



**ISAS - INTERNATIONAL SCHOOL
FOR ADVANCED STUDIES**

**DENSITY-DEPENDENT DISPERSAL AND
SPATIO-TEMPORAL DISTRIBUTION OF TWO
SPECIES IN A HETEROGENEOUS AND
PERIODICALLY FLUCTUATING ENVIRONMENT**

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1. INTRODUCTION

More than 60 years ago, mathematical ecology had its genesis through the coincident efforts of two intellectual giants A.Lodka and V.Volterra. The goal of Lodka-Volterra equation, logistic, Kolmogorov, and Gause type model was briefly, the quantification of the non-linear interactions within and between populations which can lead to periodic behaviour.

All these classical works ignored the spatial heterogeneity. The ecological situation can be understood only when population of organisms are considered in both time and space (Okubo, 1980). Many authors showed the role of space in the non-uniform distribution patterns of populations [2,5,6,8,14,23,29]. Taylor and Taylor remarked that the degree of crowding is not only a product of multiplication, but also of movement in space; and some populations disperse to avoid crowding (Namba, 1989). Shigesada and al. (1979) proposed a model of two animals species which have almost the same favorableness for the environment and disperse under population pressure due to intra and interspecific interferences. Namba (1989), in his work "Competition for space in a heterogeneous environment" analyzed the combined effects of density-dependent dispersal and spatially variable growth on distribution of competing populations. All these investigations, however, never took into account the effects of external factors of unpredictable environment. On another hand, many investigators were interested about the impact of stochastic unpredictable environment (May, 1975) and showed that the unpredictable environment strongly influenced the the population density (Nisbet and Gurney, 1982). All population, natural or artificial, are

affected to some extent by external perturbations. This variation frequently is sufficiently important that it can be regarded as a primary force in structuring many natural systems. Indeed, the existence of continual fluctuating stress on the ecosystem has led to proposals of an ecological paradigm that emphasizes population survival through the disequilibrium caused by the disturbances [27]. Classical models had assumed that birth and death rates are constant function of the population u . Obviously this is an extreme idealization even of laboratory conditions. While in the real world, outside laboratories, birth and death rates depend on some external factors of heterogeneous fluctuating environment such as temperature and humidity. This provides a possibility which cannot be explained by models that do not incorporate the effects of external factors. Therefore temporal fluctuation can be reflected in a population model through intrinsic parameters such as birth and death processes or extrinsic parameters relating to the environment. The simple and very common external factors of the varying environment are the climatic variations, which in general, change periodically with the time. A good example is the seasonal climatic variations which are quasi-cyclic.

Recently, summarizing the work of Hassell [11] and Mountford [19], (May 1989) suggested that for further studies, it is much more interesting to analyse a realistic model, in which spatial heterogeneity, environmental unpredictability, and nonlinear interactions within and between populations can swirl together to confound empirical studies aimed at understanding what prevents the long-term average density of a population from increasing indefinitely (or decreasing to zero in a time short compared with average extinction times). However, instead of using statistical approach, we will adopt a continuum mechanics approach to deduce and simplify the basic equations.

Now, a growing literature deals with the interplay between environment noise and the intrinsic dynamics of non-linear system of populations by using difference equation and by employing stochasticity in demographic or environment parameters [10,19]. Our developments are deterministic, in the mode of Namba, Nisbet and Gurney, by assuming that two species share the same space and disperse to avoid crowding. One of species is strongly affected by the external environment factors, while the second remain unaffected.

Clearly, in this work we seek to formulate a model capable of combining the spatio-temporal distribution of population which disperses, to avoid crowding in a heterogeneous space and periodically fluctuating environment.

2. CLASSICAL MODELS OF POPULATION DYNAMICS

In the natural heterogeneous and unpredictable environment, populations of many species can grow, coexist, compete and move around.

According to the first biological postulate [12]: "every living organism has arisen from at least one parent of like kind of itself", Lodka generalized the behavior of a population in the following equation

$$\frac{du}{dt} = f(u), \quad (2.1)$$

which merely tell us that the rate at which the number of individuals u in the population changes with time depends in some way on the number present. The solution of this first-order differential equation, in the simple case:

$$\frac{du}{dt} = bu,$$

is

$$u = u_0 \exp(bt), \quad (2.2)$$

where b represents the constant rate of increase per individual, birth minus death rates and is called Malthusian parameter.

The second biological postulate states that "in a finite space there is an upper limit to the number of finite being that can in some way occupy or utilize the space under consideration". This postulate leads to the best known model of a single species with density-dependent population regulation: the logistic model. In the differential form, this is

$$\frac{du}{dt} = bu - \frac{b}{k}u^2, \quad (2.3)$$

where b is the intrinsic growth rate of the species and k is the carrying capacity of the environment for this particular species.

The dynamics of the growth of a population can be described if the functional behavior of the rate of growth is known. Of course, it is this functional behavior which is usually

measured in the laboratory or in the field when the ecologist is interested in single-species population growth.

