MODELING OF BIOLOGICAL AGGREGATION PATTERNS

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ABSTRACT. Mathematical models of aggregation of biological organisms in one dimensional space are discussed taking into account the density dependent dispersive motion and the environmental potential field. Introducing three types of potential functions, the stationary distributions are analytically obtained for a single and mutually exclusive two-species populations.

1. INTRODUCTION

The aggregation phenomena of organisms and the formation of their distribution patterns can be widely observed in various biological systems, an aggregated or a clumped distribution of animals or plants, and the cell association due to the chemotaxis or mutual cohesive interactions of the cells. More interesting phenomena are the pattern formations of organisms or cells of two kinds of species, under the effect of inter-specific collective interactions, for examples, spatial segregation of habitat observed in the community of two similar species of animals or plants and phase separation of differentiated cells in the culture solution.

Here we shall present the mathematical models which phenomenologically describe these phenomena, using a nonlinear diffusion model which we previously used in the discussion on density dependent dispersive motion of insects (N. Shigesada, K. Kawasaki and E. Teramoto 1978, and N. Shigesada 1980). In the equation of continuity

$$\frac{\partial}{\partial t} n(x,t) = - \operatorname{div} J(x,t) \tag{1.1}$$

we considered the flow given by

$$J(x,t) = - \operatorname{grad}[\{\alpha+\beta n(x,t)\}n(x,t)] - n(x,t)\operatorname{grad} U(x) \tag{1.2}$$

where $n(x,t)$ is the population density, $\alpha+\beta n(x,t)$ corresponds to the density dependent diffusion coefficient and $U(x)$ is the environmental potential function.

L. M. Ricciardi (ed.), Biomathematics and Related Computational Problems, 409–419.

If we consider the one-dimensional case, the flow can be written as

$$J(x,t) = -\alpha\frac{\partial n(x,t)}{\partial x} - n(x,t)\frac{\partial}{\partial x}\{U(x)+2\beta n(x,t)\}, \quad (1.3)$$

where it is seen that the density dependent term of the dispersion coefficient can be expressed also in terms of density dependent potential function. The stationary distribution of the equation (1.1) is given by the solution of $J(x,t)=0$, that is

$$\alpha \log\frac{n(x)}{n(0)} + 2\beta\{n(x)-n(0)\} = -\{U(x)-U(0)\}, \quad (1.4)$$

and it can be shown that the solution of (1.4) is globaly stable under some suitable conditions. Here it should be noticed that when $\alpha=0$, we have two solutions of $J(x,t)=0$,

$$n(x) = 0 \quad \text{and} \quad 2\beta\{n(x)-n(0)\} = -\{U(x)-U(0)\}. \quad (1.5)$$

In the following discussions, we use these equations to discuss the stationary aggregation patterns, by introducing special types of potential functions.

2. AGGREGATION OF A SINGLE SPECIES POPULATION

Here let us consider the aggregation patterns of a sigle species population in the one-dimensional space, by introducing three types of symmetric potential functions which qualify the environmental condition and generate the initiative force of aggregation.

CASE A. $U(x) = kx^2$

At first, we consider the square potential field which produces the increasing force with distance from the origin. Though this potential field of the harmonic oscillator seems to be unrealistic in the biological systems especially at a far distance, it can be used to discuss the local properties of aggregation phenomena.

(A-a) $\alpha\neq 0$ and $\beta=0$. In this case of density independent diffusion, equation (1.4) apparently gives the normal distribution (Boltzmann distribution)

$$n(x) = (\nu/\pi)^{1/2} N\, e^{-\nu x^2} \quad \text{for} \quad -\infty<x<\infty, \quad (2.1)$$

where $\nu=k/\alpha$ and N is the total number of individuals.

