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# A DENSITY-DEPENDENT DIFFUSION MODEL OF SHOALING OF NESTING FISH

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ABSTRACT

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The shoaling of fish about a nest is considered by means of a mathematical model with a density-dependent diffusion equation. The size of the shoal is assumed to be determined by the balance between two counteracting forces: aggregation and dispersion. The parameter dependency of shoal size and density distribution within the shoal is investigated. Although the model is simple, it is expected to contribute to understand some other biological aggregations: swarm, flock, etc. The procedure of fitting data is discussed.

## INTRODUCTION

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'. Avoiding the semantic confusion between these two terms, we shall use the term 'shoal' to mean a group of fish which remain together for social reasons (Kennedy and Pitcher, 1975; Pitcher, 1983), while 'school' is defined as the structured swimming group with a synchronization or a polarization. As is clear from these definitions, schooling can be regarded as a concept included within that of shoaling (Pitcher, 1986). However, we remark that fish grouping cannot be called schooling but can be called shoaling when neither the synchronization nor the polarization is observed or identified among the behaviors of individual fish. Shoaling may correspond to 'flocking' of birds or 'swarming' of insects.

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In this paper, with a mathematical model we shall consider the shoaling of fish about the nest. In particular, we shall focus on the size of shoal, which seems to be highly correlated with some intraspecific factors, and moreover, which can be regarded as a home range for the fish group with its nest. Although fish schooling has been studied with some mathematical models (Breder, 1954; Okubo et al., 1977; Okubo, 1980, 1986; Anderson, 1981) there have been very few mathematical studies on the shoaling of nesting fish (Pitcher, 1986). It is expected that our analysis will become a starting point of such studies and moreover, will give a stimulus to the theoretical study on fish shoaling. Further, we shall discuss the fitting way of our model to a data on shoal.

## MODELLING ASSUMPTION

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. 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.

*Aggregating force.* An aggregating force is assumed to be directed to the nest. Thus, this force embodies a kind of fish's adhesion to the home range, for example, with the memory of direction to the nest. We can consider an environmental potential which has its minimum at the center of the nest and produces a force directed to the nest. We shall investigate a special type of it in the following analysis.

*Dispersing force.* A dispersing force is assumed to be given by a density-dependent diffusion (Mimura, 1980; Namba, 1980; Okubo, 1980; Teramoto, 1982). Diffusion works to make the distribution expand in the space. Though this assumption might seem to neglect too many social aspects of shoaling, 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 the stronger the tendency to avoid staying there. As far as the food distribution is spatially uniform and its depletion by feeding does not have any significant effect on the fish dynamics, this assumption is natural because the individual fish must avoid a crowded place to get a larger share of food at another less crowded place. This tendency must become more pronounced as the group size gets larger.

*Group size.* The total population of shoaling fish is assumed to be constant for a considered group. No reproduction, no migration, and no predation are assumed in the considered shoal. In such a case, the shoaling may be beneficial principally for proper sharing of food, for effective sampling, or for information transfer among the individuals. Moreover, even if there is predator density around a shoal, we can consider that the effect may be implicitly included in a parameter of environmental potential because it determines the strength of fishes' adhesion to the home range related to the strength of predation pressure.

## MODEL

We consider a shoal in 2-dimensional space. In other words, we focus on the horizontal nature of the shoal and do not explicitly consider vertical structure. Nest of the type considered is assumed to occur in sufficiently shallow water, and the fish can be considered to spread out uniformly in the vertical dimension. Further, since the aggregating force is assumed to be directed to the center of nest, and its strength is assumed to depend on the distance from the center of nest, our analysis on the 2-dimensional model can be actually regarded as that on the 1-dimensional one, as we shall see in the following section.

Our model is described as follows:

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

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

where 'grad' is a differential operator which, operating upon a function of several variables, results in a vector, the coordinates of which are the partial derivatives of the function. Also, 'div' is a differential operator that gives the scalar product of the given vector and the vector whose components are the partial derivatives with respect to each coordinate. In both cases, their concrete forms depend on the selected coordinate system (e.g., see Arfken, 1970). $n$ is the population density at a site in the space and at time $t$. $\boldsymbol{J}$ 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. $\delta$ is the diffusivity when $n$ is equal to $\kappa$, 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 nest. $U$ is a scalar function of only the distance from the origin which corresponds to the center of shoaling fishes' nest. This type of 1-dimensional density-dependent diffusion system has been studied by Shigesada et al. (1979), Shigesada

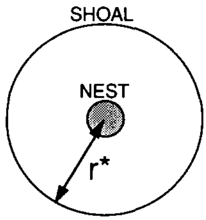


Fig. 1. Model of the fish shoal about a nest. The shoaling zone is a disk of radius $r^*$.