The usually assumption made is that the rate of growth is proportional to the number of species present. The proportionality "constant" may be dependent or independent of the number of individuals present, and it may be dependent or independent of time. In general, when the model is time independent, the population growth may be described by the autonomous equation

$$\frac{du}{dt} = ug(u), \quad (2.4)$$

where u is the number of individuals present at time t . If the model is time dependent, the population growth may be given by the nonautonomous equation

$$\frac{du}{dt} = uh(u, t). \quad (2.5)$$

Models of the preceding type are suitable for the growth of populations where the individual numbers are large. In this case u may be taken to represent the population density or perhaps the biomass of the population. Models given by (2.4) or (2.5) are generally not suitable if the individual numbers are small. The reason for this is that the differential equation models assume continuous birth and death rates, whereas in small populations that assumption is clearly false. When the average birth rates of the population is small, let say one a year, the natural model to describe the population dynamics is a difference equation, giving the change in population from one generation to the next. Hence the appropriate model for such a population is

$$u(t+1) = u(t)g(u(t)) \quad (2.6)$$

where $u(t)$ is the population number in the t -th generation or appropriate time unit, and $u(t+1)$ is the population number in the $(t+1)$ -th.

As usual we will let $u(t)$ stand for the prey density (or number, or biomass) and $v(t)$ for the predator density (or number, or biomass). Then it is assumed that the growth rate of any species at a given time is proportional to the number of that species present at that time. Further general assumptions are that the species are living in a homogeneous

environment and that age structures are not taken into account [4].

Every species in an ecological community is connected to many others. They can coexist together or compete for the use of the common resources. Each can be both a predator (if the species use the others species as a food) and prey (if one species is considered as a food of an other). These assumptions lead to a very well known model in populations dynamics, named the Lodka-Volterra equation [4].

For the prey species u it is assumed that the prey growth, if left alone, is Malthusian, i.e., the specific growth rate is constant. It is further assumed that the specific growth rate is diminished by an amount proportional to the predator density. This leads to the prey equation

$$\frac{du}{dt} = u(\alpha - \beta v), \quad \alpha, \beta > 0. \quad (2.7)$$

For the predator species v it is assumed that in the absence of prey, the predators will become extinct exponentially (just as in the radioactive decay) but that their growth rate is enhanced by an amount proportional to the prey density. This leads to the predator equation

$$\frac{dv}{dt} = v(-\gamma + \delta u) \quad \gamma, \delta > 0. \quad (2.8)$$

Putting both equations (2.7) and (2.8) together, we get a system referred as the Lodka-Volterra model for predator-prey interactions.

$$\frac{du}{dt} = u(\alpha - \beta v) \quad (2.9a)$$

$$\frac{dv}{dt} = v(-\gamma + \delta u) \quad (2.9b)$$

If the probability of an individual birth and death is constant at all points in a closed region, then movement of individuals from place to place within has no effect on the total population size.

The goal of Lodka-Volterra type model is briefly the description of the interactions within and between species and their inorganic environment. The classical modeling approach focuses on temporal evolution of populations, ignoring movement of species in the

space. All the classical works assumed a homogeneous space in an unvarying, deterministic environment and a density-dependent effect which would regulate a population to some constant value, or at worst to a stable cycle (May, 1989). These classical models for the whole population species imply only changes through time. The equations of ecosystem are then established by equating the derivative $\frac{du}{dt}$ to another relation expressing the effect of species and environmental interactions on the population u . However, spatial variation is not considered. This is unrealistic in the natural environment where the key factors differ for the same species in different places and affect different stages in the life history. This makes models for the whole species population unrealistic. The ecological situation can be understood only by taking into account the space and the time variation. Taylor and Taylor (1977), remarked that a lack of rigour in distinguishing total population from population density can imply uniform distribution of density in space. As soon as birth and death rates vary with the position the situation changes dramatically and dispersal may play a vital role in determining whether a population grows or declines.

Mathematical ecologists have produced numerous models showing how spatial aspect of species interactions can provide opportunities for coexistence [21,22,23,25,27,28,29]. Without the benefit of equation, naturalists had concluded that many species persist together only because of opportunities provided by spatial heterogeneity and dispersal.

3. SPATIO-TEMPORAL DISTRIBUTION OF DISPERSAL POPULATIONS

Space complicates ecological interactions by two fundamental mechanisms: it allows for non-uniform patterns of environment and population density and for movement (dispersal or migration) of individuals or their gametes from one location to another (Levin, 1976a). One classic definition of the aim of animal ecology is 'to discover the reasons for the distribution and abundance of animals in nature'(Elton,1927). This definition emphasizes the expectation that the same factors, both external (such as food and water, temperature, predation ect.) and internal (such as territorial behaviour, social interactions ect.) which set the overall size of a population will also determine the way in which it is distributed over the available space [27]. Nisbet and Gurney (1982) formulated their fundamental equation by assuming that, there is one elementary principle which underlies all population modelling, namely that the total number of individuals (u) in a fixed region of space can only change for four reasons:

- (a) births,
- (b) deaths,
- (c) immigration,
- (d) emigration.