(A-b) $\alpha=0$ and $\beta\neq 0$. Contrarily if we consider only the density dependent term of diffusion coefficient, we have the spatially bounded distribution instead of the normal distribution with infinite tails (Fig. 1).

$$n(x) = \mu(x^{*2}-x^2) \quad \text{for} \quad -x^*<x<x^*,$$
$$= 0 \quad \text{for} \quad |x|>x^*, \quad (2.2)$$

where

$$\mu = k/2\beta \quad \text{and} \quad x^* = (3N/4\mu)^{1/3}. \quad (2.3)$$

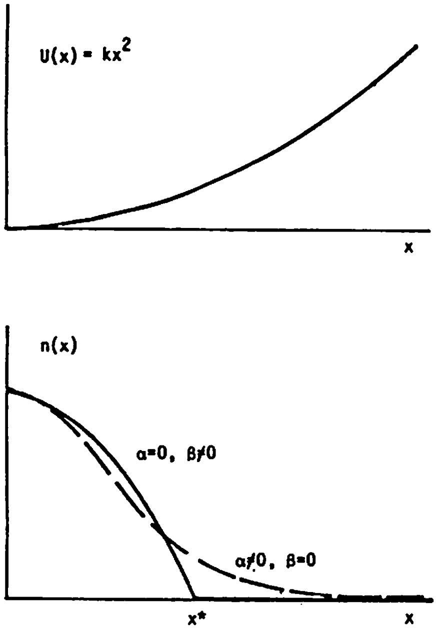

Fig. 1. Potential and distribution function of CASE A.

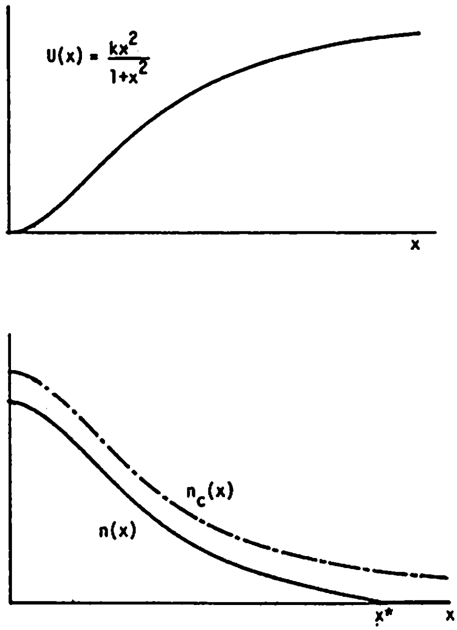

Fig. 2. Potential and distribution function of CASE B.

CASE B. $U(x) = kx^2(1+x^2)^{-1}$

This potential function gives square potential field near the origin, but the attractive force does not reach far distance, and the individuals at a distance are hard to recognize the existence of this favorable spot.

(B-a) $\alpha \neq 0$ and $\beta = 0$. If we consider the ordinary density independent dispersion, there is always the possibility that any individual has a chance to move out of the potential valley and finally the population spreads over the infinite space, thus we have no localized stationary distribution and the solution is given by

$$n(x) = 0 \qquad \text{for} \quad -\infty < x < \infty. \tag{2.4}$$

(B-b) $\alpha = 0$ and $\beta \neq 0$. In this case, there exists the critical distribution function, which is given by

$$n_c(x) = \mu(1+x^2)^{-1} \qquad \text{for} \quad -\infty < x < \infty, \tag{2.5}$$

and the critical population size

$$N_c = \mu\pi. \tag{2.6}$$

When the population size is larger than this critical value, only N_c individuals can occupy the area around the potential valley with the critical distribution $n_c(x)$ and excess number of individuals leak out of the valley and spread over the infinite space.

When $N<N_c$ they can establish a bounded aggregation (Fig. 2),

$$n(x) = \mu\{(1+x^2)^{-1}-(1+x^{*2})^{-1}\} \quad \text{for} \quad -x^* \le x \le x^*, \qquad (2.7)$$
$$= 0 \quad \text{for} \quad |x|>x^*,$$

where x^* is determined by the equation

$$f(x^*) = \arctan x^* - x^*(1+x^{*2})^{-1} = N/2\mu. \qquad (2.8)$$

CASE C. $U(x) = k\{K|x| - \int_0^{|x|} n(x,t)dx\}$

This density dependent potential function indicates that there is a maximum critical density K and the potential is given by the number of allowable vacant rooms S(x) in the inside space as shown in Fig. 3, and if the space is over crowded it acts as repulsive force. Because of the symmetry property of the potential function, we shall consider only positive part of space x.

