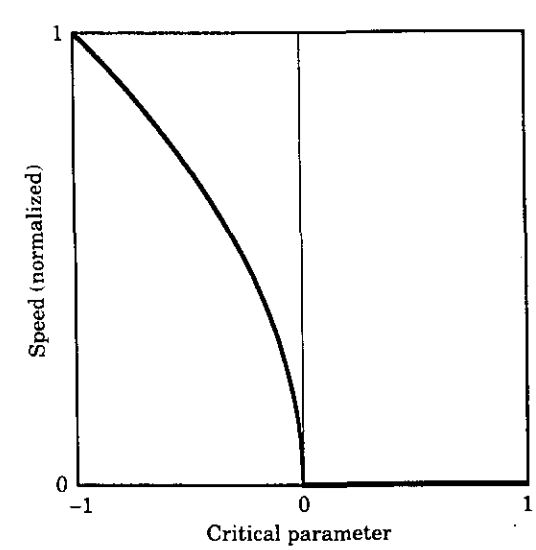

FIG. 1. Change of the centroid speed for different critical parameters $\theta = 5\beta\epsilon/J - 1$. The normalized speed $|V/\beta^{-1/2}|$ vs. θ is shown. θ changes its sign at the critical point $5\beta\epsilon/J = 1$. We therefore distinguish between the two regions $\theta < 0$ and $\theta > 0$. For the polarized state, $\theta < 0$, the most probable speed is given by $|V| = |\theta/\beta|^{1/2}$. For the non-polarized state, $\theta > 0$, the most probable speed is given by $|V| = 0$.

mined self-consistently using the solution of the linearized Langevin equation. Thus we arrive at the following equation of self-consistency for the variance of the school velocity, $Z(t) \equiv \langle V^2(t)\rangle$:

$$\frac{\mathrm{d}}{\mathrm{d}t}Z(t) = 2\left\{\kappa\left(1-5\frac{\beta\epsilon}{J}\right)-\kappa\beta Z(t)\right\}Z(t)+6\frac{\epsilon}{N}. \quad (37)$$

This equation is derived in Appendix B. The solution of this equation takes the following asymptotic form:

$$Z(t) = Z_{\mathrm{st}}\frac{\tau}{1+\tau} \quad (38)$$

where

$$\tau = \frac{\beta}{1-5\beta\epsilon/J}\left\{Z(0)+\frac{3\epsilon/N}{\kappa(1-5\beta\epsilon/J)}\right\} \times \exp\left[2\kappa\left(1-5\frac{\beta\epsilon}{J}\right)t\right] \quad (39)$$

for small ϵ/N and $\langle V^2(0)\rangle$, and for large t; where

$$Z_{\mathrm{st}} = \langle V^2\rangle_{\mathrm{st}} = \frac{1}{\beta}\left(1-5\frac{\beta\epsilon}{J}\right)+\mathcal{O}(\epsilon/N). \quad (40)$$

It should be noted that $\langle V^2(t)\rangle$ expresses the fluctuation of $V(t)$ for rather small t, but in the intermediate time region, $\tau \approx 1$, the order of magnitude of $\langle V^2(t)\rangle$ becomes quite different from the initial value of the order of ϵ/N, and begins gradually to show the feature of the order parameter. Thus, the above enhancement of the fluctuation can be regarded as the essential mechanism of the formation of macroscopic order: namely, schooling structure. The time for this onset of schooling structure is given by $\tau \approx 1$; thus we have

$$t_0 \approx -\frac{1}{2\kappa(1-5\beta\epsilon/J)}\ln\left[\frac{\beta}{1-5\beta\epsilon/J}\left\{\langle V^2(0)\rangle + \frac{3\epsilon/N}{\kappa(1-5\beta\epsilon/J)}\right\}\right]. \quad (41)$$