In a small time interval Δt the change in population Δu can thus always be written as

$$\Delta u = (B - D + I - E)\Delta t, \quad (3.1)$$

where $B\Delta t$, $D\Delta t$ are respectively the total numbers of births and deaths during Δt , while $I\Delta t$ and $E\Delta t$ are the total numbers of individuals entering and leaving the region during the same time interval. The wide variation in the mathematical form of population equations found in the literature correspond to different assumptions concerning the terms, B , D , I and E in this fundamental equation.

These assumptions are of two types. First we need to specify the type of information on B , D , I , or E which is to be incorporated in the model. This determines the

class of mathematical equations which will be used. Then we must specify the function form for each of the quantities. For instance, if we are modelling a population density-dependent, age-specific mortality we must specify the death rate as a function of age and of population size. It is important that this should be done as late as possible in the analysis in order to distinguish general principles from special results caused by particular choices of B , D , I , or E . Immigration or emigration occur only by moving from one region to another.

In the life time of most animals there occurs a time when the site of inhabitation is abandoned in favor of migration. Thus, in an environment changing through space and time, the most probable strategy for a new individual to adapt to survive and reproduce may not necessarily consist of remaining to compete with its parents or congeners, but may rather consist of migration elsewhere to find empty niche to habitat (Taylor and Taylor, 1977). As a result, the spread of population, i.e., dispersal takes place. Such animal movement include nomadism, whereby animals wander with no particular direction in search of sustenance, in a manner that resembles the random walk; and migration, which may be periodic when animals move from one habitat to another in a repetitive cycle, or nonperiodic. In addition, animals may display a restricted movement as they carry on their daily activities within a given domain of their habitat (home range). Animals utilize spatial selectivity in their movement. A similar restriction can also be applied to time. The utilization of time by animals is not uniform. They do not always move around, but sometimes rest.

The spatial distribution of patterns of animal population in its natural environment may be realized as a result of various kinds of biological effects, for example, heterogeneity of environment conditions, mutually attractive or repulsive interactions of individuals and localization of egg-laying process can be the principal causes of spatial pattern formation. Species interaction is directly related to the net population flux through an arbitrary small piece of space, and thus a proper expression is unattainable without knowledge of the mechanism of movement of the organism. Many organisms in the natural environment are subject to biodiffusion, i.e, there exist some forces acting on individual organism.

Neither Patlk's model nor The Fokker-Planck equation for biodiffusion which describe the diffusion of population species in a randomly fluctuating environment, takes into account interference between individuals, although the parameters of these models may be regarded as being dependent upon the population density in general.

Shigesada and Teramoto (1978) presented a mathematical model of advection and diffusion to explain the spatial distribution of animal populations that are principally controlled by interference between individuals and other environmental conditions. The formulation of this model is based on the assumption that animals move under the influence of the following fundamental forces:

(1) a dispersive force associated with random movement of animals;

(2) an attractive force, which induces directed movement of animals toward favorable environments;

(3) population pressure due to interference between individual animals.

Thus, Shigesada and Teramoto presented their equation for the one dimensional model

$$\frac{\partial S}{\partial t} = \frac{\partial^2}{\partial x^2} [\{\alpha(x) + \beta(x)S\}S] + \frac{\partial}{\partial x} \left\{ \frac{\partial \Phi}{\partial x} S \right\}. \quad (3.2)$$

Here $S(x, t)$ is the density of animals; $\alpha(x) + \beta(x)S$ represents the virtual diffusivity, dependent upon spatial inhomogeneity and population pressure; and $\Phi(x)$ denotes the potential of the environmental attraction, which induces the advection velocity

$$V(x) = -\frac{\partial \Phi}{\partial x} \quad (3.3)$$

toward favorable region. Shigesada and Teramoto derive equation (3.2) from a microscopic model in which individuals perform a biased random walk.

The steady-state distribution of animals for the above is obtained by equating the right-hand side of (3.2) to zero and integrating with respect to x :

$$\frac{d}{dx} \{(\alpha + \beta S)S\} + \frac{\partial \Phi}{\partial x} S = -J \quad (\text{constant}) \quad (3.4)$$

where J represents the flux of organisms. When an animal is displaced in a closed region this flux must vanish.

One year later, Shigesada and al. extended their model to the populations of two animal species that have almost the same affinity for the environment and are under the influence of population pressure due to intra-and interspecific interference. They showed, by computer simulations, that coexistence of two similar and competing species, which cannot coexist in the absence of dispersal, is realised if environmental heterogeneity and non-linear dispersive forces are introduced. However, they assumed that the environmental heterogeneity modifies only the dispersive forces and does not alter the growth rate and competitive interactions. The growth rate and the ranks of competitive ability also varies as the environmental conditions change and some inferior competitors can survive in heterogeneous environments, because of their wider tolerance to the environment conditions.