(1980) and Teramoto and Seno (1988) as a model for insects' or cells' aggregation phenomena (also see Okubo, 1980).

To consider the size of a stabilized shoal, we shall investigate the stationary solution of our model. By our assumption, the stationary distribution $n^*$ is a function of only the distance, $r$, from the origin, and the shoaling zone is modelled by a disk region (Fig. 1). It is given by solving $J = 0$:

$$-\delta\left(\frac{n^*}{\kappa}\right)^m \frac{\mathrm{d}n^*}{\mathrm{d}r} - n^* \frac{\mathrm{d}U}{\mathrm{d}r} = 0 \tag{3}$$

In addition, the conservation of total number of population in the shoal implies the following:

$$2\pi \int_0^{r^*} n^* r \,\mathrm{d}r = N \tag{4}$$

where $N$ is a constant of group size, and the factor $2\pi$ 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:

$$n^*(r^*) = 0 \tag{5}$$

The existence of such a finite $r^*$ is a characteristic nature of density-dependent diffusion (Okubo, 1980). By means of (3), (4) and (5) (Appendix A), we can obtain:

$$n^* = \left(\frac{m\kappa^m}{\delta}\right)^{1/m} [U(r^*) - U(r)]^{1/m} \tag{6}$$

$$\int_0^{r^*} [U(r^*) - U(r)]^{1/m} r \,\mathrm{d}r = \frac{N}{2\pi}\left(\frac{\delta}{m\kappa^m}\right)^{1/m} \tag{7}$$

Equation (7) determines the shoal size $r^*$.

A special environmental potential is:

$$U(r) = \mathrm{sgn}(\gamma)\ kr^{\gamma}$$

where $k$ is a positive constant. Although $\gamma$ is also a real constant, the characteristic of considered potential field so significantly depends on the sign of $\gamma$ that we shall consider separately the cases of positive and negative $\gamma$:

$\gamma = \alpha > 0$

In this case, the potential field produces increasing force with distance from the origin. Although this potential field of the harmonic oscillator seems to be unrealistic in some biological systems, especially at a far distance, it may be useful to discuss the relatively small scale of aggregation as an approximated field for such cases. Substituting this potential into (6) and (7), we obtain:

$$n^* = \left(\frac{r^*\eta}{\alpha}\right)^{1/m}\left[1 - \left(\frac{r}{r^*}\right)^{\alpha}\right]^{1/m} \tag{8}$$

$$r^* = \left[\frac{\alpha^{1+1/m}}{2\pi\eta^{1/m}} \frac{N}{B\left(\frac{2}{\alpha}, 1 + \frac{1}{m}\right)}\right]^{1/(2+\alpha/m)} \tag{9}$$

where $\eta \equiv m\kappa^m k\alpha/\delta$, and $B$ is the Beta function defined by:

$$B(a, b) \equiv \int_0^1 x^{a-1}(1-x)^{b-1}\,dx \qquad (0 < a, b) \tag{10}$$

As easily seen in (8), the stationary distribution becomes more platykurtic (flatter) as $m$ gets larger, while it becomes more leptokurtic (steeper) as $m$

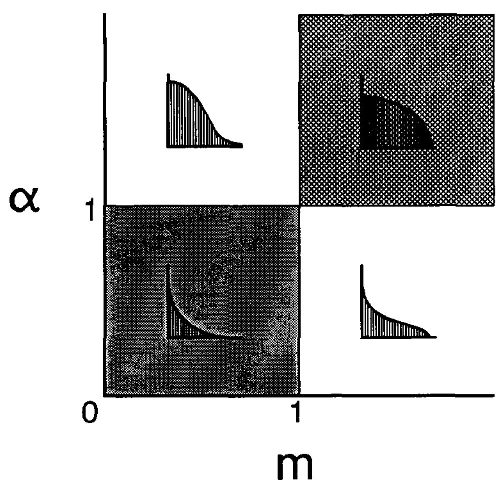


Fig. 2. $(m, \alpha)$-dependency of density distribution within shoal when $\gamma = \alpha > 0$. Each boundary is included within the shadowed region. Depending on those parameters, the distribution shows a variety of patterns.

