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A Density-dependent Diffusion Model on Biological Aggregation Phenomena: An Analysis on Fish Shoaling

Hiromi SENO
Information Processing Center of Medical Sciences, Nippon Medical School
Sendagi 1-1-5, Bunkyo-ku, 113 Tokyo
Japan

生物集合に関する密度依存型拡散方程式モデル
：ある群魚(shoaling)についての考察

日本医科大学基礎医学基礎医学情報処理室　　瀬野裕美

As a mathematical model for the biological aggregation phenomena, we consider a density-dependent diffusion equation system with a potential term without growth term and focus on their stationary solutions to investigate the effect of density-dependency type of diffusion and potential on them. The model is applied to analyze a type of fish grouping, "shoaling". The result gives a new information to understand the phenomenon.

Introduction

In the last decades, some density-dependent diffusion equations were investigated to reveal some of their interesting features different from those of density-*independent* diffusion equations (Shigesada *et al.*, 1979; Mimura, 1980; Namba, 1980, 1989; Teramoto and Seno, 1988; Seno, 1989, 1991c). For a review of prototypes of studies on density-dependent diffusion equations, see Okubo (1980).

In some cases, it is very difficult to deal analytically with dynamical aspects of density-dependent diffusion system, so that it cannot help simulating mainly by computers. On the other hand, although the dynamical aspect is worth while being investigated, the stationary solution may sometimes be sufficient to give interesting results to contribute to understanding of a biological phenomenon (Teramoto and Seno, 1988; Seno, 1990, 1991a, 1991b). Despite that very few biological systems could be regarded stationary, a stationary solution in a model may be useful as an approximation to consider a quasi-stationary biological system.

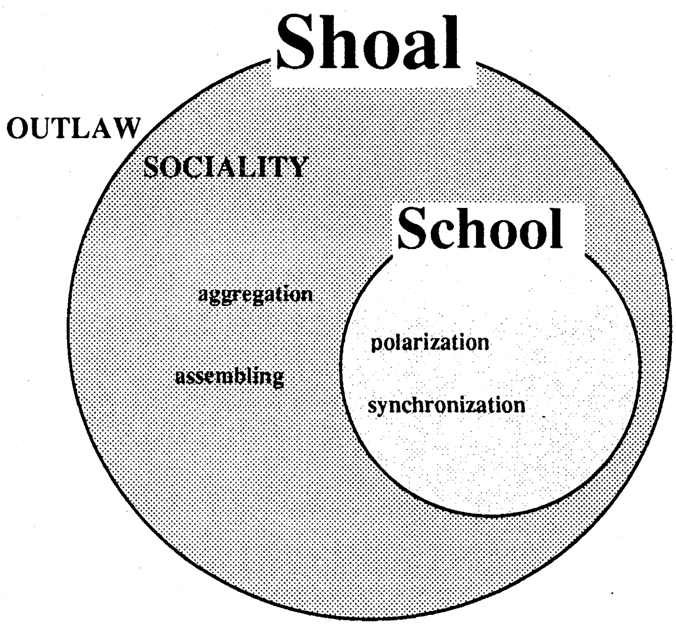

Fig. 1. Category of Fish Grouping (after Pitcher, 1986).

As an application of density-dependent diffusion model for the real phenomeno, we will deal with a type of fish grouping. Fish grouping is very frequently observed in nature. Each grouping might have its behavioral reason in the biological sense (Shaw, 1978; Partridge, 1982; Pitcher, 1986). It is often called "shoaling" or "schooling" (see Fig. 1). Following Parr (1927), Breder (1954), and Okubo *et al.* (1977), we consider the stabilized shoal size in terms of the balance of two counteracting forces aggregating and dispersing ones (see Fig. 2). However, differently from them, we shall not consider the shoal size to be the result of the two counteracting forces *among* individual fish. Instead, our purpose is to discuss shoal size as resulting from two counteracting forces on each individual (Seno, 1990, 1991b). The model is applied to analyze the data for the shoaling of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika (Nakai, private communication). The result gives a new information to consider the shoaling.

