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SPATIAL DISTRIBUTION OF RAPIDLY DISPERSING ANIMALS IN HETEROGENEOUS ENVIRONMENTS

Nanako SHIGESADA

Department of Biophysics
Kyoto University
Kyoto
Japan

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Nanako Shigesada

Department of Biophysics, Kyoto University, Kyoto, Japan

1. Introduction

Ecological models incorporating spatial heterogeneity of habitats are of profound importance in understanding the movements of organisms and their effects on the stability of spatial distributions of populations under natural circumstances. Equations describing the time development of the spatial distribution of a population in a heterogeneous environment fundamentally involves two terms, dispersal and growth, which are both functions of space. There have been several distinct approaches to the analysis of such models depending on the system under investigation and the type of method being applied (See reviews by Okubo (1980) and Levin (1981)). Among them, models for a single species in one dimensional space have been extensively studied for various types of ecological systems. Okubo (1980) analyzed effects of various kinds of spatially varying dispersal on the spatial structure of populations. Gurney and Nisbet (1974) and Namba (1980) included a spatially varying growth term in their model. In population genetics, Fleming (1975) studied the effect of environmental heterogeneity on the viability of individuals of a single species and presented the condition for the existence of clines in a one-dimensional space. As for two-species systems, the effect of dispersal with directed movements was taken into consideration by Comins and Blatt (1974) and Shigesada et al. (1979), and the effect of spatially varying growth was considered by Pacala and Roughgarden (1982) and Kawasaki and Teramoto (1979). However, these models incorporated the effect of heterogeneity either in dispersal or growth, but not in both processes.

Recently, Fife and Peletier (1981) studied a single species model in population genetics, in which effects of environmental heterogeneity were incorporated in both dispersal and growth processes. Shigesada and Roughgarden (1982) also considered these effects in a two-competing species model. The latter authors analyzed the time development of spatial distribution and its stability for the special case in which the dispersal process occurs much rapidly compared with the growth process of the species. In this paper we examine Shigesada and Roughgarden's model on a more mathematical basis by using a multiple scale method, and present a general formula for the time development of spatial distributions of populations. From the assumption of rapid dispersal, the original partial differential equation is reduced to an ordinary differential equation so that the analysis becomes much easier. We apply this method to a few systems with a single and with two competing species, and compare the results from this method with those from computer calculations.

2. Application of the multiple scale method to a single species population dynamics with dispersal

Consider a single-species population in a bounded heterogeneous habitat. Individuals of the species undergo dispersal both by random motion and by directed movement toward favorable places in the habitat. The population density also changes due to birth and death, which are usually dependent on both the position and population density. If $n(t,x)$ denotes the population density at time t and position x, the dynamical equation for the spatial distribution of the population in a one-dimensional bounded region $\sigma \equiv [0,L]$ is given by

$$\frac{\partial}{\partial t} n(t,x) = -\frac{\partial}{\partial x} J(x,n) + \varepsilon G(x,n), \qquad x \in \sigma, \tag{1}$$

where

$$J(x,n) = -\alpha\frac{\partial}{\partial x} n - \frac{dU(x)}{dx}\cdot n \quad . \tag{2}$$

The term $J(x,n)$ is the flux of population due to the dispersal process. Namely, $-\alpha\frac{\partial}{\partial x}n$ (α is a positive constant) represents the flow associated with random movements of individuals, and the term $-\frac{d}{dx}U(x)\cdot n$ (where we assume that $U(x)$ has a continuous derivative) represents the flow due to directed movements of individuals toward favorable environments. Here we designate $U(x)$ as the "environmental potential", which induces the advection velocity, $-\frac{d}{dx}U(x)$, toward favorable regions. The second term of (1), $\varepsilon G(x,n)$ represents the net growth rate due to birth and death. For convenience in later discussions, we express the net growth rate by the product of the factor ε and G so that the dispersal term $-\frac{\partial}{\partial x}J$ and G are of the same order of magnitude. We assume here that $G(x,n)$ is a bounded piecewise continuous function of x and has a continuous derivative with respect to n. We also incorporate an intraspecific competition in the function G such that G becomes negative as n exceeds a certain positive number k.

