Mathematical analysis on fish shoaling by a density-dependent diffusion model

Hiromi Seno [*,a], Katsuki Nakai [b]

[a] Department of Mathematics, Faculty of Science, Hiroshima University, Higashi-hiroshima, Hiroshima 724, Japan
[b] Lake Biwa Museum Project Office, Shiga Prefecture Board of Education, Uchidehama 14-15, Otsu 520, Japan

Abstract

Shoaling by juveniles of a cichlid fish *Lepidiolamprologus elongatus* in Lake Tanganyika, central Africa, is considered by means of a mathematical model with a density-dependent diffusion equation. The spatial size of shoaling is assumed to be determined by the balance between two counteracting forces: aggregation and dispersion. The data on the spatial size of shoaling and the group size are analyzed by the model. Then those tendencies of aggregation and dispersion are quantified. The result gives qualitative information to understand shoaling.

Keywords: Aggregation; Diffusion; Fish; School organization

1. Introduction

In the last decades, some density-dependent diffusion equations were investigated to reveal some of their interesting features that are different from those of density-*independent* diffusion equations (Shigesada et al., 1979; Mimura, 1980; Namba, 1980; 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 systems, so that simulation by computers is inevitable. On the other hand, although the dynamical aspect is worth while investigating, the stationary solution may sometimes be sufficient to give interesting results contributing to the understanding of a biological phenomenon (Teramoto and Seno, 1988; Seno, 1990, 1991a,b). Despite that very few biological systems can be regarded as being stationary, a stationary solution in a model may be useful as an approximation to consider a quasi-stationary biological system.

As an application of density-dependent diffusion model for the real phenomenon, we deal with a type of fish grouping. Fish grouping is very commonly observed in nature. It is often called "shoaling" or "schooling" (see Fig. 1). Each grouping might have its behavioral reason in the biological sense (Shaw, 1978; Partridge, 1982;

---

* Corresponding author. Present address: Department of Information and Computer Sciences, Nara Women's University, Kita-Uoya, Nishimachi, Nara, Japan.
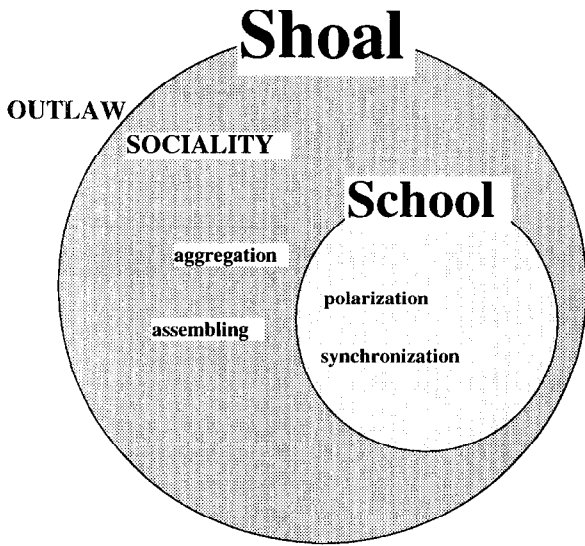
Fig. 1. Category of fish grouping (after Pitcher, 1986).

Pitcher, 1986). 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: aggregation and dispersion (see Fig. 2). However, different from the authors mentioned, we do not consider the shoal size to be the result of the two counteracting forces *among* individual fishes. Instead, our pur-
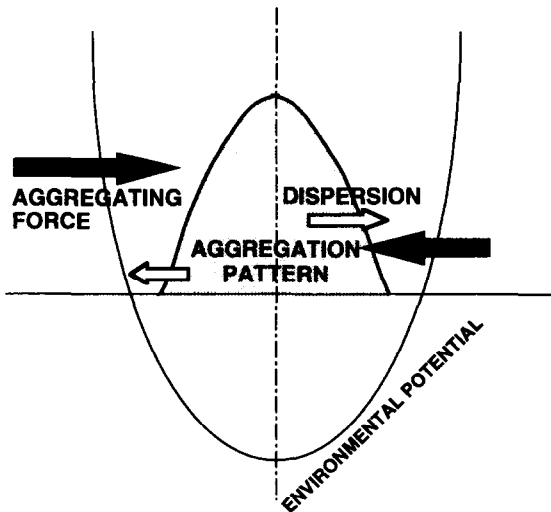

Fig. 2. Modelling of biological aggregation pattern formation.

pose is to discuss shoal size as resulting from two counteracting forces on each individual (Seno, 1990, 1991b). Our model is applied to analyze the data for the shoaling of the juveniles under parental guarding of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika, central Africa. The result gives qualitative information to consider shoaling.