The time changes of population densities $S_1(x, t)$ and $S_2(x, t)$ are given by

$$\frac{\partial S_1}{\partial t} = \frac{\partial^2}{\partial x^2} \{(\alpha_1 + \beta_{11}S_1 + \beta_{12}S_2)S_1\} + \frac{\partial}{\partial x} \left\{ \gamma_1 \frac{\partial \Phi}{\partial x} S_1 \right\} \quad (3.5a)$$

$$\frac{\partial S_2}{\partial t} = \frac{\partial^2}{\partial x^2} \{(\alpha_2 + \beta_{21}S_1 + \beta_{22}S_2)S_2\} + \frac{\partial}{\partial x} \left\{ \gamma_2 \frac{\partial \Phi}{\partial x} S_2 \right\}, \quad (3.5b)$$

where $\alpha_i + \beta_{ij}S_j (i, j = 1, 2)$ are the virtual diffusivities of the i -th species, which depend upon spatial inhomogeneity and intra-and interspecific population pressure, and $\gamma_i (i = 1, 2)$ are the coefficients of affinity for the environment.

If two similar species have slightly different preference to the environmental conditions because of distinctive adaptabilities, there occurs severe competition only in the overlapping zone when their main habitats meet in some region [27].

Until now we have been concerned primarily with diffusional aspects of animal movements, and ignoring the growth or decay of the populations. Under optimum condition, most populations have a very high potential for growth. However, in spite of this potential, the number observed in populations of many species appear to be regulated within certain limits, because of the effects of environment heterogeneity in the habitat.

To study such an effect in the habitat, we must consider growth function and diffusion

coefficients for each species as space-dependent.

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 involve two terms, dispersal and growth, which are both functions of space [5].

4. ON THE REACTION-DIFFUSION EQUATION FOR BIOLOGICAL SYSTEM:

As the relations describing the growth, decay, and interaction of biological populations are very closely analogous to the laws of chemical kinetics in general, mathematical methods and analyses underlying the reaction-diffusion systems in chemistry may often be applicable to an ecosystem with diffusing populations. In this context the book by (Nicolis and Prigogine, 1978) is very useful. In recent years reaction-diffusion equation have been frequently used to model ecological system. The formalism they provide is rich enough to include all reasonable forms of intra- and interspecific interactions, also making possible to account for the effects of dispersal. A good general reference is the book by (Okubo, 1980). Reaction-diffusion systems have received much attention particularly when two or more equations are coupled through nonlinear terms to model predator-prey and competitive interactions between species [7]. The diffusion is almost invariably always to be Fickian. This has been criticized by a number of authors, notably by Cohen and Murray [1] in their work "A generalized diffusion model for growth and dispersal in a population". They believed that, with complexity of ecological system it seems too restrictive to describe spatial effects (other than convection) with the simply Fickian. They have shown that an approach based on a Landau-Ginzburg free energy model is more general and contains the Fickian law model as a special case.

We see now another approach: a modelling procedure which has found wide application in such situation is the use of partial differential equations which describe the changes with respect to both space and time of population density.

$$\frac{\partial u}{\partial t} = D\Delta(u) + f(x, u, t), \quad (4.1)$$

where u is the population density depending on space x , time t , and D the diffusion coefficient, while $f(x, u, t)$ represents the reaction terms. The underlying assumption made by the authors which used this model is that dispersal is due to random motion of individuals. There is, however, ample evidence that for some species migration to avoid crowding, rather than random motion is primarily cause of dispersal [20,23]. Gurney and MacCAMY (1977) adopt a continuum viewpoint and use standard techniques

of continuum mechanics to deduce and simplify the basic equations.

Gurney and Nisbet (1975), based the analysis on probabilistic consideration They showed that the population is growing with a local growth rate $G(x)$ which in their case did not depend on the population density and disperse with a local population current density $J(x, t)$. In the general case $G(x)$ is a function depending on the density u , the space x and time t . Then they proposed that the population density $u(x, t)$ satisfy the equation

$$\frac{\partial u}{\partial t} = G(x)u - \nabla \cdot J(x, t), \quad (4.2)$$

where $J(x, t)$ is the local density flux. Such flux can be induced by some forces which can be decomposed into random and non-random components.