(C-a) $\alpha\neq0$ and $\beta=0$ In this case, we have the differential equation

$$\alpha\frac{dn(x)}{dx} = -k\{K-n(x)\}n(x). \qquad (2.9)$$

The solution of this equation is given by, for sufficiently large value of N,

$$n(x) = K\{1+e^{\nu K(x-N/2K)}\}^{-1} \quad \text{for} \quad 0\le x<\infty. \qquad (2.10)$$

This is the well known Fermi distribution, and $\nu=k/\alpha$.

(C-b) $\alpha=0$ and $\beta\neq0$. From $J(x,t)=0$, we have

$$n(x) = 0 \quad \text{or} \quad \frac{dn(x)}{dx} = -\mu\{K-n(x)\},$$

and for large value of N we have

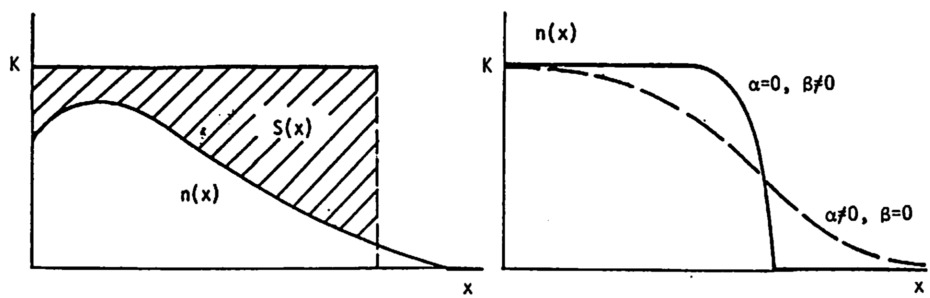

Fig. 3. Vacant room potential and distribution function of CASE C.

$$n(x) = K\{1 - e^{-\mu(x^*-x)}\} \quad \text{for} \quad 0\leq x\leq x^*, \qquad (2.11)$$
$$\quad = 0 \quad \text{for} \quad x>x^*,$$

where

$$x^* = (N/2K) + (1/\mu). \qquad (2.12)$$

3. TWO SPECIES POPULATION WITH EXCLUSIVE INTERFERENCE

Here we shall consider the stationary distribution of two species population, assuming that both species have a preference for similar enviroment and the predominant species 1 exerts the repulsive pressure on the species 2. The population flows of these two species are given by

$$J_1(x,t) = -\frac{\partial}{\partial x}\{\beta_1 n_1(x,t)^2\} - n_1(x,t)\frac{\partial}{\partial x} U_1(x),$$
$$J_2(x,t) = -\frac{\partial}{\partial x}\{\beta_2 n_2(x,t)^2\} - n_2(x,t)\frac{\partial}{\partial x}\{U_2(x)+\gamma n_1(x,t)\}, \qquad (3.1)$$

where we assumed $\alpha_1=\alpha_2=0$ and the repulsive pressure of species 1 is represented by an additional term $\gamma n_1(x,t)$ in the potential function for species 2. The stationary distributions are again given by the solutions $J_1(x,t)=J_2(x,t)=0$.

CASE A. $U_1(x) = k_1x^2$ and $U_2(x) = k_2x^2$.