2. Modelling assumptions

Aggregating force. An aggregating force is assumed to be directed to the center of an 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). The environmental potential mathematically embodies the tendency of aggregation, for example, to reduce the vulnerability to predation.

Dispersing force. We can assume that the density-dependence 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 is the tendency to avoid staying there.

Group size. The total number of shoaling individuals is assumed to be conserved for a considered group, realizing a quasi-stationary situation. No reproduction, no migration, and no predation are assumed during the considered period which is sufficient for the shoal to be stabilized under balance of the two counteracting forces.

3. Model

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

$$\frac{\partial n(x, t)}{\partial t} = -\operatorname{div} J(x, t) \tag{1}$$

$$J(x, t) = -\delta \left(\frac{n(x, t)}{\kappa} \right)^m \text{grad } n(x, t)$$

$$- n(x, t) \cdot \text{grad } U(x). \tag{2}$$

where grad is a differential operator that, 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). $n(x, t)$ is the population density at spatial site x at time t. The 2-dimensional vector $J(x, t)$ represents the flux of population density at spatial site x at time t, which is the 2-dimensional vector. The first term of the right-hand side of Eq. 2 represents the density-dependent diffusion force, that is, the dispersing force, which becomes stronger as the density gets higher. δ is a constant which means the diffusivity when n is equal to a constant κ, which represents a conventional reference density (Okubo, 1980). The power m is the index of strength of density-dependency of the diffusion, that is, the index of strength of the tendency to avoid crowding: the larger the index m, the stronger is this tendency. The second term means the aggregating force directed to the shoal center, due to the environmental favorability for the fish population. $U = U(r)$ is a scalar function of only the distance r from the shoal center.

To consider the size of the stabilized shoal, we investigate the stationary solution $n(x, t \to \infty) = n^*(r)$ of our model, given by solving $J = 0$. In addition, the conservation of the total population in the 2-dimensional shoal implies the following:

$$2\pi \int_0^{r^*} n^*(r) \cdot r \, dr = N = \text{constant},$$

where N is a constant of group size, and the factor 2π results from integration with respect to the angle expanded by the shoal around the center. r^* is an unknown constant which denotes the edge of the population distribution $n^*(r)$, that is, the radius size expanded by the shoal. Since the population density should be zero at the edge of the shoal, the following relation is required:

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

The existence of such a finite r^* is a characteristic of density-dependent diffusions (Okubo, 1980). At last, following Seno (1990), we can obtain

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

where r^* is the unique positive solution for

$$\int_0^{r^*} \{ U(r^*) - U(r) \}^{1/m} \cdot r \, dr$$

$$= \frac{N}{2\pi} \cdot \left(\frac{\delta}{m\kappa^m} \right)^{1/m}.$$

In the case of 3-dimensional space, the same argument can be applied, while the aggregating group is regarded as having the shape of a 3-dimensional ball. The aggregating force directed to the center of the ball works on each individual in it. The resulting equation is fundamentally the same as in the 2-dimensional case, except for the following conservation relation to determine the stationary shoal size r^*:

$$\int_0^{r^*} \{ U(r^*) - U(r) \}^{1/m} \cdot r^2 \, dr$$

$$= \frac{N}{4\pi} \cdot \left(\frac{\delta}{m\kappa^m} \right)^{1/m}.$$

In order to analyze the data sampled in the field, the environmental potential U in our model requires a specific form, as follows:

$$U(r) = \begin{cases} \gamma \cdot kr^\gamma & \text{if } \gamma > 0; \\ -\gamma \cdot kr^\gamma & \text{if } \gamma < 0, \end{cases}$$