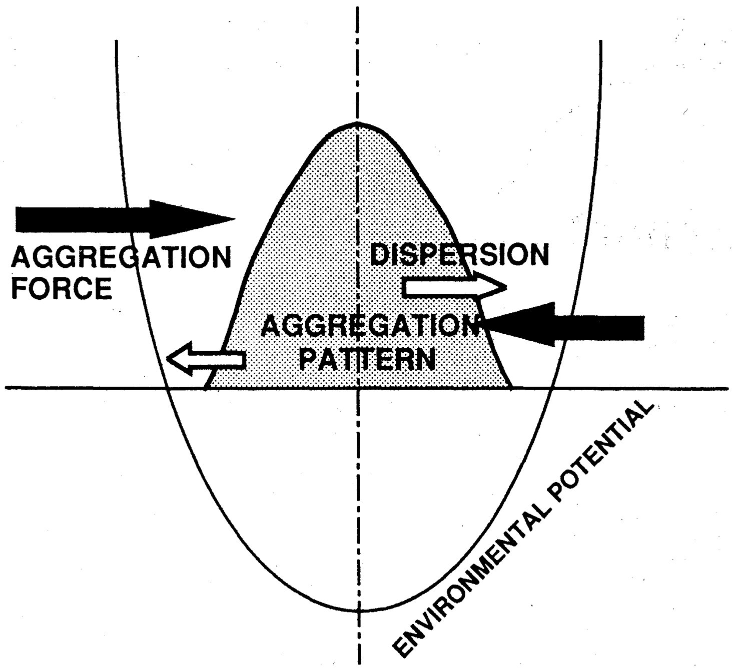

Fig. 2. Modelling of biological aggregation pattern formation.

MODELLING ASSUMPTION

Aggregating Force: An aggregating force is assumed to be directed to the center of aggregating group. We can consider an environmental potential which has its minimum at the center and produces a force directed to it (see Fig. 2).

Dispersing Force: We can assume that the density-dependency of diffusivity is a consequence of intraspecific competition for food among fish in the shoal. At a site in the shoal, the higher the density is, the stronger is the tendency to avoid staying there.

Group Size: The total population of shoaling fish is assumed to be conserved for a considered group. No reproduction, no migration, or no predation are assumed in the considered shoal.

MODEL

At first, we consider a shoal in 2-dimensional space. Since the aggregating force is assumed to be directed to the grouping center and its strength is assumed to depend only on the distance from the center. Our model is described as follows (Seno, 1990, 1991b):

$$\frac{\partial n}{\partial t} = -\operatorname{div}\mathbf{J} \tag{1}$$

$$\mathbf{J} = -\delta\left(\frac{n}{\kappa}\right)^{m} \operatorname{grad} n - n \operatorname{grad} U \tag{2}$$

n is the population density at a site in the space and at time t. $\mathbf{J}$ is the flux of population density which is the 2-dimensional vector. The first term of the right-hand side of (2) represents the density-dependent diffusion force, which becomes stronger as the density gets higher. δ is the diffusivity when n is equal to κ which represents a conventional reference density. The power m is the index of strength of density-dependency of the diffusion. The second term means the aggregating force directed to the grouping center. U is a scalar function of only the distance from the origin which corresponds to the center of shoaling fish.

To consider the size of stabilized shoal, we shall investigate the stationary solution of our model, given by solving $\mathbf{J} = \mathbf{0}$. In addition, the conservation of total population in the shoal implies the following:

$$2\pi\int_{0}^{r^*} n^*\cdot r\mathrm{d}r = N ,$$

where N is a constant of group size, and the factor 2π is resulted from integration with respect to the angle expanded by the shoal around the nest. r^* is an unknown constant which denotes the edge of the distribution n^*, that is, the shoal size. Thus, the special following relation is required:

$$n^*(r^*) = 0.$$

The existence of such a finite r^* is a characteristic nature of density-dependent diffusion (Okubo, 1980). At last, we can obtain

$$n^* = \left(\frac{m\kappa^m}{\delta}\right)^{1/m} \cdot \{U(r^*) - U(r)\}^{1/m}$$

$$\int_0^{r^*} \{U(r^*) - U(r)\}^{1/m} \cdot r\mathrm{d}r = \frac{N}{2\pi} \cdot \left(\frac{\delta}{m\kappa^m}\right)^{1/m}.$$

In the case of 3-dimensional space, the same argument can be applied, while the aggregating group has the shape of 3-dimensional ball and the attractive force directed to the center of the ball works on each individual in it. The resulted equation is fundamentelly the same as above, except for the following conservation relation:

$$\int_0^{r^*} \{U(r^*) - U(r)\}^{1/m} \cdot r^2\mathrm{d}r = \frac{N}{4\pi} \cdot \left(\frac{\delta}{m\kappa^m}\right)^{1/m}.$$