Random forces are related to the random motion of the individuals themselves and can be included in the diffusion process. In many cases they are enclosed in the diffusivity terms. The transport behaviour of the population as a whole will then be considered as the simple linear diffusion normally observed in physical systems, and can be expressed as

$$J = -D\nabla u, \quad \text{Fick law.} \quad (4.3)$$

This model is obtained from the assumption of random motion

The non-random forces are not directly related to diffusion, but it brings about a regular motion of individuals and acts to change the spatial distribution of population. In some cases it counteracts diffusion and causes a concentration (aggregation) of population in specific places, and in other cases it augments diffusion (dispersal). (Gurney and Nisbet, 1975) proposed two models of non-random forces:

(a) the biased random motion model

$$J = -d\nabla u - \mu u \nabla u, \quad (4.4)$$

(b) the directed motion model

$$J = -\lambda u \nabla u, \quad (4.5)$$

where d , μ and λ are positive constants. The model (a) and (b) respectively were obtained from the microscopic assumption that individuals move down the gradient of the

population density and that movement of individuals is largely random but with some bias in the direction down the gradient of the population density (see Gurney and Nisbet, 1975, 1976, and Namba, 1980 for details). Model (b) and (a) may also be considered as some kind of the diffusion model with coefficients dependent on population density. These models are called density-dependent dispersal models.

Namba (1989), basing his idea on Shigesada and Teramoto's model, investigated the combined effect of density-dependent dispersal and spatial variable growth on distributions of competing populations. However, he did not consider the usual competitive dynamics, which are expressed through decrease of growth rate in the presence of competing populations. It suggested that "extrinsic population control by Malthusian killing agencies is partly an illusion borne of man's obsession with mortality" (Taylor and Taylor) [31]. Thus, it may be more rational to expect migration before population densities rise so high as to cause severe competition, unless migration brings a great risk. For this reason Namba ignored density dependence in growth rates, to focus his attention on density dependence in dispersal rates, or competition for space. In this case the growth rate of both populations depend on the spatial position reflecting the environmental heterogeneity. This may be interpreted as an approximation when the population densities are far below the carrying capacities of the environment because of movements to avoid crowding. Namba also neglected the random diffusion in his model and considered only purely density-dependent terms. The environment is assumed to have a favorable habitat for growth of population surrounded by largely hostile universe. This assumption may be ecologically reasonable: the border of a habitat must be hostile for any population since, or else the population can further extend its range. From this assumption it is possible to consider a kind of non-linear-interaction diffusion model that is similar to the models of Shigesada and al, Gurney and Nisbet.

$$\frac{\partial u_1}{\partial t} = \frac{\partial^2}{\partial x^2} [(u_1 + \alpha_1 u_2)u_1] + G_1(x)u_1 \quad (4.6a)$$

$$\frac{\partial u_2}{\partial t} = \frac{\partial^2}{\partial x^2} [(u_2 + \alpha_2 u_1)u_2] + G_2(x)u_2 \quad (4.6b).$$

If $\alpha_i = 0$ or $u_j(t, x) = 0$, then each of the two equations in system (4.6) reduces to

$$\frac{\partial u_i}{\partial t} = d_i \frac{\partial^2}{\partial x^2} (u_i)^2 + G_i(x) u_i. \quad (4.7)$$

Using a quadratic form for $G(x)$ Namba arrived to the following model

$$\frac{\partial u_1}{\partial t} = \frac{\partial^2}{\partial x^2} [(u_1 + \alpha_1 u_2) u_1] + r_1 \left[1 - \left(\frac{x}{x_1} \right)^2 \right] u_1 \quad (4.8a)$$

$$\frac{\partial u_2}{\partial t} = \frac{\partial^2}{\partial x^2} [(u_2 + \alpha_2 u_1) u_2] + r_2 \left[1 - \left(\frac{x}{x_2} \right)^2 \right] u_2. \quad (4.8b)$$

With this model, he showed that the coexistence of two species is possible in the presence of competition for the space if there exist the coexistence of the stationary solutions. That is, a solution in which $u_1(x, t)$ and $u_2(x, t)$ are positive for some x . He formulated a sufficient condition for coexistence of positive stationary solutions of his model by assuming that,

$$G_2(x) = \beta G_1(x), \quad (4.9)$$

that is, $G_1(x)$ and $G_2(x)$ are proportional to each other. This means ecologically that the favorable habitats for two populations coincide and that the hostile regions are also the same for both species. Namba made for convenience, an additional assumption to obtain a positive stationary solution in some cases. First, he considered a positive stationary solution $(\bar{u}_1(x), \bar{u}_2(x))$, which satisfies

$$\bar{u}_2(x) = \gamma \bar{u}_1(x); \quad (4.10)$$

that is, the solution $\bar{u}_2(x)$ itself is proportional to $\bar{u}_1(x)$. Then the stationary problem corresponding to the system (4.6) can be written, making use only $G_1(x)$ and $\bar{u}_1(x)$;

$$0 = d_1(1 + \alpha_1 \gamma) \frac{\partial^2}{\partial x^2} (\bar{u}_1)^2 + G_1(x) \bar{u}_1 \quad (4.11a)$$

$$0 = d_2 \gamma (\gamma + \alpha_2) \frac{\partial^2}{\partial x^2} (\bar{u}_1)^2 + \beta \gamma G_1(x) \bar{u}_1. \quad (4.11b)$$