where k is a positive constant. γ is a real constant. When $1 < \gamma$, the aggregating force is the stronger in the location further from the shoal center and is zero at the center: the long-distance force. On the other hand, when $\gamma < 1$, the aggregating force has the inverse tendency, so that the force is the weaker in the location further from the center and is the strongest at the center; the short-distance force. If $\gamma = 1$, the aggregating force has a positive strength independent of the
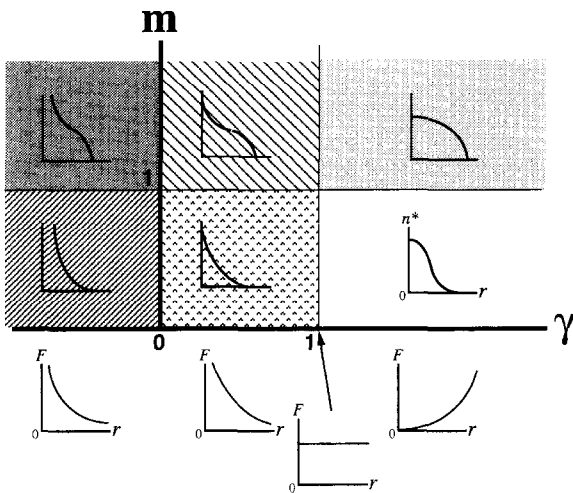
Fig. 3. Parameter dependency of the stationary distribution n^* and the strength of aggregating force F (for detailed explanation, see text).

distance from the shoal center: the position-independent force. We do not consider the case when $\gamma = 0$; then $n^* \equiv 0$ for any r, which means all individuals disperse. The above tendencies are emphasized more as the absolute value $|\gamma|$ gets larger. The fish distribution in the shoal is determined by those parameters γ and m (Seno, 1990; see Fig. 3). Eventually, the relation between the shoal size r^* and the group size N can be expressed in the following form:

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

that is,

$$\log N = \left(d + \frac{\gamma}{m}\right) \cdot \log r^* + \text{constant},$$

where $d = 2$ and $d = 3$ in the 2-dimensional and 3-dimensional case, respectively. We will use this proportional relation to investigate the data of the juvenile shoaling of the cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika, central Africa.

4. Shoaling of *Lepidiolamprologus elongatus*

The shoaling considered in this paper is of juveniles under parental guarding of the sub-

strate-brooding cichlid fish, *Lepidiolamprologus elongatus*, endemic to Lake Tanganyika, central Africa. Breeding parents of this species guard their brood through the fertilized egg, yolk-sac embryo (= larva), and free-swimming juvenile (= fry) stages. After yolk absorption (about 10 days after spawning), juveniles appear out of a shelter hole and form a shoal in water column right above the shelter during daytime, where they feed on zooplankters (Nakai et al., 1991; Nakai, 1994). At night, the juveniles rest on the bottom around the shelter hole (Nakai, personal observation). Since most of the breeding pairs successively utilize the same spawning/brooding sites all year round (Nakai, 1994), the shoals of juveniles are continuously formed in almost the same location. The shoals usually disappear 3 months or more after spawning when the juveniles reach sufficient body size for independence from their parents (Nagoshi, 1985).

The present analysis deals with shoals of juveniles aged 0–60 days, when the brood seldom suddenly decreases in size nor wholly disappears (except for "slaughter" on broods, see below), but usually keeps a relatively stable size, even though the brood size gradually decreases day by day probably due to predation. Here, we should mention that the daytime predation on broods was sufficiently infrequent for the assumption of "no predation" during the period considering the balance of two counteracting forces. The spatial size of each shoal was directly measured in the field, and the number of juveniles in the shoal, that is the brood size, was later counted on the photograph taken at the same time as measurement of the spatial shoal size. Since each shoal of juveniles was continuously observed after being spawned, the exact age of the shoal was known. Accordingly, the age of the shoal was represented as the number of days after appearance of the shoal.

5. Analysis of data

Although it is expected that some photographs of the shoal will give the information of distribution of fish in the shoal, we now deal only with

the data of the spatial shoal size and the brood size, which are easier to be estimated than the fish distribution in the shoal. We use Eq. 3 and estimate the slope of the line fitted to the graph of log(spatial shoal size)–log(brood size) (Figs. 4 and 5), and lastly calculate the value of γ/m by the least square method. As easily seen in Fig. 4, those plots by the 2-dimensional model do not

seem to show any significant linear correlation between log(spatial shoal size) and log(brood size), while those by the 3-dimensional model do (Fig. 5). This means that the 3-dimensional model could reflect better the spatial characteristics of the considered shoal.