A Special Environmental Potential: $U(r) = \mathrm{sgn}(\gamma)\cdot k\, r^{\gamma}$, where k is a positive constant. Although γ is also a real constant, the characteristic of considered potential field so significantly depends on the sign of γ that we should consider separately the cases of positive and negative γ, especially in terms of the embodied distribution n^*, which can be obtained in a explicit form (Seno, 1990, 1991b). The individual distribution in the aggregating pattern is determined by those parameters γ and m (Seno, 1990; see Fig. 3). However, independently the sign of γ, the relation between the shoal size r^* and the group size N can be expressed in the following form:

$$r^* \propto N^{1/(d + \gamma/m)}, \qquad (3)$$

where $d = 2$ and $d = 3$ respectively in 2-dimensional case and in 3-dimensional case. We will use this proportional relation to investigate the data of the

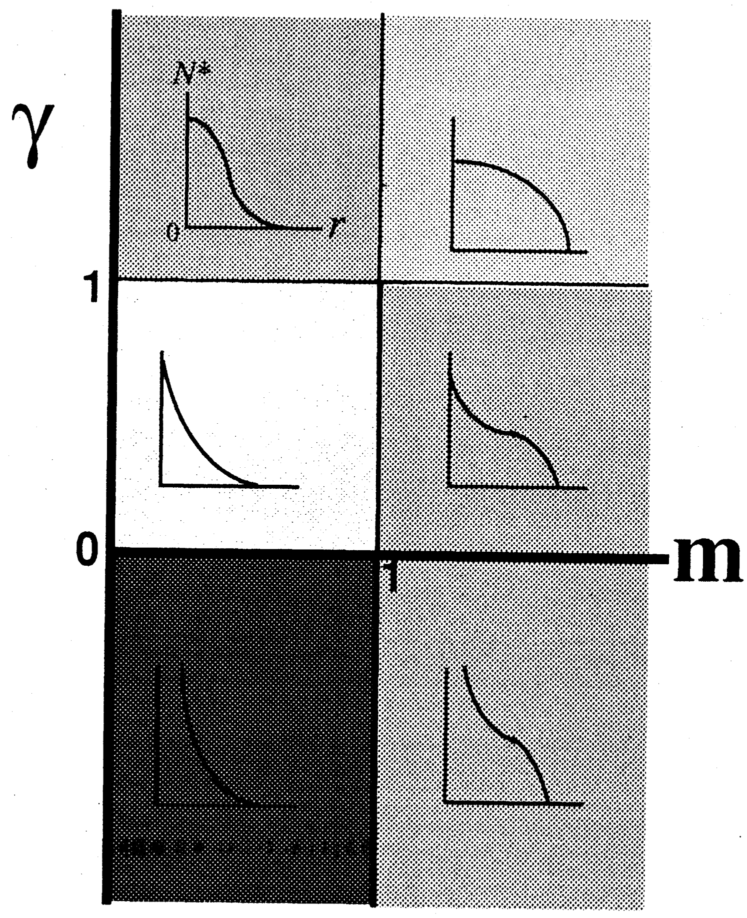

Fig. 3. Parameter dependency of the shape of stationary distribution of the model (Seno, 1990).

shoaling of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika, observed by Nakai (1991, private communication).

ANALYSIS ON THE DATA OF A SHOALING

A detail data of the shoaling of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika is obtained by the observasion (Nakai, private communication). It will be expected that some photographs of the shoal give the information of the distribution of fish in the shoal. But, now, we deal only with the data of the group size and the shoal size, which are easier to be estimated than the fish distribution in the shoal. We will use the relation (3) and estimate the slope of the line fitted to the graph of log(the spatial size of shoal)-log(the group size), and lastly calculate the value γ/m (Fig. 4; Fig. 5).