From the previous considerations, we know that each equation of the system (4.11) has a solution with free boundaries. However, these two solutions must coincide. Thus a

compatibility condition can be obtained as a condition on the ratio of coefficients of the system (4.11);

$$\frac{d_2\gamma(\gamma + \alpha_2)}{d_1(1 + \alpha_1\gamma)} = \frac{\beta\gamma}{1}. \quad (4.12)$$

The author determined γ from the above condition;

$$\gamma = \frac{d_1\beta - d_2\alpha_2}{d_2 - d_1\alpha_1\beta}. \quad (4.13)$$

In order to have u_1 and u_2 non-negative, γ must be positive. Then, they obtained a sufficient condition for the existence of a positive stationary solution of their system (4.6).

Theorem 1. Suppose that $G_1(x)$ and $G_2(x)$ are chosen so that the reduced equation (4.7) has a positive stationary solution with free boundaries. Further assume that $G_1(x)$ and $G_2(x)$ satisfy the relation (4.9). Then the system (4.6) has a positive stationary solution with free boundaries,

$$(1) \text{ if } \alpha_1\alpha_2 > 1 \text{ and } \frac{d_2}{d_1} \frac{1}{\alpha_1} < \beta < \frac{d_2}{d_1} \alpha_2 \quad (4.14a)$$

or

$$(2) \text{ if } \alpha_1\alpha_2 < 1 \text{ and } \frac{d_2}{d_1} \alpha_2 < \beta < \frac{d_2}{d_1} \frac{1}{\alpha_2}, \quad (4.14b)$$

if $G_1(x)$ and $G_2(x)$ specifically satisfy the specific form in (4.8), then β equals $\frac{r_2}{r_1}$. However, note that the sufficient conditions (4.14) for existence of a positive stationary solution do not depend on the specific form of function $G_1(x)$ and $G_2(x)$ so long as the reduced equation (4.7) has a positive stationary solution. Hitherto, it is found that when either of condition (4.14) is satisfied, system (4.6) has three solutions $(u_1^*(x), 0)$, $(0, u_2^*(x))$ and $(\bar{u}_1(x), \bar{u}_2(x))$ see (Fig.4.1). However the stability of these solution is not yet known. Moreover, the author had not determined whether a positive solution may exist or not when conditions (4.14) are not satisfied. Even if conditions (4.14) are satisfied, they have not determined whether or not the stationary solutions is uniquely determined. In other words, it is not certain whether there exists another positive stationary solution of system (4.6) in which $u_1(x)$ and $u_2(x)$ are not proportional.

However, it is certain that there always exist two stationary solutions $(u^*(x), 0)$ and $(0, u_2^*(x))$. If β becomes large enough to satisfy either of conditions (4.14) then a positive

stationary solution $(\bar{u}_1(x), \bar{u}_2(x))$ appears. If β increases further to violated the upper condition, then the solution disappears (see Fig.4.2). If the positive stationary solution is stable and a solution with positive initial data approaches it, then two populations can coexist permanently. However, if it is unstable and a solution approaches either of two solutions $(u_1^*(x), 0)$ and $(0, u_2^*(x))$, one population must go to extinction. Namba also showed numerically that question of extinction can arise when the initial data of either of population is too small compared with the other one. The population, which has a large initial data forces the other population to extinction, see for example Fig.4.3(a) and (b), which is the cases with $r_2 (= r_1\beta)$ sufficiently large to satisfy the first condition of (4.14). In Fig.4.3(b), the initially superior population u_2 survives and u_1 extincts. It is not true that any solution with non-negative initial value data approaches the positive solution. Depending also on their spatial position in the favorable region of growth, the species can go to extinction (stationary solution) or to a positive stationary solution. If the initial date is confined to a border region, it may vanish because of the finite speed of propagation. This means ecologically that a population may extinct before it can reach a favorable habitat if the initial distribution ranges within a severely harsh region. Furthermore, we can expect that there exists no stable positive stationary solution. Thus, when two populations are competing for space through repulsive forces to enforce migration, one of them may be extinct because of harshness of the border environment, although it never goes to extinction in the absence of the rival species.