The onset time t_0 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. This qualitative gradual change is an essential aspect of onset process of macroscopic order or schooling structure. This time becomes larger, as the non-linearity β and the sum of the initial fluctuation $\langle V^2(0)\rangle = \Sigma_{i=1}^{N}\langle v_i^2(0)\rangle/N^2$ (of order ϵ/N) and the strength of the random force $(\epsilon/N)\kappa^{-1}$ become small. The mechanism for fluctuation enhancement is found to be *synergism* (or *co-operative effect*) of initial fluctuations, random force and non-linearity of the system (Suzuki, 1978*a*, *b*, 1981). It should be also noted that eqn (38), of which the functional form may be dependent on approximations, yields an asymptotically correct value of $\langle V^2(t)\rangle$ for infinite time: namely, it describes qualitatively a global feature of the system.

The universal functional form of $\langle V^2(t)\rangle$ can be obtained by a scaling theory of transient phenomena near the instability point, or the master equation approach. The asymptotically rigorous solution is expressed as (Suzuki, 1976*a*, *b*, 1977*a*, *b*, *c*, 1978*a*, *b*, 1981, 1984, 1985)

$$\langle V^2(t)\rangle = \langle V^2\rangle_{\mathrm{st}}\frac{1}{\sqrt{2\pi}}\int_{-\infty}^{+\infty} e^{-q^2/2}\frac{q^2\tau}{q^2\tau+1}\,\mathrm{d}q \quad (42)$$

in the limit $(\epsilon/N) \to 0$, for τ and $\langle V^2(0)\rangle/(\epsilon/N)$ fixed. It should be remarked that the previous solution (38) obtained by the dynamical molecular field theory agrees qualitatively with the solution (42), and the timescale of onset of macroscopic order (41), i.e. $\tau \approx 1$, is also correct even in this limit.

4. Comparison with Experimental Results

Experimental observation for transient phenomena of the formation of schooling structure has been performed in detail by Aoki (1980) on *Gnathopogon elongatus elongatus* school. He quantitatively studied the temporal evolution of the schooling structure from the non-polarized to polarized state in a tank-enclosed eight-fish school of *Gnathopogon* of body length 50–65 mm. He measured a time change of the position of the center of the school: namely, the velocity of the school changing with time in process of development of school structure from initial inactive state to rectilinear movements as a whole. Figure 2 shows the temporal evolution of the squared velocity of the center of the school, $Z(t) = \langle V^2(t)\rangle$, where the experimental points exhibit the square of the averaged absolute value of the school velocity, i.e. $\langle|V(t)|\rangle^2$, instead of mean squared velocity of the school, i.e. $\langle V^2(t)\rangle$. Aoki's observations signify that when a fish accidentally swims outward from the school in the state of amoebic movement, its nearest-neighbor companions draw toward and follow it: that is, fluctuation or random motion of individuals in a school causes the trailer with which nearest neighbors equalize their velocities, on the assumption of equivalence among fish. If this initial fluctuation is sufficiently large, the order (i.e. polarization) locally