gets smaller. In Fig. 2, we schematically show how the distribution pattern depends on the parameters $m$ and $\alpha$. It is clearly shown that those parameters reflect the density distribution within the shoal and that an appropriate selection of them can realize a variety of distribution patterns. From (9) we remark that:

$$r^* \propto N^{1/(2+\alpha/m)} \tag{11}$$

$\gamma = -\alpha < 0$

Contrary to the previous case, the aggregating force does not reach a far distance, and the individuals at a far distance have tendency to very low adhesion to the home range. Besides, with this potential function, the potential field diverges at the origin, and so does the stationary distribution. Although such a distribution is unrealistic, this potential function can be useful to approximate the density distribution relatively far from the nest. In the same way as before, we can obtain the stationary distribution and the shoal size in this case:

$$n^* = \left(\frac{\eta}{r^*\alpha}\right)^{1/m}\left\{\left(\frac{r^*}{r}\right)^{\alpha} - 1\right\}^{1/m} \tag{12}$$

$$r^* = \left[\frac{\alpha^{1+1/m}}{2\pi\eta^{1/m}} \frac{N}{B\left(\frac{2}{\alpha} - \frac{1}{m}, 1 + \frac{1}{m}\right)}\right]^{1/(2-\alpha/m)} \tag{13}$$

where $\eta$ is as before. In Fig. 3, it is schematically shown how the distribution pattern depends on $m$ and $\alpha$.

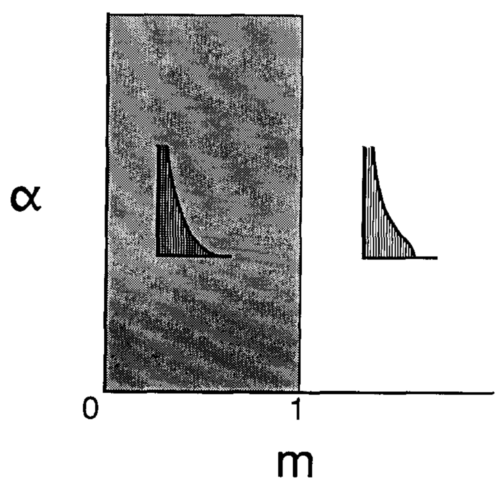


Fig. 3. $(m, \alpha)$-dependency of density distribution within shoal when $\gamma = -\alpha < 0$. Each boundary is included within the shadowed region.

We note that, independently the sign of $\gamma$, the relation between the shoal size $r^*$ and the group size $N$ can be expressed in the following form:

$$r^* \propto N^{1/(2+\gamma/m)} \tag{14}$$

## DISCUSSION

We have shown that the balance between two counteracting forces of aggregating and dispersing determines a unique size of the shoal. Our model may be useful as a rough description of shoaling. Indeed, although it is likely that each parameter embodies several biological factors which determine the shoal pattern, it is expected that some significant aspects of the fishes' shoal, or at least some debating points on it, may be revealed by fitting our model to the data.

Assuming that the data of fish population distribution $n^*$ and of total population $N$ are obtained for a shoal, we can then estimate the parameters in our model, $m$, $\alpha$ and $\eta$, making use of the following relation given by (3):

$$\log \left| \frac{\mathrm{d}(n^*)^m}{\mathrm{d}r} \right| = \log \eta + (\gamma - 1) \log r \tag{15}$$

where the left-hand side can be obtained as the data with its relation to the distance $r$ from the center of nest. As for a possible practical way to obtain the relation corresponding to (15) from the data, see Appendix B. Here we discuss a way to estimate the parameters through (15): At first, the parameter $m$ must be appropriately selected to satisfy a linear relation between the value of the left-hand side of (15) and $\log r$. Next, making use of the graph of (15) for a selected $m$, we can determine $\gamma$ from the slope and $\eta$ from the cross point with the axis. With all these selected parameters, we can obtain the shoal size $r^*$ through (9) or (13), and can compare it with the observed size.