The result is shown in Fig. 6. It is shown that the value γ/m does not seem to have any signifi-
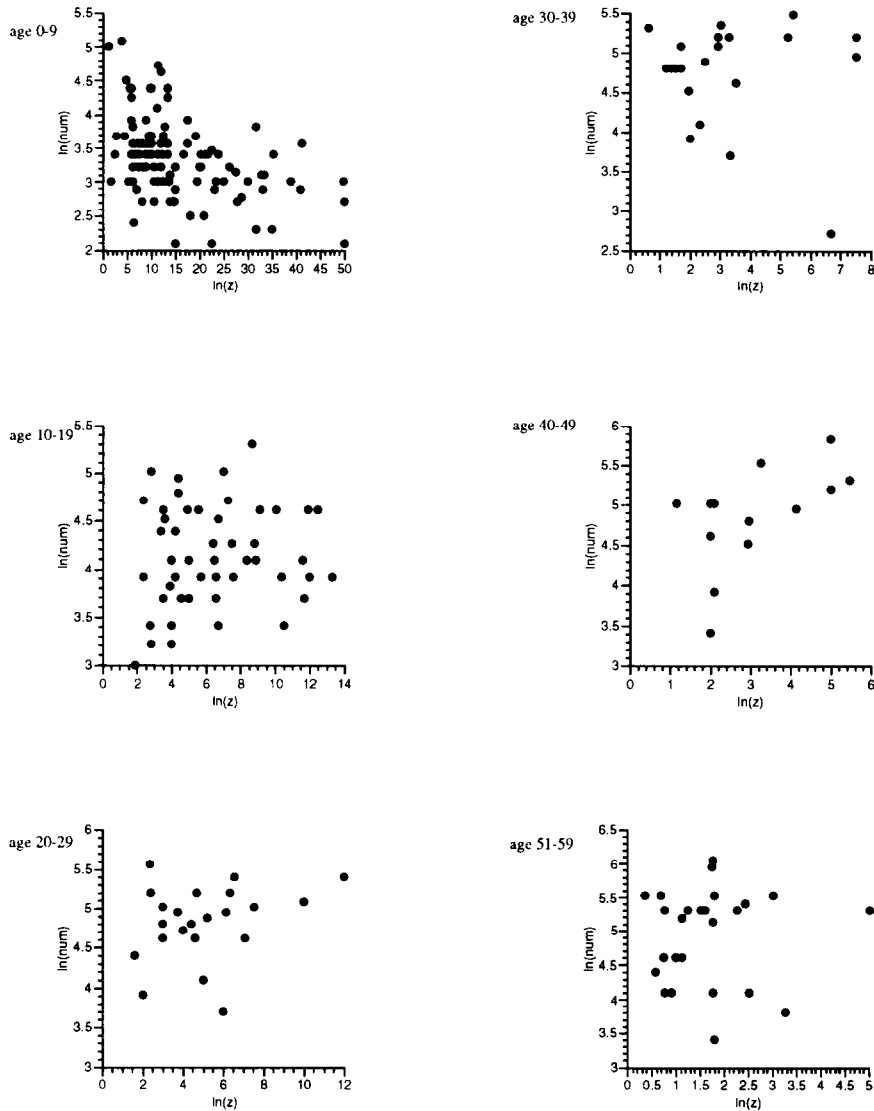