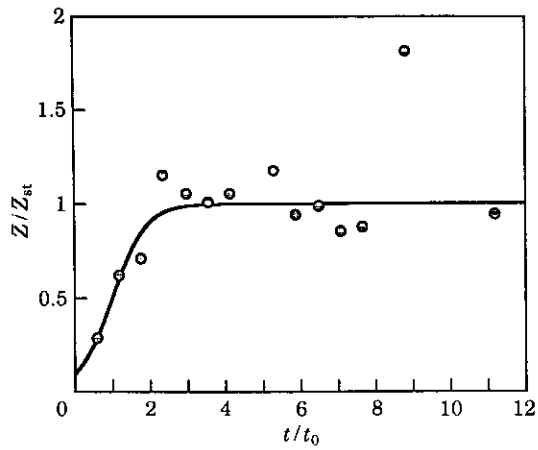

FIG. 2. Transient behavior of formation of polarized school structure. The squared velocity of the center of *Gnathopogon* school, composed of eight individuals, is shown as a function of time, $Z(t) = \langle V^2(t) \rangle$. The experimental points, which were calculated from Aoki's data (Aoki, 1980; fig. 44), can satisfactorily fit by the theoretical curve based on eqn (38) with onset-time of the schooling structure, $t_0 = 0{\cdot}85$ sec, initial variance $Z(0) = 2{\cdot}1\ \mathrm{cm^2\,sec^{-2}}$, and steady swimming speed squared $Z_{st} = 22{\cdot}0\ \mathrm{cm^2\,sec^{-2}}$. These values were estimated from the experimental data by using the least-squares method (SALS). Time t and squared velocity $Z(t)$ are normalized with t_0 and Z_{st} respectively.

appearing in a school grows rapidly to a high degree of parallel orientation throughout the school. He showed the validity of the equivalence: namely, the absence of leaders in the *Gnathopogon* school. While the number of the constituent members of his experimental school may not be so large, his experimental observations and results completely confirm the theoretical predictions of the analysis developed here, and the fundamental concept—synergism.

Moreover, Aoki (1980) also measured the mean angular deviation of individuals from the direction of movement of the school, which shows a degree of irregularity in orientation among fish within the school. The deviation was settled lower at the onset of the schooling structure. Here again the experimental results qualitatively agree with eqn (29), the variance of individual velocity in the school.

5. Discussion

In this paper we have discussed *collective properties* of the fish school, where the composite individuals are treated similarly to gas molecules obeying Newton's laws of motion. A statistical mechanical treatment of the formation process of fish schooling and a fundamental concept (i.e. synergism) were proposed. The non-linear Langevin equation describing the collective motion of the fish school was derived, and an asymptotic solution illustrating the evolution of the schooling structure was obtained.

Many species of ichthyoid, including in crustacean form, in steady state either polarized schools, in which the composite individuals swim with similar orientation, or non-polarized 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 example, (i) herring schools are polarized in the day but form non-polarized and loose aggregation at night (Buerkle, 1983); (ii) anchovy schools increase their inter-fish distance at night compared to daytime, with the formation of swarms, and the nearest-neighbor distance shows very great variation (Aoki & Inagaki, 1988); (iii) threespine sticklebacks form a non-polarized school which remains 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 (e.g. a predator) as a cohesive unit, the individuals being close and parallel to each other—external stimuli force sticklebacks to organize into a polarized school (Keenleyside, 1955). (iv) Mysid shrimps can also exhibit schooling and swarming behavior (Clutter, 1969). Moreover, Partridge (1980) made time-series analysis with European minnows (*Phoxinus phoxinus*) and showed that correlation between instantaneous velocities of fish increased with school size and as the inter-fish distance decreased. These observations may prove eqns (28), (29) and (36) to be qualitatively accurate.

Instead of eqn (28), the spatial size of the school $\langle \xi^2 \rangle$ with more rigorous accuracy can be obtained self-consistently by using the one-body approximation (e.g. Szabo & Ostlund, 1982) as follows. First we calculate the grouping force $\boldsymbol{F}_0^{(g)}(\xi)$ in the school with spherical symmetry, which has an arbitrary spherical distribution of the constituent bodies, $\rho_0(\xi)$, where all directions are equivalent because here we do not consider the gravity, and then we solve the Langevin equation (27) with $\boldsymbol{F}_0^{(g)}(\xi)$, which is attractive toward the center of the school; thus we get a new $\rho_1(\xi)$. Second we calculate $\boldsymbol{F}_1^{(g)}(\xi)$ with $\rho_1(\xi)$, and then we resolve eqn (27) with $\boldsymbol{F}_1^{(g)}(\xi)$. We repeat these procedures until $\rho_{i+1}(\xi) = \rho_i(\xi)$; thus the self-consistent solution $\langle \xi^2 \rangle_{sc}$ can be obtained as a variance of individual configuration in a school. Here there is a similarity to Hartree's treatment of the atomic problem, which is to replace the many-electron problem by the problem of solving the motion of one electron in a certain self-consistent field. The above calculations may be practicable by means of a computer.