Selected values of $m$ and $\gamma$ can be tested through the relation (14). Indeed, by sampling shoal sizes with a variety of total population, we can obtain the data of relation between the spatial shoal size and the total population in it. Then, making use of (14), we can compare the data to the result by our model with a value $\gamma/m$.

It is likely that some dynamical parameters may change nonlinearly as the spatial shoal size expands. In such a case, since $m$ and $\gamma$ might be functions of $r^*$, the adaptability of a set of $m$, $\gamma$ and $\eta$ determined from a data set might be restricted only for a special range of shoal size.

As the parameters $m$ and $\gamma$ respectively represent the strength of density-dependency of the shoaling fishes' diffusion and the strength of adhesion to the nest, the estimation of those parameters is expected to show intuitively some aspects of the nesting fishes' shoal.

Such data-fitting seems to be possible for some cases of larval nesting shoals: for example, smallmouth-bass nesting behavior has been studied in North American lakes and streams, and observed is the shoaling of larval fish about the nest, a phenomenon that takes place during a period of a few weeks following hatching (D.L. DeAngelis, private communication). During this time, the male parent guards an area about the nest against possible predators on the nest. During hours of light, the larval fish forage for zooplankton. But we have not yet obtained data enough to carry out the fitting.

Although our model was discussed with respect to shoals of fish about a nest, it can be applied to other biological aggregating phenomena: for example, insects' swarming, animals' flocking, etc. With some mathematical models in the previous works (as for review, see Okubo, 1986), our model is expected to contribute to considering such biological aggregating phenomena.

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APPENDIX A

In this appendix, explained is the derivation of equations (6) and (7). To obtain the stationary solution for (1), it is required to solve (3). Equation (3) has a trivial solution $n^* = 0$. But we shall focus on the non-trivial solution for (3) with assumption of its stability. When $m = 1$, the non-trivial solution has been proved to be globally stable as the stationary solution for (1) (Shigesada et al., 1979). After some modifications of (3), it is found to satisfy the following equation:

$$\frac{\delta}{m\kappa^m}\frac{\mathrm{d}(n^*)^m}{\mathrm{d}r} = -\frac{\mathrm{d}U}{\mathrm{d}r}$$

This can be easily solved:

$$(n^*)^m = -\frac{m\kappa^m}{\delta}U + C$$

where $C$ is determined by equation (5), and consequently (6) is obtained. Equation (7) is obtained by substituting (6) into (4).

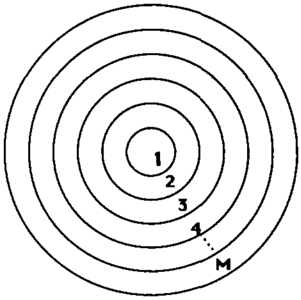


Fig. 4. Division of shoaling zone into $M$ rings. As for the detail explanation, see the text.

## APPENDIX B

We explain here a possible practical way to obtain the relation (15), making use of a set of data on fish distribution within shoal. Assume that the distribution is stationary and that it is possible, with a sampling technique, to count the number of individuals within a shoal. Approximating the shoal with a disk region, let us divide the shoal region into a number, say $M$, of rings which have common center and width, say $\Delta r$, given by $\Delta r \equiv r^*/M$. Then, number each ring as the 1st, ..., the $M$th (see Fig. 4). Put the counted population $n_i^*$ $(i = 1, 2, \ldots, M)$ within each ring. It is clear that:

$$N = \sum_{i=1}^{M} n_i^*$$

Now, making use of well-known discretization for derivative, we approximate the $r$-derivative as follows:

$$\frac{\mathrm{d}n^*}{\mathrm{d}r} \approx \frac{n_{i+1}^* - n_i^*}{\Delta r} \qquad (i = 1, 2, \ldots, M-1)$$

At last, with a modification for convenience, the relation (15) gives the following approximated form:

$$(m-1) \log n_i^* + \log\left|\frac{n_{i+1}^* - n_i^*}{\Delta r}\right| = \log \eta + (\gamma - 1) \log(i+1)\, \Delta r - \log m$$

where $i = 1, 2, \ldots, M-1$. With a routine mentioned in the main text, we can determine the parameters $m$, $\gamma$ and $\eta$ through this relation with a set of data.

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