Fig. 4. Data of the shoaling of the cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika, central Africa. The vertical axis is of the group size, while the horizontal is of the spatially horizontal shoal size, that is, the 2-dimensional extension length of the shoal. The data is grouped with respect to the age represented by the number of days after the appearance of shoal.
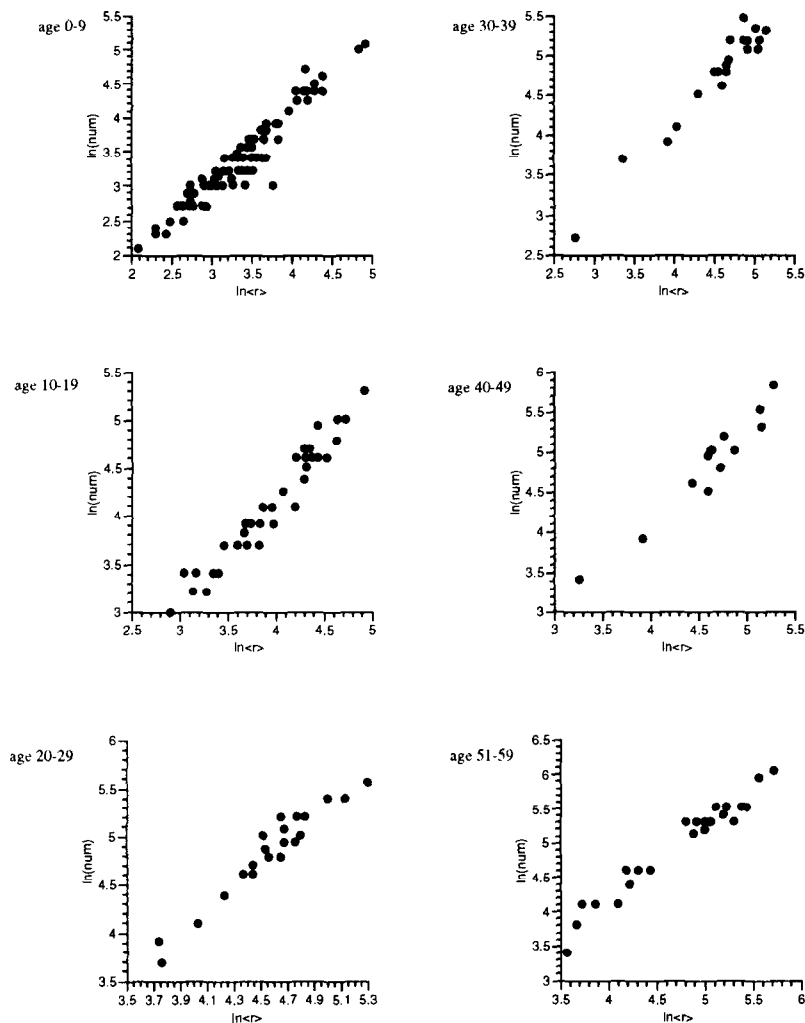
Fig. 5. Data of the shoaling of cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika. The vertical axis is of the group size, while the horizontal is of the 3-dimensional shoal size, which is the radius of a ball corresponding to the shoal. The radius ⟨r⟩ is calculated regarding the shoal as a ball which has the volume equivalent to that of the ellipsoid of revolution given by the 3-dimensional data on the size of shoaling.

cant variation in the later period (10 + days after the appearance of shoaling), while it takes a significantly different value in the earlier period (age 0–9 days). This might mean that the ratio (the strength of aggregating tendency)/(the strength of dispersal tendency) is almost constant during the period of shoaling except for the earlier, relatively short, period.

This significantly different result for the shoal of 0–9 days of age might be due to the vulnerabil-

ity to predation specific to the period. The juveniles of 0–9 days of age (younger juveniles) have a semi-transparent and less pigmented body of about 7–10 mm total length (for description, see also Mihigo, 1986). When the guarding parents are temporally absent, the juveniles are immediately subject to predation by almost all fishes residing or foraging around them. That is, the younger juveniles should be defended against any approaching fish which is regarded as a "poten-
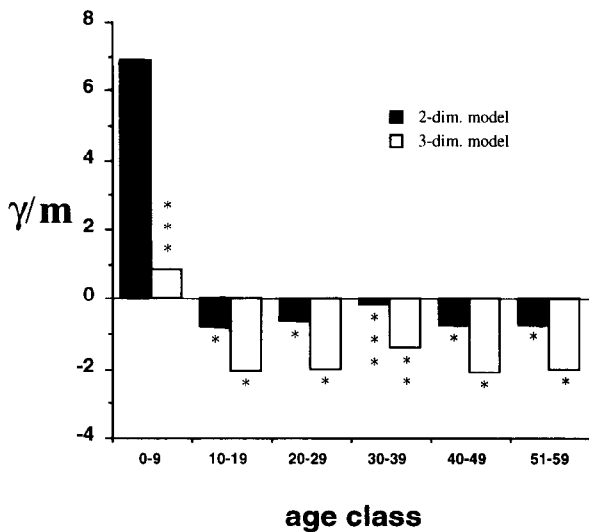
Fig. 6. γ/m estimated for the data of the shoaling of the cichlid fish, *Lepidiolamprologus elongatus*, in Lake Tanganyika. The result of t-test is overlaid: $^{*} P < 0.01$; $^{**} P < 0.02$; $^{***} P < 0.03$; non-significant in the age 0-9 class of 2-dimensional model case.

tial predator" for the juveniles of this period. The juveniles older than approximately 10 days after yolk absorption (older juveniles) gradually become beige-colored and well-pigmented, and reach the large body size sufficient to be free from predation by many potential predators, although some fish still exist specialized in hunting those juveniles under parental guarding (= "brood predators" in Nakai, 1994, or "fry eaters" in Hori, 1987). This difference in vulnerability to predation between the younger and the older juveniles may explain our result.