That the dependance of $\langle \xi^2 \rangle$ upon the school size N (i.e. $\langle \xi^2 \rangle$ is expected to be scaled as N^ν) signifies the following. If the exponent $\nu = 0$, individuals do

not exclude each other because the spatial size of a school is independent of N; on the other hand if $\nu = 2/3$, the exclusion is extremely strong so that at a minimum-approach distance an infinitely strong repulsion begins to act on individuals, and the resultant structure of grouping may become regular and geometric as in a crystal lattice; here N is assumed to be sufficiently large. Hence with exponent $\nu = 1/3$ [eqn (28)], which is greater than 0 and less than 2/3, the population pressure is not so high (Morisita, 1954). From Parr–Breder's description of the attractive–repulsive interaction (8) with the infinite-range attraction and the soft-core repulsion, it can be expected that ν is around 1/3, and the average density $\bar{\rho}$ is scaled as $N^{1-3\nu/2}$, where the exponent is positive. Note, however, that the number density observed by Misund (1991) is almost independent of school size N, hence $\nu \approx 2/3$.

Here we also found out the critical relation between the arrayal coupling constant J and the strength of noise or randomness of individual movements ϵ, such that in swarming phase, where $J < 5\beta\epsilon$, the center of the school hardly moves, whereas in schooling phase, with $J > 5\beta\epsilon$, the fish form a tighter group with a rectilinear movement, where β shows the non-linearity of the system—biologically, $\beta^{-1/2}$ is the steady swimming speed of fish. These parameters may depend on the species of fish: for example, tropical fish that inhabit a coral reef usually form swarms; migrant fish generally form highly organized schools. The critical relation can be rewritten in the form:

$$\begin{cases} 5\dfrac{\epsilon/\beta^{-\frac{1}{2}}}{J\beta^{-\frac{1}{2}}} > 1 & \text{for swarming} \\[2ex] 5\dfrac{\epsilon/\beta^{-\frac{1}{2}}}{J\beta^{-\frac{1}{2}}} < 1 & \text{for schooling.} \end{cases} \tag{43}$$

The numerator $\epsilon/\beta^{-1/2}$ represents the magnitude of the random movement in a school, and the denominator $J\beta^{-1/2}$ denotes the mean strength of the arrayal interaction with which one individual is influenced by the other individuals as a whole. This illustrates that as the strength of the arrayal interaction becomes large, at $J\beta^{-1/2} = 5\epsilon/\beta^{-1/2}$, the polarized schooling structure is self-organized. It shows the principal feature of order–disorder transitions (Haken, 1983). Systems, being composed of many subsystems, change their macroscopic behavior (i.e. school velocity and density) dramatically when certain parameters are varied.

The theoretical analysis of the collective motion of the fish school and the experimental observations reported above demonstrate that fluctuating movements of constituents can greatly modify the macroscopic behavior of a system. When the fluctuations grow in amplitude, the transition phenomena can occur that is quite unexpected from a deterministic point of view. It corresponds to situations in which the system no longer adjusts its macroscopic behavior to the average properties of the individuals, which is proportional to $J\beta^{-1/2}$, but responds in a definite way, as investigated in this paper: even though the steady swimming speed of individuals $\beta^{-1/2}$ and the arrayal interaction $J\beta^{-1/2}$ are large, if the randomness of individual movements $\epsilon/\beta^{-1/2}$ is large enough, the individual properties of rectilinear movement are never seen at a hierarchical level above and the system remains stationary. Thus we see that the interplay between the fluctuations and the non-linearities of the system, which construct this hierarchical structure of schooling, leads to drastic modifications of macroscopic behavior of the system, from polarized schooling to non-polarized swarming.