We assume that some animals are located initially in the closed region σ, where there is no population flow through the boundaries, so that the model is subject to the initial and boundary conditions:

$$\begin{aligned} &n(0,x) = s(x) \geq 0 \quad (\neq 0)\ , \\ &J(x,n) = 0 \quad \text{at } x=0 \text{ and } L, \end{aligned} \tag{3}$$

where $s(x)$ is continuous in σ.

In some ecological situations, dispersal and growth processes take place in different time scales. It is frequently seen in nature that the change in population density as a result of the dispersal process occurs more rapidly than the change due to the growth process. For example, some animals undergo daily migration, seeking resources and settling places, while they reproduce once or twice a year. Here we focus our attention on the cases where ε is small enough so that a rapid change in the spatial distribution of population due to the dispersal process occurs initially, followed by a slow long-term change in the population size due to the growth process. We can choose the scales of independent variables so as to set the order of magnitude of the dispersal rate to be $O(1)$. In this case we can analyze our model by the multiple scale (two-timing) method (Neyfeh,1973), and obtain a truncated expansion valid for all t up to $O(1/\varepsilon)$.

Let us introduce the following two different time scales, T_0, T_1 defined as

$$T_0 = t, \qquad T_1 = \varepsilon t \quad .$$

We consider the solution of (1) as a function of these two time scales, $n(t,x) = n(T_0,T_1,x;\varepsilon)$ and we attempt to find the solution in the following form, which is valid for times as large as $O(1/\varepsilon)$:

$$n(t,x) = n(T_0,T_1,x;\varepsilon) = n^0(T_0,T_1,x) + \varepsilon n^1(T_0,T_1,x) + \cdots, \tag{4}$$

where the remainder is $O(\varepsilon^2)$ and n^1 is bounded for all T_0. We now carry out a perturbation procedure by noting that the time derivative is transformed according to

$$\frac{\partial}{\partial t} = \frac{\partial}{\partial T_0} + \varepsilon\frac{\partial}{\partial T_1} \quad . \tag{5}$$

Upon inserting (4) and (5) into (1) and equating coefficients of like powers of ε, we obtain

$$\frac{\partial}{\partial T_0} n^0 = -\frac{\partial}{\partial x} J(x,n^0), \tag{6}$$

$$n^0(0,0,x) = s(x),$$

$$J(x,n^0) = 0 \quad \text{at } x=0 \text{ and } L;$$

$$\frac{\partial}{\partial T_0} n^1 + \frac{\partial}{\partial x} J(x,n^1) = -\frac{\partial}{\partial T_1} n^0 + G(x,n^0), \tag{7}$$

$$n^1(0,0,x) = 0,$$

$$J(x,n^1) = 0 \quad \text{at } x=0 \text{ and } L.$$

The general solution of (6) is written in the form

$$n^0(T_0,T_1,x) = N^0(T_1)f(T_0,x) \quad , \tag{8}$$

where $f(T_0,x)$ is the solution of the following equation,

$$\frac{\partial}{\partial T_0} f = -\frac{\partial}{\partial x} J(x,f), \tag{9}$$

$$f(0,x) = \frac{s(x)}{\int_\sigma s(x)dx} \quad ,$$

$$J(x,f) = 0 \quad \text{at } x=0 \text{ and } L.$$

By integrating (9) over σ, we find $\int_\sigma f(T_0,x)dx = 1$. Thus, $f(T_0,x)$ may be regarded as the probability density of the spatial distribution of population in σ, since $f(T_0,x) \geq 0$. Equation (9) is a so-called regular Sturm-Liouville problem, and its solution is written as

$$f(T_0,x) = \sum_{i=1}^{\infty} c_i \exp\{-\lambda_i T_0\}\phi_i(x) \quad , \tag{10}$$