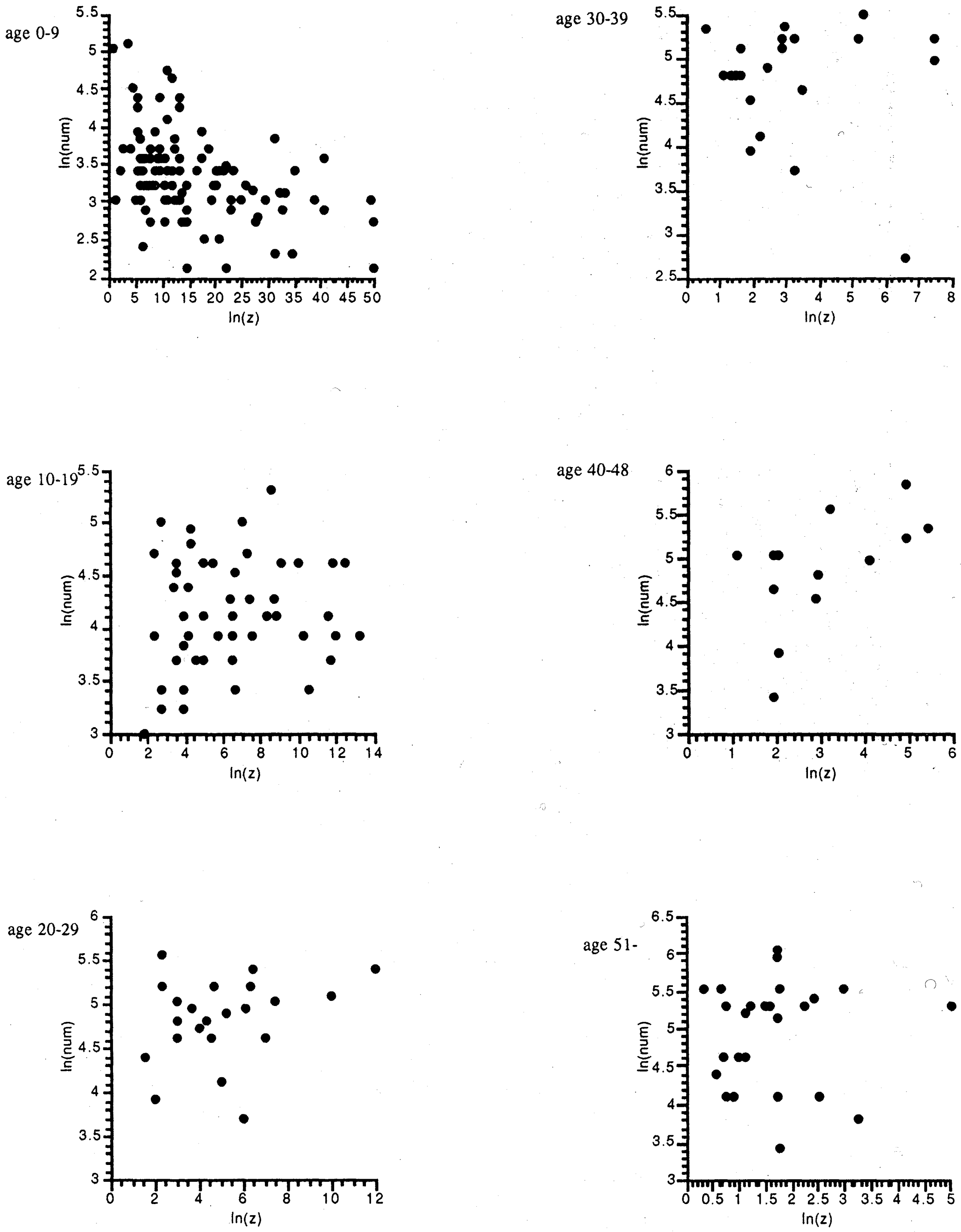

Fig. 4. Data of the shoaling of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika. The vertical axis is of the group size, while the horizontal is of the spatially horizontal size, that is, the 2-dimensional extension length of the shoal.