However, we should note that, since the least square method to estimate the slopes of fit lines was applied all the plots, the distinct result for the shoal of age 0-9 days might be just an arithmetic ghost due to specifically distributed values of some of the data. Indeed, as seen in Fig. 5, the slope around 1.0 seems to be fit also for that of age 0-9 day. If so, it would result that the ratio (the strength of aggregating tendency)/(the strength of dispersal tendency) is almost constant around -2.0 over the whole period in which the shoal exists.

It should be remarked that, with the 3-dimensional model, γ results in a positive value around 1 and less than 1 for the shoal of 0-9 days of age, and negative values for those of 10 + days. This means that, for the shoal of 0-9 days, the aggregating force has the tendency of short-distance, whereas the strength decreases very slowly in the distance from the shoal center. The latter is because γ is near 1. As mentioned above, for the juveniles of age 0-9 days, the vulnerability to predation is so much higher than for the older juveniles, that each individual juvenile is under a high risk. Thus, it would be essentially necessary for each individual to have the memory of the direction to the shelter, which is now the shoal center. In addition, the informational communication among juveniles would be still premature for the younger shoal, that is, the behavior as a group would not be yet founded. In such a case, each juvenile must behave by itself, not relying on the information from the others in the shoal. Therefore, each individual must have the aggregating tendency almost independent of its position in the shoal. On the other hand, for the older juveniles, the vulnerability to predation becomes lower, and the informational communication among juveniles has been sufficiently founded. Then, juveniles can rely on the information from the others and can behave relatively free from the memory of the direction to the shelter. This can be a reason for the result of γ for 10 + days of age. As mentioned before, this argument might be applied also for 0-9 day age. If so, it might be concluded that the informational communication among juveniles is founded in the very early period after the foundation of shoal.

The main purpose of the present work is to analyze the relation between the spatial shoal size and the brood size, through the mathematical model assuming the balance of two counteracting forces. Although the quantity of γ/m might be expected to characterize some intrinsic tendency of shoal and to give an indication of disappearance of shoal, it could not be in the framework of the present analysis. In fact, all shoals of juveniles eventually disappeared as they grew, but other reasons can be considered for such disap-

pearances. "Slaughter" on broods, which may be accidentally caused not by brood predators (daytime visual predators) but by nocturnally foraging predators, may explain some cases (see also Nakai et al., 1990). No indication for such accidental disappearances caused by a solely external factor would be detected beforehand. Other shoal disappearances may be attributed to qualitative change of the parents with a brood of sufficiently grown juveniles, who must prepare for the next spawning or must protect their newly spawned brood against their previous one, because large (previously-cared) juveniles can be a strong predator on the newly appearing juveniles which are vulnerable to almost all fish. Then, we should take the "parental" force into account, which will oblige the shoal of juveniles to move away or disappear. In the present model, the effect of such parental force might be regarded as involved in those parameters m and γ.

However, in the present analysis, the juveniles dealt with were young enough to neglect such later disappearances caused by the parental force. Further, the shoals of juveniles could be formed only under safety warranted by parental guarding; they became almost demersal without guarding such as experimental removal of parents or their independence. In addition to the above circumstantial evidence in the field, another explanation based on the characteristics of γ and m is possible for the lack of indication of disappearance: γ and m are contemporarily decreasing as the fish grows in the shoal. At any rate, disappearance of broods could not be easily indicated by the quantity of γ/m nor be explained by the unbalance of the two counteracting forces assumed in the present model.

It is still better to mention that we dealt with a variety of brood size (a part of small-sized broods being attributable to the accidental "slaughter"), and that the statistical operation may enshadow the variation of the quantity, that is, the data dealt with involve so various observed shoals that some disappear in the earlier age class than others. To get more information, making use of this model, the analysis on the density distribution in the shoal is necessary.

6. Conclusion

The model introduced in this paper is shown to have a potential to give some useful information on the shoaling dynamics. The shoaling of the juvenile cichlid fish, *Lepidiolamprologus elongatus*, is the case. It is indicated that the shoal in the earlier period has the intrinsic character different from that in the latter period.