where ϕ_i are the eigenfunctions of (9) and λ_i are the eigenvalues, which are nonnegative and can be arranged in the following increasing sequence (Berg and McGregor, 1966):

$$0 = \lambda_1 < \lambda_2 < \lambda_3 < \cdots$$

Thus $f(T_0,x)$ is bounded for all x and T_0 and asymptotically approaches an equilibrium $f^*(x)$, which is the solution of $J(x,f^*)=0$:

$$f(T_0,x) \xrightarrow{T_0 \to \infty} f^*(x) = \frac{\exp\{-\frac{U(x)}{\alpha}\}}{\int_\sigma \exp\{-\frac{U(x)}{\alpha}\}\,dx} \quad . \tag{11}$$

The function $N^0(T_1)$ remains arbitrary, but we can determine it at the next stage of the perturbation.

To this end, let us integrate (7) over σ and put $N^1(T_0,T_1) = \int_\sigma n^1(T_0,T_1,x)dx$. We then have

$$\frac{\partial}{\partial T_0} N^1(T_0,T_1) = -\frac{\partial}{\partial T_1} N^0(T_1) + \int_\sigma G(x,N^0(T_1)f(T_0,x))dx \quad . \tag{12}$$

Since $n^1(T_0,T_1,x)$ is required to be bounded for all T_0, $N^1(T_0,T_1)$ should also be bounded for all T_0. However, the solution of (12), $N^1(T_0,T_1)$, will become unbounded, because of the occurrence of secular terms, unless we require the right hand side of (12) to tend to zero as $T_0 \to 0$. So let us try to set the unknown function $N^0(T_1)$ equal to the solution of the following equation,

$$\frac{\partial}{\partial T_1} N^0(T_1) = \int_\sigma G(x,N^0(T_1)f^*(x))dx \tag{13}$$

$$N^0(0) = \int_\sigma s(x)dx,$$

which is obtained if we substitute $f^*(x)$ into $f(T_0,x)$ in (12) and set the right hand side of (12) equal to zero. The solution of (13), $N^0(T_1)$, is bounded for all T_1 because we imposed the condition that $G(x,n)$ becomes negative for large n.

Now let us examine whether the solution of (12), $N^1(T_0,T_1)$, is actually bounded for all T_0. By substituting (13) into (12), and integrating over T_0, we obtain the equation,

$$N^1(T_0,T_1) = \int_0^{T_0}\int_\sigma \{-G(x,N^0 f^*(x)) + G(x,N^0 f(T_0',x))\}dxdT_0'. \tag{14}$$

The right hand side is verified to be bounded for all T_0 if we apply the mean value theorem and take Eq.(10) into consideration. Thus the assumption of N^0 as the solution of (13) proves to be appropriate. However, it should be noted here that $N^1(\infty,T_1)$ becomes divergent as the length of the habitat L becomes infinite, since the eigenvalue $\lambda_2 \to 0$ as $L \to \infty$.

To summarize the above analysis, we can conclude that:

The solution of (1), which is valid for times up to $O(1/\varepsilon)$, is given by

$$n(t,x) = N^0(\varepsilon t)f(t,x) + O(\varepsilon) \ , \tag{15}$$

where $f(t,x)$ is the probability density of the spatial distribution given by (10), and $N^0(\varepsilon t)$ is the solution of the ordinary differential equation (13), which usually can be solved easily, as will be shown in the following sections.

Note here that $\int_\sigma n(t,x)dx = N^0(\varepsilon t) + O(\varepsilon)$, since $\int_\sigma f(t,x)dx = 1$, so that we can regard $N^0(\varepsilon t)$ as the total size of the population in σ. Thus we can see from (15) that when we focus our attention on the behavior of the rapid dispersal process (in the time range of $O(1)$), the distributional pattern changes so as to satisfy (10), approaching an equilibrium $f^*(x)$ without change in the total population size ; on the other hand, when we turn our attention to the long-term behavior (in the time range of $O(1/\varepsilon)$), the total population size $N^0(\varepsilon t)$ changes so as to satisfy Eq.(13), while the probability density of the spatial distribution always remains in the stationary state, $f^*(x)$. In the following section, we will apply the above method to a typical system of a single species.