The solution n (x) is given by (2.2), that is

$$n_1(x) = \mu_1(x_1^2-x^2) \quad \text{for} \quad -x_1<x<x_1, \qquad (3.2)$$
$$\quad = 0 \quad \text{for} \quad |x|>x_1,$$

where

$$\mu_1 = k_1/2\beta_1 \quad \text{and} \quad x_1 = (3N_1/4\mu_1)^{1/3}.$$

The differential equation $J_2(x,t)=0$ can be analysed by substituting (3.2) for $n_1(x)$ and we can obtain the following results depending upon the population size N_2 and the values of the parameters

$$B = \mu_2/\mu_1 \quad \text{and} \quad \Gamma = \mu_1\gamma/k_2.$$

(A1) $\Gamma < 1$. When $\gamma<k_2/\mu_1$, the effect of environmental attractive force dominate the pressure of species 1 and species 2 can also occupy the central area. The stationary distribution $n_2(x)$ is given by a monotone decreasing function of the distance $|x|$ from the origin.

(A1-i) $N_2/N_1\leq B(1-\Gamma)$.

$$n_2(x) = \mu_2(1-\Gamma)(x_2'^2 - x^2) \quad \text{for} \quad -x_2'\leq x\leq x_2', \qquad (3.3)$$
$$\quad = 0 \quad \text{for} \quad |x|\geq x_2'.$$

where

$$\mu_2 = k_2/2\beta_2 \quad \text{and} \quad x_2' = \{3N_2/4\mu_2(1-\Gamma)\}^{1/3} \leq x_1.$$

(A1-ii) $N_2/N_1 \geq B(1-\Gamma)$.

$$\begin{aligned} n_2(x) &= n_2(0) - \mu_2(1-\Gamma)x^2 && \text{for} \quad -x_1 \leq x \leq x_1, \\ &= \mu_2(x_2^2 - x^2) && \text{for} \quad x_1 < |x| \leq x_2, \\ &= 0 && \text{for} \quad |x| > x_2, \end{aligned} \tag{3.4}$$

where

$$x_2 = [x^3 + \frac{3N_1}{4\mu_2}\{\frac{N_2}{N_1} - B(1-\Gamma)\}]^{1/3} > x_1,$$

$$n_2(0) = \mu_2(x_2^2 - \Gamma x_1^2).$$

(A2) $\Gamma > 1$. When $\gamma > k_2/\mu_1$, the population of species 2 is pushed out of the central part of potential valley by the repulsive pressure of species 1 and the distribution function $n_2(x)$ is given by a concave function in the interval $(-x_1, x_1)$.

(A2-i) $N_2/N_1 > B\Gamma(\sqrt{\Gamma}-1)$. In this case, the stationary distribution is also given by equations (3.4) and it has a finite positive value at the origin.

(A2-ii) $N_2/N_1 < B\Gamma(\sqrt{\Gamma}-1)$. The stationary distribution $n_2(x)$ splits into two parts and, in general, it approaches different unsymmetrically separated distribution, depending upon the initial distribution $n_2(x,0)$. Especially if $N_2/N_1 < B\Gamma(\sqrt{\Gamma}-1)/2$ and the initial distribution is located only at one side of region $x>0$ or $x<0$, it can not squeese through the barrier of species 1. Each of the separated distribution has the pattern given by

$$\begin{aligned} n_2(x) &= 0 && \text{for} \quad 0 \leq x \leq x_0, \\ &= \mu_2(\Gamma-1)(x^2 - x_0) && \text{for} \quad x_0 < x \leq x_1, \\ &= \mu_2(x_2^2 - x^2) && \text{for} \quad x_1 < x \leq x_2, \\ &= 0 && \text{for} \quad x > x_2 \quad . \end{aligned} \tag{3.5}$$

Fig. 4 shows the distribution patterns in four cases discussed above and the domains of these characteristic patterns in the parameter space are shown in Fig. 5.