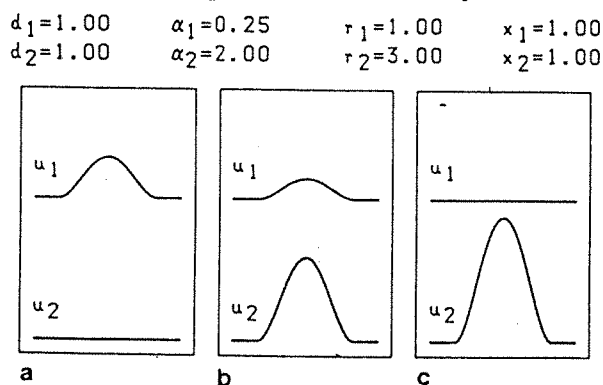


Fig.4.1 example of stationary solutions of system (4.6). (a) $(u^*(x), 0)$; (b) the positive stationary solution $(\bar{u}_1(x), \bar{u}_2(x))$; (c) $(0, u_2^*(x))$. Note that they have same boundaries $x = \pm x_i^*$

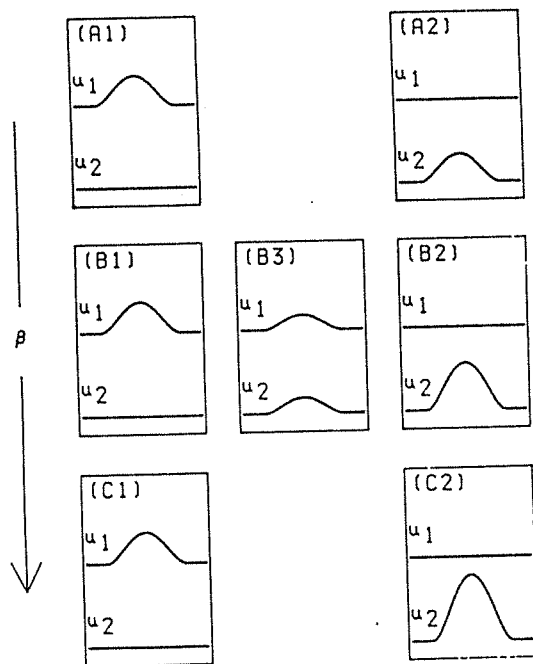


Fig.4.2 The relation between the value of β and the number of stationary solution. In case (B), there exist three stationary solutions including a positive one since β satisfies conditions (4.14)

From the practical point of view, the question of whether all the competing species in a given space can persist or coexist together for all the time is one of the most important problems. This question was aborded by Hutson and Vickers (1982), and they formulated the following criterion of permanent coexistence of different populations (see also Levin, 1976b):

- (a) *The criterion should be global.* That is, it should be independent of the initial values of the populations (so long as these are all nonzero).
- (b) *The existence of a stable limit cycle should not be ruled out.* Cyclic behavior is completely consistent with the persistence of species so long the cycle lies away from the boundary. Indeed, even such unpleasant dynamics as associated with a "strange attractor" should be allowed if the attractor is at nonzero distance from the boundary.

(c) *The population vector should not be near the boundary for more than a finite time.* For if it is, over a large time interval the probability of extinction of species (due say to small random fluctuations in the environment) is large, and the system cannot be regarded as modeling persistence of species in any realistic sense.

As we can see, Namba's sufficient conditions (4.14) satisfy all these criterions. Therefore, Namba's model is useful for modeling the dynamics of permanent coexistent populations in a bounded space. However, the omitting of an explicit dependence of demographic parameters (birth or death rates) on environment fluctuations in his model is unrealistic.

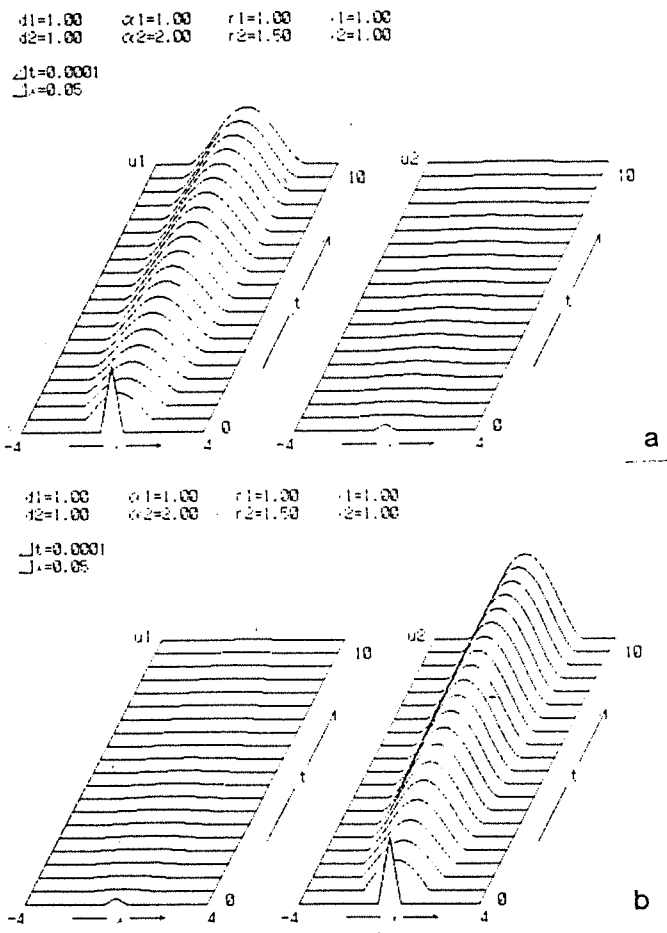


Fig.4.3a-b. Example of numerical solution of system (4.8), in case of $\alpha_1\alpha_2 > 1$. However, in a and b, nothing other than the initial data differs. The first conditions (4.14) is satisfied in a and b