Moreover, we have discussed self-organizing dynamics of school formation, i.e. transient phenomena and the onset of macroscopic order, by using non-linear Langevin equation near the instability point. The process from initial non-polarized form to polarized schooling structure is shown as follows (Sakai, 1973; Inagaki *et al.*, 1976; Aoki, 1980). First, individuals do not yet move but gather; individuals accidentally removed from companions appear; then the other individuals are quickly attracted toward them and follow them, and the fish as a whole tend to perform a rectilinear movement; thus forming a polarized structure. We have seen that the essential mechanism of the onset of polarized schooling structure is the macroscopic enhancement of fluctuation from the initial microscopic one, where synergism or co-operative effect of initial fluctuation, random force and non-linearity of the system plays an important role.

Pelagic fish schools, such as Pacific mackerel migrating over enormous distances, are much more highly organized than those of tropical fish that inhabit a coral reef. This fact suggests the evolutionary advantage of schooling on the migration. 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 a comfortable place, and what distribution of the assembly of schools arises in the sea as a result? 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). The environment also has influences on the strength of its fluctuating movement. If fish swim in a "bad" environment with stress factor, the fluctuating movements of the composite individuals of a school may be enhanced. Hence, not only the swimming activity but also the fluctuation of the individual behavior determines the migration in heterogeneous environment. Furthermore, the fluctuation is important for the random search of 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 composite individuals 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 non-linear Langevin equation (31) describing the motion of fish school. With the noise-induced transition of schooling structure, the mathematical functional form of the resultant distribution of the assembly of schools changes (Niwa, 1991). This is another important character of fish schooling.

So far we have assumed that the swimming abilities of schooling members, which depends on body length, are similar, so that there are no 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, hence there is a certain permitted limit in 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 assumed that each individual efficiently interacts with the average velocity of the entire school. However, the average that 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 its near neighbors than by the distant members of the school. The contribution of each fish to the average is inversely proportional to either the square (owing to vision), or the cube (owing to the lateral line's sensitivity to water displacement) of the distance (Partridge, 1980, 1982).

Similarly, a more detailed description of the attractive–repulsive interaction (taking into account both short-range attractions and hard-core repulsions) is required in order to explain the observed results. A general theory on fish-school behavior must take these considerations into account.

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APPENDIX A

To derive eqn (12) in the main text (the attractive force acting on one body in a school uniformly distributed over a sphere of radius R) we consider eqn (10) in the text, written in cylindrical co-ordinates, r, φ, z, which are related to the Cartesian co-ordinates, x, y, z, by the well-known formulas:

$$x = r\cos\varphi,$$
$$y = r\sin\varphi, \tag{A.1}$$
$$z = z.$$

The attractive interaction produced on one body in the school is a central force because of the symmetry of the system. For simplicity, the origin of the co-ordinates is assumed to be fixed at the center of the school. We calculate the force acting on the body at position $\boldsymbol{x}$ on the z-axis, expressed as components in cylindrical co-ordinates:

$$(r_x, \varphi_x, z_x) = (0, 0, r), \tag{A.2}$$

where the distance between the body and the center of the school, $|r| \leqslant R$.

First we consider the first term of eqn (8) in the text, namely, the attractive two-body interaction between i-th and j-th body, $\boldsymbol{F}_{ij}^{\mathrm{atr}} = a(\boldsymbol{x}_j - \boldsymbol{x}_i)/|\boldsymbol{x}_j - \boldsymbol{x}_i|$. Assuming the linear superposition of forces owing to many bodies in the school, we may write the force due to a system of bodies located at $\boldsymbol{x}_j, j = 1, 2, \ldots, N$, as the vector sum:

$$\boldsymbol{F}^{\mathrm{atr}}(\boldsymbol{x}) = \frac{1}{N}\sum_{j=1}^{N} a\frac{\boldsymbol{x}_j - \boldsymbol{x}}{|\boldsymbol{x}_j - \boldsymbol{x}|}. \tag{A.3}$$