The analysis presented in this paper is applicable to the shoaling of the other species. Then, it will be interesting to reveal the difference of intrinsic character among a variety of shoals and to approach the more detail nature of shoaling dynamics. Moreover, our modelling analysis may be able to be applied to the other aggregation phenomena, for instance, "flocking" of birds or "swarming" of insects. We expect that our analysis will be also useful to understand such phenomena.

Acknowledgment

References

Arfken, G., 1970. Mathematical Methods for Physicists. Academic Press, New York, 815 pp.
Breder, C.M., 1954. Equations descriptive of fish schools and other animal aggregations. Ecology, 35: 361–370.
Hori, M., 1987. Mutualism and commensalism in the fish community in Lake Tanganyika. In: S. Kawano, J.H. Connell and T. Hidaka (Editors), Evolution and Coadaptation in Biotic Communities. Tokyo University Press, Tokyo, pp. 219–239.
Mihigo, N.Y.K., 1986. Description of larvae and juveniles of cichlid in Lake Tanganyika (Osteichthyes: Cichlidae) (1). Afr. Study Monogr. Kyoto Univ., 6: 29–36.

Mimura, M., 1980. Stationary pattern of some density dependent diffusion systems with competitive dynamics. Hiroshima Math. J., 11: 621–635.

Nagoshi, M., 1985. Growth and survival in larval stage of the genus *Lamprologus* (Cichlidae) in Lake Tanganyika. Verh. Int. Ver. Limnol., 22: 2663–2670.

Nakai, K., 1994. Foraging of brood predators restricted by territoriality of substrate-brooders in a cichlid fish assemblage. In: H. Kawanabe, J. Cohen and K. Iwasaki (Editors), Mutualism and Community Organization: Behavioral, Theoretical and Food Web Approaches. Oxford University Press, Oxford, pp. 84–108.

Nakai, K., Yanagisawa, Y., Sata, T., Niimura, Y. and Gashagaza, M.M., 1990. Lunar synchronization of spawning in cichlid fishes of the tribe Lamprolonini in Lake Tanganyika. J. Fish Biol., 37: 589–598.

Namba, T., 1980. Density dependent dispersal and spatial distribution of a population. J. Theor. Biol., 86: 351–363.

Okubo, A., 1980. Diffusion and Ecological Problems: Mathematical Models. Springer-Verlag, New York.

Okubo, A., Sakamoto, W., Inagaki, T. and Kuroki, T., 1977. Studies on the schooling behavior of fish. V. Note on the dynamics of fish schooling. Bull. Jpn. Soc. Sci. Fish, 43: 1369–1377.

Parr, A.E., 1927. A contribution to the theoretical analysis of the schooling behavior of fishes. Occasional Papers of the Bingham Oceanographic Collection, No. 1.

Partridge, B.L., 1982. Structure and function of fish schools. Sci. Am., 245: 114–23.

Pitcher, T.J., 1986. Functions of shoaling behaviour in teleosts. In: T.J. Pitcher (Editor), The Behavior of Teleost Fishes. The Johns Hopkins University Press, Baltimore, MD, pp. 294–337.

Seno, H., 1989. The condition for population persistence in a patchy environment: Critical patch size problems for some basic models. Biophysics (The Biophysical Society of Japan), 164: 41–45 (in Japanese).

Seno, H., 1990. A density-dependent diffusion model on nesting fish's shoal. Ecol. Model., 51: 217–226.

Seno, H., 1991a. Rank-size relation of a multi-species system with an exclusive interference relation. Trans. Jpn. Soc. Ind. Appl. Math., 1: 81–100 (in Japanese).

Seno, H., 1991b. Distribution pattern around the shelter of shoaling fish. Suuri-kagaku, 334: 78–80 (in Japanese).

Seno, H., 1991c. Predator's invasion into an isolated patch with spatially heterogeneous prey distribution. Bull. Math. Biol., 53: 557–577.

Shaw, E., 1978. Schooling fishes. Am. Sci., 66: 166–175.

Shigesada, N., 1980. Spatial distribution of dispersing animals. J. Math. Biol., 9: 85–96.

Shigesada, N., Kawasaki, K. and Teramoto, E., 1979. Spatial segregation of interacting species. J. Theor. Biol., 79: 83–99.

Teramoto, E. and Seno, H., 1988. Modeling of biological aggregation patterns. In: L.M. Ricciardi (Editor), Biomathematics and Related Computational Problems. Kluwer Academic Publishers, Dordrecht, pp. 409–419.