3. Population with general logistic growth

Here we will consider the case in which the growth term is of the general logistic type,

$$G(x,n) = \{a(x) - b(x)n\}n \tag{16}$$

where $a(x)$ and $b(x)$ (>0) are assumed to be piecewise continuous functions of x in σ. The intrinsic growth rate $a(x)$ may have both positive and negative values in the habitat and if regions satisfying $a(x) < 0$ predominate in σ, the population may fail to grow in this habitat as a whole. Thus we are interested in the conditions under which the population can grow in the habitat and how the total population size changes to approach an equilibrium state.

Substituting (16) into (13), we have the equation for the total population size $N^0(\varepsilon t)$ that

$$\frac{d}{dT_1} N^0(T_1) = (A - BN^0)N^0 \ , \qquad N^0(0) = \int_\sigma s(x)dx \ , \tag{17}$$

where

$$A = \int_\sigma a(x)f^*(x)dx, \qquad B = \int_\sigma b(x)f^{*2}(x)dx,$$

$$f^*(x) = \exp\{-\frac{U}{\alpha}\} \Big/ \int_\sigma \exp\{-\frac{U}{\alpha}\}\, dx \ .$$

The solution of (17) is given by

$$N^0(\varepsilon t) = \frac{AN^0(0)}{BN^0(0) + (A - BN^0(0))\exp\{-\varepsilon tA\}} \tag{18}$$

which becomes, as $\varepsilon t \to \infty$

$$\begin{aligned} N^0(\varepsilon t) \quad &\to \quad \frac{A}{B} \qquad \text{when} \quad A \geq 0 \ , \\ &\to \quad 0 \qquad \text{when} \quad A < 0. \end{aligned} \tag{19}$$

Thus if the average growth rate with respect to $f^*(x)$ is positive i.e.

$$A = \int_\sigma a(x)f^*(x)dx > 0, \tag{20}$$

then the population can grow in this habitat, and otherwise, the population becomes extinct. In other words, the condition $A > 0$ represents the invasion condition for the population. The value of A depends on the function $U(x)$, and hence even if the average of the intrinsic growth rate $a(x)$ over σ, $\int_\sigma a(x)dx$, is negative, A may be positive when $U(x)$ has such an appropriate form that directed movements are induced toward the region where $a(x)$ is positive.

As we noted previously, the two-timing expansion (15) is applicable as long as we are concerned with the time scale up to $O(1/\varepsilon)$, so that it is not necessarily uniformly valid for all time. However, in the case of the logistic growth of (16), it turns out to be a fairly good approximation even for a longer time range when ε is sufficiently small. Fig.1 shows that the truncated solutions (18) agree well with numerical results derived from (1).

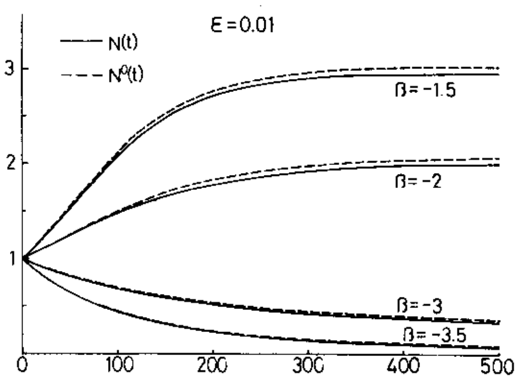

Fig.1. Time variation of the total population sizes of single species. The solid curves are $N(t)=\int_\sigma n(t,x)dx$ derived from (1) by computer calculation. The broken curves are the truncated solutions of (18), N^0. Parameter values are $\alpha=1$, $b(x)=1$, $\varepsilon=0.01$, $L=4$ and advection velocity, $-dU/dx=1$, so that animals are attracted in the positive direction of the x axis. The intrinsic growth rate is $a(x)=\beta+x$. Results for $\beta=-1.5$, -2, -3 and -3.5 are plotted. The critical value of β for invasion in the multiple scale method is -3.074 at which $A=0$.