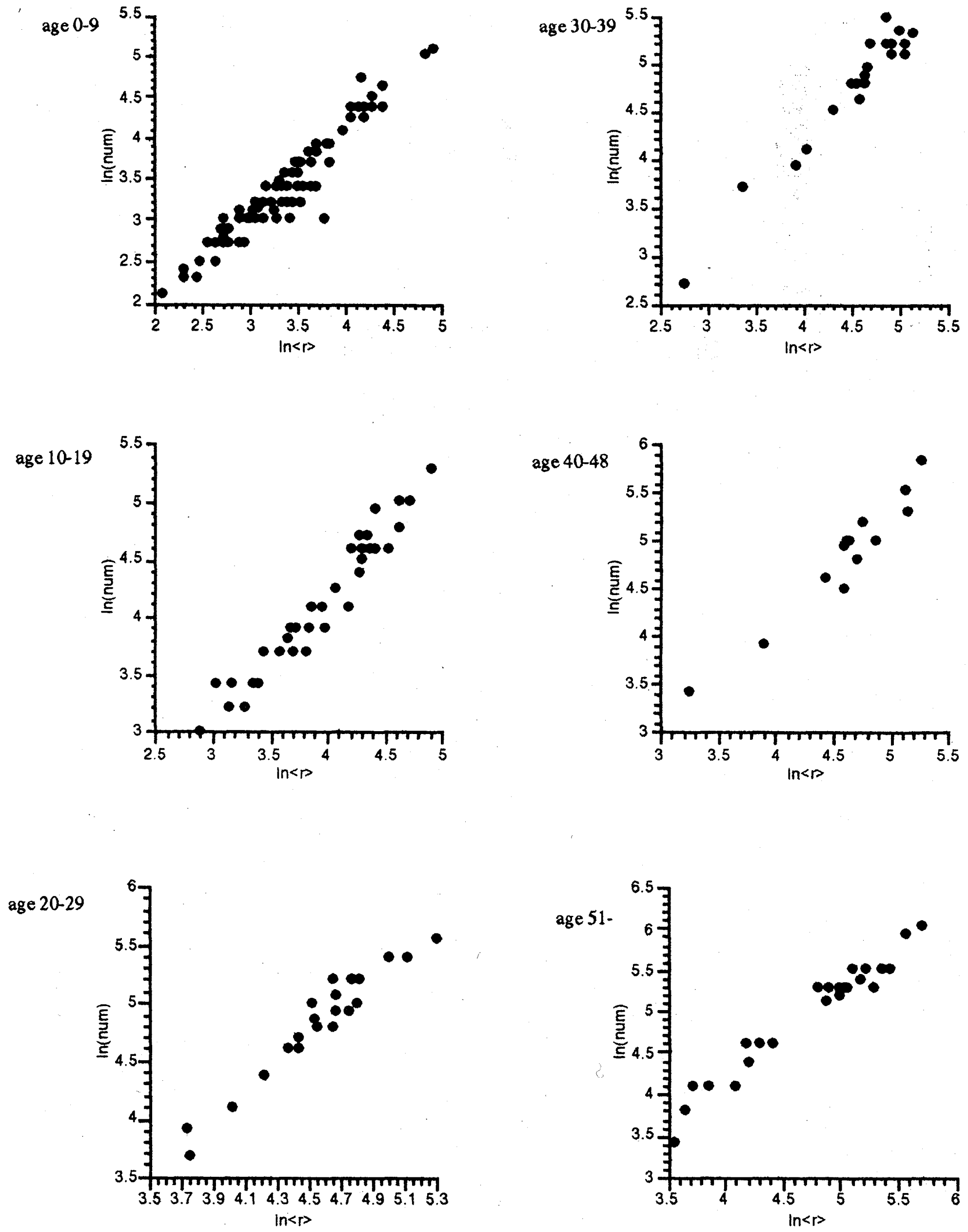

Fig. 5. Data of the shoaling of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika. The vertical axis is of the group size, while the horizontal is of the 3-dimensional shoal size, which is the radius of the ball corresponding to the shoal. The radius <*r*> is calculated regarding the shoal as the ball which has the volume equivalent to that of the ellipsoid of revolution given by the data on the size of shoaling.

Fig. 6. γ/m estimated for the data of the shoaling of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika. The result of t-test is shown: *: $p < 0.01$; **: $p < 0.02$; ***: $p < 0.03$; non-significant in the age 0-9 class of 2-dimensional model case.

The result is shown in Fig. 6. It is shown that the value γ/m does not seem to have any significant variation in the period later after the appearance of shoaling, while it may take a significantly different value in the earlier period after the appearance of shoaling. This means that the ratio (the strength of aggregation tendency)/(the strength of dispersal) is almost constant during the period of shoaling. It is observed that the shoal disappears at a morning for those fish to disperse away. Although the quantity γ/m might be expected to characterize the intrinsic tendency of shoal and to make the indication of the disappearance of shoal, it is not. The reason may be that γ and m are contemporarily decreasing as the fish in the shoal grows. Another possible reason is that the statistical operation enshadows the variation of the quantity, because the dealt data involves so various observed shoals that some disappear in the ealier age class and the others in the later age class. The analysis on the density distribution in the shoal is necessary, made use of this model.

CONCLUSION

The model introduced here is shown to be useful to investigate the aggregation phenomena in nature. It is so simple and so fundamental that it may give the information on the phenomena as the zenoth approximate analysis. Such information is sometimes still useful to consider the real phenomena. The shoaling of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika, is the case. Moreover, it is easy to improve the model to fit the characteristics of the considered real phenomenon. Thus, it is expected that the analysis on the data by this model gives some new information for various kinds of real phenomena.

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