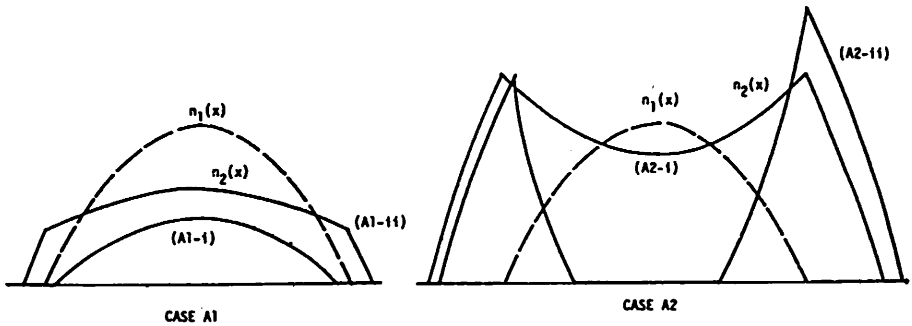

Fig. 4. Distribution functions $n_1(x)$ and $n_2(x)$ of CASE A. Four types of patterns of $n_2(x)$ for given $n_1(x)$ are shown.

CASE B.

$$U_1(x) = k_1 x^2 (1+x^2)^{-1}$$

and

$$U_2(x) = k_2 x^2 (1+x^2)^{-1}.$$

The potential valley presented by these functions have the limiting carrying capacities. As we have shown in the last section, when the population size N_1 is smaller than the critical value $N_{1C}=\mu_1\pi$, the stationary distribution $n_1(x)$ is given by

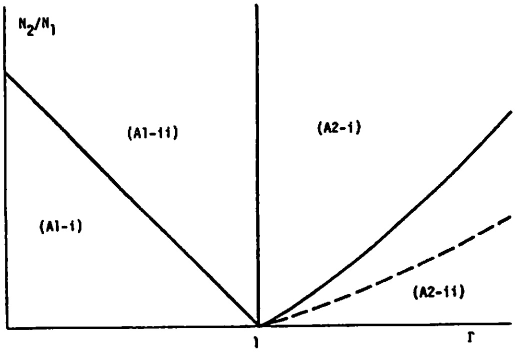

Fig. 5. Domains of four types of distribution patterns.

$$\begin{aligned} n_1(x) &= \mu_1\{(1+x^2)^{-1} - (1+x_1^2)^{-1}\} && \text{for} \quad 0\le|x|\le x_1, \\ &= 0 && \text{for} \quad |x|>x_1 . \end{aligned} \qquad (3.6)$$

where

$$f(x_1) = \arctan x_1 - x_1(1+x_1^2)^{-1} = N_1/2\mu_1. \qquad (3.7)$$

When $N_1 \geq N_{1C}$, $n_1(x,t)$ finally approaches the same critical distribution (2.5) of the population size N_{1C}, which is obtained by taking the limit $x_1\to\infty$ in (3.6) and (3.7). On the other hand, the critical population size N_{2C} is determined depending upon the population size N_1 and the value of parameter $\Gamma=\mu_1\gamma/k_2$.

(B1) $\Gamma < 1$. When $\gamma<k_2/\mu_1$, the distribution has a maximum at the origin just as the case of square potential (A1) and we have the following solutions $n_2(x)$.

(B1-i) $N_2/\mu_2<(1-\Gamma)N_1/\mu_1$.

$$\begin{aligned} n_2(x) &= \mu_2(1-\Gamma)\{(1+x^2)^{-1} - (1+x_2'^2)^{-1}\} && \text{for} \quad 0\le|x|\le x_2' , \\ &= 0 && \text{for} \quad |x|>x_2' , \end{aligned}$$

(3.7)

where x_2' is determined by

$$f(x_2') = N_2/2(1-\Gamma)\mu_2.$$

(B1-ii) $(1-\Gamma)N_1/\mu_1<N_2/\mu_2\le\pi-\Gamma N_1/\mu_1=N_{2C}(N_1,\Gamma)/\mu_2$.

$$\begin{aligned} n_2(x) &= n_2(0) - \mu_2(1-\Gamma)x^2(1+x^2)^{-1} && \text{for} \quad 0\le|x|\le x_1, \\ &= n_2(0) - \mu_2\{x^2(1+x^2)^{-1} - \Gamma x_1^2(1+x_1^2)^{-1}\} && \text{for} \quad x_1<|x|\le x_2, \\ &= 0 && \text{for} \quad |x|>x \quad , \end{aligned}$$