To further examine the validity of our expansion, we will compare the invasion condition (20) with the exact one which is analytically derived from Eq.(1) combined with (16). When the population is rare throughout the whole habitat, we obtain the invasion condition for the population satisfying Eq.(1) with (16) by analysing the following linearized equation about the solution $n=0$:

$$\frac{\partial}{\partial t} n = -\frac{\partial}{\partial x} J(x,n) + \varepsilon a(x)n \ , \quad x \in \sigma \tag{21}$$

$$J(x,n) = 0 \quad \text{at } x=0 \text{ and } L.$$

If the equilibrium state $n=0$ is dynamically unstable, the population can grow in the habitat; namely, the population, even when rare, can invade the habitat. If $n=0$ is stable, on the other hand, the population finally becomes extinct in the habitat. Previously, Fleming (1975) performed a stability analysis of (21) for the special case of $U(x)=0$ and has presented a useful theorem on the stability condition. By applying his theorem with slight modifications to our model, we have invasions conditions for our system as follows:

i) $A > 0$, or

$$\text{ii) when } A < 0,\ \varepsilon > \inf\left\{\frac{\int_\sigma n_x^2 \exp\{-\frac{U}{\alpha}\}\,dx}{\int_\sigma a(x)n^2\exp\{-\frac{U}{\alpha}\}dx} : \int_\sigma a(x)n^2\exp\{-\frac{U}{\alpha}\}dx > 0\right\} \tag{22}$$

Now if ε tends to zero, the above condition is reduced to $A > 0$, which exactly coincides with our conclusion (20).

To comfirm the above result for a specific example, let us consider the special case that has been analytically solved by Pacala and Roughgarden (1982):

$$\begin{aligned} a(x) &= s_1>0 \text{ (const.)} && \text{for } 0\le x< L_1, \\ &= s_2<0 \text{ (const.)} && \text{for } L_1\le x\le L_1 + L_2 \ , \\ U(x) &= 0 \ . \end{aligned} \tag{23}$$

The invasion condition derived from (21) was given by the above authors as

$$\sqrt{s_1}\,\mathrm{Tan}\left(\frac{L_1}{\sqrt{\alpha}}\sqrt{\varepsilon s_1}\right) - \sqrt{-s_2}\,\mathrm{Tanh}\left(\frac{L_2}{\sqrt{\alpha}}\sqrt{-\varepsilon s_2}\right) > 0 \quad . \tag{24}$$

When we are concerned with the case,

$$L_1\sqrt{\frac{\varepsilon s_1}{\alpha}} \ll 1, \qquad L_2\sqrt{\frac{-\varepsilon s_2}{\alpha}} \ll 1,$$

(24) is expanded as

$$A + \frac{\varepsilon}{3\alpha}\,(L_1^3 s_1^2 + L_2^3 s_2^2) + \cdots > 0,$$

where $A = s_1 L_1 + s_2 L_2$. As expected, we have again $A > 0$ as the invasion condition with a correction of order $O(\varepsilon)$.

4. Multi-species system.

We now extend the previous study to multi-species systems. Consider an M-species system which satisfies the following equation,

$$\frac{\partial}{\partial t} n_i = -\frac{\partial}{\partial x} J_i(x,n_i) + \varepsilon G_i(x,n_1,n_2,\ldots,n_M), \quad x \in [0,L] \equiv \sigma \qquad (25)$$

$$\text{for } i = 1,2,\ldots,M,$$

where we put

$$J_i(x,n_i) = -\alpha_i \frac{\partial}{\partial x} n_i - \frac{d}{dx} U_i(x)\cdot n_i . \qquad (26)$$