If the bodies are so numerous that they can be described by a probability density $\rho(\boldsymbol{x}')$, the sum is replaced by an integral:

$$\boldsymbol{F}^{\mathrm{atr}}(\boldsymbol{x}) = \int a\frac{\boldsymbol{x}' - \boldsymbol{x}}{|\boldsymbol{x}' - \boldsymbol{x}|}\rho(\boldsymbol{x}')\mathrm{d}^3\boldsymbol{x}', \tag{A.4}$$

where $\mathrm{d}^3\boldsymbol{x}' = r'\mathrm{d}r'\mathrm{d}\varphi'\mathrm{d}z'$ is a three-dimensional volume element at $\boldsymbol{x}'$. Then, the component of the resultant attractive force in the direction of the z-axis, $F_z^{\mathrm{atr}}(\boldsymbol{x})$, is expressed as

$$\frac{F_z^{\mathrm{atr}}(\boldsymbol{x})}{a} = -\int_{z'=-R}^{z'=R}\int_{r'=0}^{r'=\sqrt{R^2-z'^2}}\int_{\varphi'=0}^{\varphi'=2\pi}\frac{r - z'}{\sqrt{r'^2 + (r - z')^2}}\rho(\boldsymbol{x}')r'\,\mathrm{d}r'\,\mathrm{d}\varphi'\,\mathrm{d}z', \tag{A.5}$$

where $\rho(\boldsymbol{x}')$ is given by eqn (11) in the text. The other components of $\boldsymbol{F}^{\mathrm{atr}}(\boldsymbol{x})$ acting on the body on the z-axis of the co-ordinates vanish, because of the spherical symmetry of the system. Consequently we have the attractive term of the grouping force:

$$\frac{F^{\mathrm{atr}}}{a} = -\frac{r}{R} + \frac{r^3}{5R^3}. \tag{A.6}$$

Second, for the repulsive term of eqn (8), i.e. $\boldsymbol{F}_{ij}^{\mathrm{rep}} = -b(\boldsymbol{x}_j - \boldsymbol{x}_i)/|\boldsymbol{x}_j - \boldsymbol{x}_i|^3$, Gauss's law holds (e.g. Jackson, 1975). Hence we have

$$\frac{F^{\mathrm{rep}}}{b} = \frac{r}{R^3}. \tag{A.7}$$

In summary, the grouping force acting on one body in the school can be written as

$$F^{(\mathrm{g})} = F^{\mathrm{atr}} + F^{\mathrm{rep}} = -\left(\frac{a}{R} - \frac{b}{R^3}\right)r + \frac{a}{5}\frac{r^3}{R^3}. \tag{A.8}$$

Substituting $r = |\boldsymbol{x}_i - \Sigma_{j=1}^{N}\boldsymbol{x}_j/N|$, we can obtain eqn (12) in the text.

APPENDIX B

We formally integrate the equation obtained by linearizing eqn (31) in the text:

$$V(t)=\int_0^t \bar{\eta}(t')\exp\left[\kappa\left(1-5\frac{\beta\epsilon}{J}-\beta\langle V^2\rangle\right)(t-t')\right]\mathrm{d}t'+V(0)\exp\left[\kappa\left(1-5\frac{\beta\epsilon}{J}-\beta\langle V^2\rangle\right)t\right]. \quad \text{(B.1)}$$

Then the variance of the school velocity is written as

$$\langle V^2(t)\rangle=-\frac{3\epsilon/N}{\kappa(1-5\beta\epsilon/J-\beta\langle V^2\rangle)}\left\{1-\exp\left[2\kappa\left(1-5\frac{\beta\epsilon}{J}-\beta\langle V^2\rangle\right)t\right]\right\}. \quad \text{(B.2)}$$

Thus, after differentiation with respect to time t, we get the non-linear differential equation of self-consistency for the variance, $Z(t)\equiv\langle V^2(t)\rangle$:

$$\frac{\mathrm{d}}{\mathrm{d}t}Z(t)=2\kappa\left\{1-5\frac{\beta\epsilon}{J}-\beta Z(t)\right\}Z(t)+6\frac{\epsilon}{N}. \quad \text{(B.3)}$$