(3.8)

where

$$n_2(0) = \mu_2\{x_2^2(1+x_2^2)^{-1} - \Gamma x_1^2(1+x_1^2)^{-1}\},$$

$$f(x_2) = (N_2/2\mu_2) + \Gamma(N_1/\mu_1). \tag{3.9}$$

Here, taking the limit $x_2 \to \infty$, we can obtain the critical distribution of species 2. From (3.11) and $f(\infty)=\pi/2$, the critical population size of species 2 for given values of N_1 and $\Gamma<1$ is given by

$$N_{2C}(N_1,\Gamma) = \mu_2\{\pi - \Gamma(N_1/\mu_1)\}. \tag{3.10}$$

(B2) $\Gamma > 1$. In this case the distribution function (3.8) becomes concave function in the interval $(-x_1,x_1)$.

(B2-i) $\Gamma x_1^2(1+x_1^2)^{-1}<x_2^2(1+x_2^2)^{-1}$. Here x_1 and x_2 are determined as functions of N_1/μ_1 and N_2/μ_2 bythe equations (3.7) and (3.9) respectively and it is easily seen that this condition holds only when $x_1 \leq 1/\sqrt{\Gamma-1}$. The domain in $(N_1/\mu_1,N_2/\mu_2)$ space in which this condition holds is shown in Fig. 7. The upper boundary of this domain which gives the critical size of species 2 is again expressed by the same equation with (3.10). The stationary distribution $n_2(x)$ is also given by (3.8) which has finite positive value at x=0 in this case.

(B2-ii) $\Gamma x_1^2(1+x_1^2)^{-1}>x_2^2(1+x_2^2)^{-1}$. In this case the distribution of species 2 splits into two parts and we have

$$\begin{aligned} n_2(x) &= 0 && \text{for} \quad 0\leq|x|\leq x_0, \\ &= \mu_2(\Gamma-1)\{(1+x_0^2)^{-1} - (1+x^2)^{-1}\} && \text{for} \quad x_0<|x|\leq x_1, \\ &= \mu_2\{(1+x^2)^{-1} - (1+x_2^2)^{-1}\} && \text{for} \quad x_1<|x|\leq x_2, \\ &= 0 && \text{for} \quad |x|>x_2, \end{aligned} \tag{3.11}$$

where x_0 and x_2 are determined by the equations

$$\begin{aligned} (\Gamma-1)x_0^2(1+x_0^2)^{-1} &= x_1^2(1+x_1^2)^{-1} - x_2^2(1+x_2^2)^{-1}, \\ (\Gamma-1)f(x_0) + f(x_2) - \Gamma f(x_1) &= N_2/2\mu_2. \end{aligned} \tag{3.12}$$

It can be also shown that, when $x_1>1/\sqrt{\Gamma-1}$, the critical size of species 2 is determimed by taking the limit $x_2 \to \infty$,

$$N_{2C}(N_1,\Gamma)/\mu_2 = \pi - 2\Gamma f(x_1) + 2(\Gamma-1)f(x_0). \tag{3.13}$$

The distribution patterns discussed above are shown in Fig. 6 and their domains in $(N_1/\mu_1,N_2/\mu_2)$ space are shown in Fig. 7 with the critical size $N_{2C}(N_1,\Gamma)$.

CASE C.
$$U_1(x) = k[K|x| - \int_0^{|x|} n_1(x,t)dx],$$
$$U_2(x) = k[K|x| - \int_0^{|x|} \{n_1(x,t)+n_2(x,t)\}dx].$$

Here, for simplicity, we use the same values of parameters for both species, $\beta_1=\beta_2=\beta$, $k_1=k_2=k$, $\mu_1=\mu_2=k/2\beta=\mu$ and $\Gamma=\gamma\mu/k$. We assume also that the species 1 can invade the room which is being already occupied by the species 2 and puts the pressure on them.