$n_i(t,x)$ is the population density of the i-th species, and α_i, $U_i(x)$ and εG_i are respectively the diffusion constant, the environmental potential and the growth rate of the i-th species. These parameters are defined in the same way as in the single species system. The model is subject to the following initial and boundary conditions:

$$n_i(0,x) = s_i(x) \geq 0 \ (\not\equiv 0),$$

$$J_i(x,n_i) = 0 \quad \text{at } x = 0 \text{ and } L.$$

The multiple scale method can be applied to the above equation in a similar way as in the case of the single species system, and the solution, which is valid for all t up to $O(1/\varepsilon)$, is given by

$$n_i(t,x) = N_i^0(t) f_i(t,x) + O(\varepsilon), \quad i=1,2,\ldots,M, \qquad (27)$$

where $f_i(t,x)$ is the probability density for the spatial distribution of the i-th species and satisfies the following equation:

$$\frac{\partial}{\partial t} f_i = -\frac{\partial}{\partial x} J_i(x,f_i), \quad i=1,2,\ldots,M \qquad (28)$$

$$f_i(0,x) = \frac{s_i(x)}{\int_\sigma s_i(x)dx}$$

$$J_i(x,f_i) = 0 \quad \text{at } x = 0 \text{ and } L.$$

$N_i^0(t)$ is the total population size of the i-th species in σ and satisfies the dynamical system,

$$\frac{d}{dt} N_i^0 = \varepsilon \int_\sigma G_i(x, N_1^0 f_1^*, N_2^0 f_2^*, \ldots, N_M^0 f_M^*)dx, \quad i=1,2,\ldots,M \qquad (29)$$

$$N_i^0(0) = \int_\sigma s_i(x)dx,$$

where

$$f_i^*(x) = \exp\{-\frac{U_i}{\alpha_i}\} \Big/ \int_\sigma \exp\{-\frac{U_i}{\alpha_i}\}dx \quad .$$

Now, let us consider a special case of a two competing species system, which has the following generalized Lotka-Volterra type growth functions,

$$G_i(x,n_1,n_2) = \{a_i(x) - \sum_j b_{ij}(x) n_j\}\, n_i, \quad i=1,2, \qquad (30)$$

where we assume that $a_i(x)$ and $b_{ij}(x)(>0)$ depend on position x.

As is well known, if neither of these two species undergoes dispersal (namely when $J_1=J_2=0$), they can coexist at a position x if and only if

$$\frac{b_{11}(x)}{b_{21}(x)} > \frac{a_1(x)}{a_2(x)} > \frac{b_{12}(x)}{b_{22}(x)} \qquad (31)$$

and otherwise, one of the species always becomes extinct at x. Since the environment is heterogeneous, (31) may be satisfied at some places in the habitat, but not at other places. In such a case, we are interested in how the total population sizes of the two species in the habitat change with time, if both species undergo dispersal according to equation (26).

The equations for the population sizes in the multiple scale method are obtained by substituting (30) into (29):

$$\frac{d}{dt} N_i^0 = \varepsilon\{A_i - \sum_j B_{ij} N_j^0\} N_i^0 , \quad i=1,2, \tag{32}$$

where

$$A_i = \int_\sigma a_i(x) f_i^*(x) dx$$

$$B_{ij} = \int_\sigma b_{ij}(x) f_i^*(x) f_j^*(x) dx \quad .$$

Thus if

$$\frac{B_{11}}{B_{21}} > \frac{A_1}{A_2} > \frac{B_{12}}{B_{22}} \quad , \tag{33}$$

the two species can coexist at least for times as large as $O(1/\varepsilon)$, and otherwise, one of the species tends to extinction.

Here it should be noted that Eq.(32) is analogous to the niche-partitioning theory of the MacArthur and Levins (1967), if we take the real habitat space as the niche space. Namely, we can see that $f_i^*(x)$ and $\varepsilon a_i(x)$ correspond to their utilization function and resource function. Thus (32) may be interpreted as a behavioral version of the MacArthur-Levins formula for habitat partitioning by competing species.