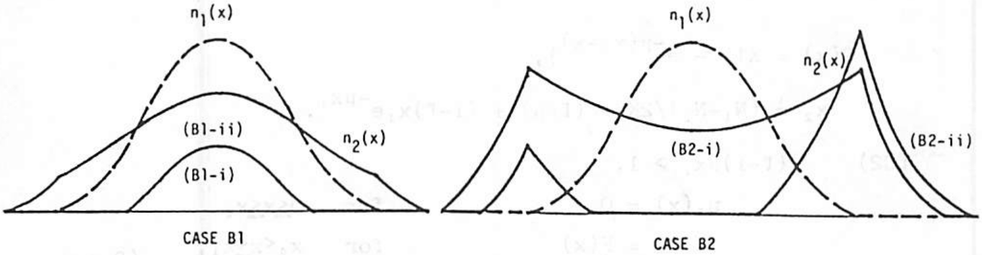

Fig. 6. Distribution functions $n_1(x)$ and $n_2(x)$ of CASE B. Four types of patterns of $n_2(x)$ for given $n_1(x)$ are shown.

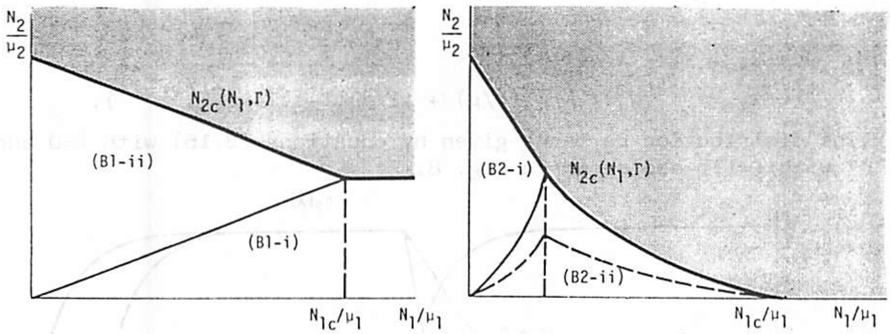

Fig. 7. Domains of four types of patterns of distribution $n_2(x)$.

As we have shown in the last section (C-b), the solution $n_1(x)$ is given by

$$n_1(x) = K\{1 - e^{-\mu(x_1-x)}\} \quad \text{for} \quad 0 \le x \le x_1, \qquad (3.14)$$
$$= 0 \quad \text{for} \quad x > x_1,$$

where

$$x_1 = (N_1/2K) + (1/\mu).$$

In the present case, the species 1 puts the repulsive pressure on the species 2 through the contest of room occupation, even if $\Gamma=0$, and the species 2 scarecely get into the central part of potential valley. $n_2(x)$ is obtained as follows.

(C1) $(\Gamma-1)\mu x_1 \le 1.$

$$n_2(x) = F(x) \quad \text{for} \quad 0 \le x \le x_1,$$
$$= G(x) \quad \text{for} \quad x_1 < x \le x_2, \qquad (3.15)$$
$$= 0 \quad \text{for} \quad x > x_2,$$

where

$$F(x) = Ke^{-\mu(x_1-x)}[\{1-e^{-\mu(x_2-x_1)}\} + (1-\Gamma)(x_1-x)],$$

$$G(x) = K\{1 - e^{-\mu(x_2-x)}\},$$

$$x_2 = (N_1+N_2)/2K + (\Gamma/\mu) + (1-\Gamma)x_1e^{-\mu x_1}.$$

(C2) $(\Gamma-1)\mu x_1 > 1.$

$$n_2(x) = \begin{cases} 0 & \text{for } 0\le x\le x_0, \\ F(x) & \text{for } x_0<x\le x_1, \\ G(x) & \text{for } x_1<x\le x_2, \\ 0 & \text{for } x>x_2 . \end{cases} \qquad (3.16)$$

where

$$x_0 = x_1 - 1/\mu(\Gamma-1),$$

$$x_2 = (N_1+N_2)/2K + (\Gamma/\mu) + (1/\mu)(\Gamma-1)\{1-e^{-1/(\Gamma-1)}\}.$$

The distribution patterns given by equations (3.15) with $\Gamma=0$ and (3.16) with $\Gamma=1.5$ are shown in Fig. 8.