Now we carry out a numerical calculation of (25) for a two competing species system with the following parameters:

$$\begin{aligned} &J_1 = -0.5\frac{\partial}{\partial x} n_1 - 0.2 n_1 , \quad J_2 = -0.5\frac{\partial}{\partial x} n_2 + n_2 , \quad L = 2, \\ &G_1 = (1 - 0.1x - n_1 - n_2) n_1 , \quad G_2 = (1 + 0.5x - n_1 - n_2) n_2 . \end{aligned} \tag{34}$$

We also calculate the total population sizes $N_1(t) = \int_\sigma n_1(t,x)dx$, $N_2(t) = \int_\sigma n_2(t,x)dx$, and compare them with the truncated solution by the multiple scale method given by (32), $N_1^0(t)$ and $N_2^0(t)$. With the parameters chosen in (34), $a_1(x)/a_2(x) < b_{11}/b_{21}$, b_{12}/b_{22} for any $x \in \sigma$, and hence only the 2nd species can survive everywhere in σ in the absence of dispersal. However, if both species undergo dispersal, (32) has a stable positive equilibrium state, because the condition (33) is satisfied (A_1=0.91, A_2=1.77, B_{11}=0.53, B_{12}=B_{21}=0.40, B_{22}=1.04), so that both species tend to coexist as a whole in the multiple scale method. In Fig.2, we show the time developments of the population sizes for three cases, ε =0.01, 1 and 10. The solid and broken lines represent the numerical solutions of $N_1(t)$ and $N_2(t)$ derived from (25) for the case of (34) (hereafter called the exact solution), and the truncated solutions of (32), respectively. From this figure, we can see that for ε=0.01, the dynamical behavior of the truncated solution closely coincides with that of the exact solution, and the coincidence persists even for times longer than $O(1/\varepsilon)$. However, as ε increases so that the growth term becomes dominant in Eq.(25), the truncated solution deviates from the exact one with the lapse of time, and finally the first species becomes extinct in the exact solution, whereas in the truncated solution it remains positive for all time (the case of ε=10). In the above example, we chose parameters such that the two species undergo dispersal with directed movement toward different favorable places. Thus they segregate their habitats from each other, occupying those places in which they can grow at higher rates. This segregation facilitates the coexistence of species by relaxing the competition between the species.

Further computer calculations with various parameter values have shown that as long as ε is small, the time developments of population sizes according to (32) approximate exact ones fairly well for various kinds of potential functions $U_i(x)$ and growth function G_i.

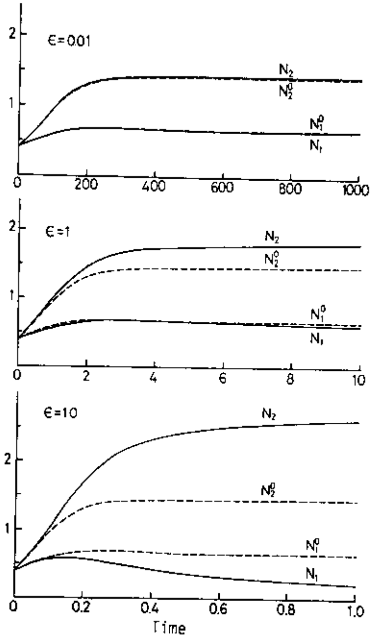

Fig. 2. Time variations of the total population sizes of the two competing species. The solid curves are $N_1(t) = \int_\Omega n_1(t,x)dx$ and $N_2(t) = \int_\Omega n_2(t,x)dx$ derived from Eq. (25) for the case of M=2 by computer calculation. The broken curves are the truncated solutions derived from (32), $N_1^0(t)$, $N_2^0(t)$. Parameter values are given by (34). Results for $\varepsilon = 0.01$, 1 and 10 are plotted. The agreement between the two curves becomes better as ε decreases.

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