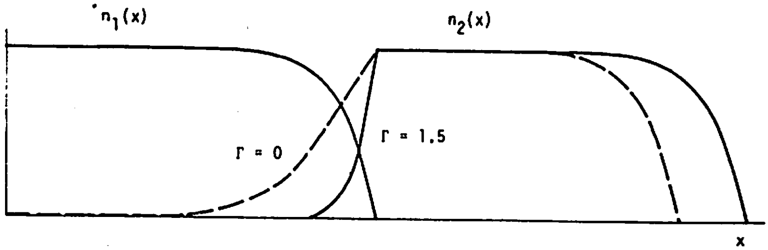

Fig. 8. Distributions $n_1(x)$ and $n_2(x)$ of CASE C.

4. DISCUSSION

The stationary distribution patterns of biological aggregation, which are derived by the density dependent dispersive motion under the environmental attractive potential field, were studied using three types of potential functions, (A) square potential (B) local square potential valley and (C) density dependent vacant room potential.

It has been shown that, if we consider ordinary density independent dispersive motion ($\beta=0$), the population can not be stuck in the finite range of space by the attractive potential force and it approaches a stationary distribution with infinite tails, except when the potential valley is spatially bounded by the infinite walls of potential barriers. Especially, in the case (B) of local potential valley, whole population gradually spreads out over infinite space and the aggregation pattern which could be temporarily realized finally disappears. On the other hand, when we consider only the density dependent term of dispersive coefficient ($\alpha=0$), the population can forms a spatially bounded aggregation pattern without dropouts, except the case of local potential valley, in which only restricted number ($N<N_C$) of individuals can remain in the aggregation surrounding the bottom of valley.

The stationary aggregation patterns of two species populations with interspecific interference were also studied assuming that both species have a preference for similar environmental condition, but the predominant species 1 exerts the repulsive pressure on the species 2. The populations of two species show different spatial patterns, depending upon the value of $\Gamma=(k_1/2\beta_1 k_2)\gamma$, where γ is the parameter specific to the repulsive pressure of the predominant species 1. As shown in Figs. 4 and 5 (also in Figs. 6 and 7), the effect of the repulsive pressure appears explicitly when $\Gamma>1$, however when the weaker species 2 has a certain degree of population size, they can intrude into the central part of potential valley.

Finally, as the examples, the time development of the distributions of two species in the cases (A1-i) and (A2-i) are shown in Fig. 9.

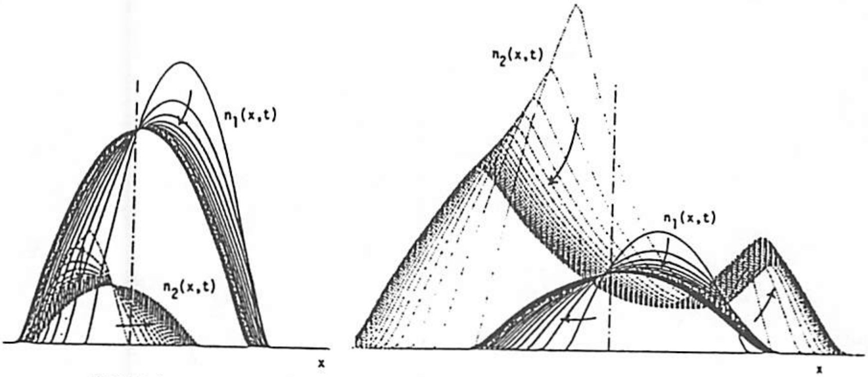

Fig. 9. Time development of distribution patterns of two species populations (case A).

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