Up to now, we were concerned with the model in which the population grow and disperse in a limited heterogeneous space, under an unvarying environment. But real environmental is uncertain and stochastic; it can be periodical for certain species and stochastic for others. As we mentioned in the introduction of this work, all the populations, natural or artificial, are affected by the external environment perturbations. The importance of this effect in natural ecosystem was appreciated by Nicholson, who asserted that any periodic change of climate tends to impose its period upon oscillations of internal origin or to cause such oscillations to have a harmonic relation to periodic climatic changes (Nisbet and Gurney, 1976).

5. THE EFFECTS OF UNPREDICTABLE STOCHASTIC ENVIRONMENTS

The magnitudes of real populations of plants and animals are rarely governed by simple non-linear equation that could crisp illustrations of chaotic behaviour (May, 1989). Rather such populations are typically affected by the interaction with many others and by unpredictable environmental fluctuations. Some years ago, one of the major theoretical and empirical challenges in ecology was elucidating the role of various kinds of heterogeneity, such as environmental fluctuations in the dynamics of the populations and the organisation of communities. There is substantial evidence that stochastic environmental fluctuations have a strong role in population and community processes (May, 1974). Birth rate, carrying capacities, competition coefficients and other parameters which characterize natural biological systems all, to a greater or lesser degree, exhibit random fluctuations. Consequently equilibrium is an average situation around which the system fluctuates. In the early 1958s Elton had observed that the "chief cause of fluctuations in animal numbers is the instability of the environment. The climate in most countries is always varying ...". There exist some trenchant affirmations of the view that such environment must be stochastic not deterministic.

For deterministic environments, May states that, we seek the constant equilibrium population U_i^* , and then study their stability, which follows from the dynamics of the interactions between and within species. In particular, for relatively small amplitude disturbances, the interactions are summarized and the stability set by the community matrix of interacting species.

Once environmental stochasticity is admitted, so that some of the parameters are fluctuating randomly about their mean values, we obviously can no longer speak of the population $U(t)$ at time t , but only of its probability distribution. Such a distribution function, $f(u, t)$, gives the probability to observe $u = 0, 1, 2, \dots, N$, animals at time t . More generally, for community with m species, there will be a multivariate probability distribution function, $f(u_1, u_2, \dots, u_m; t)$. By taking the usual statistical moments of this distribution, we get the mean numbers of animals at time t ; these may, or may not be equal

to the deterministic populations $U_i(t)$ which is obtained from the deterministic equation in which all the environmental parameters are fixed at their mean values. Similarly one may obtain the variances of fluctuating populations, and so on.

Furthermore, the analogue of the equilibrium population, $U_i^*(t)$, which were the time-independent solutions of the deterministic population equations, is the time-independent probability distribution function, $f^*(u)$. *This equilibrium probability distribution is to the stochastic environment as the stable equilibrium point is to the deterministic one.*

In the deterministic case, May studied the response to a specific disturbance from the equilibrium configuration; in the stochastic environment, an incessant sequence of such perturbations is built into the fabric of the model. The relation between deterministic and stochastic case is illustrated for the two interacting populations, U_1 and U_2 , in fig 5.1. Fig 5.1(a) shows a stable equilibrium point, corresponding to constant population U_1^* and U_2^* . If disturbed from this point, the dynamics of the population interactions brings the system back: for small disturbances, these dynamics are described by the community matrix, and the characteristic time to return to equilibrium is measured by the (negative) real parts of the matrix's eigenvalues λ . In the stochastic environment, Fig. 5.1(b), there is no longer an equilibrium point, but rather a probabilistic "smoke cloud," described by the equilibrium probability distribution. There is now a continuous spectrum of disturbances, generated by the environmental stochasticity, and the system is in tension between two countervailing tendencies. On the one hand, the random environmental fluctuations (measured by a characteristic variance σ^2) act to spread the cloud, to make the probability distribution more diffuse, while on the other hand the dynamics of the stabilizing population interactions tend to restore the population to their mean values, to compact the cloud. For a relatively compact probability cloud, the interaction dynamics are again measured by the eigenvalues of the same community matrix as for the deterministic case, the matrix being evaluated using the mean values of the environmental parameters.

We see immediately that, if the stabilizing effects of the interactions are "strong" compared to the diffusive effects of random environmental fluctuations, the probability

cloud will be compact, and may for many practical purposes be indistinguishable from the deterministic equilibrium point. In such cases, the deterministic model will be entirely relevant. Conversely, if the stability provided by the population interactions is "weak" compared with the environmental variance, then (even though the deterministic model may be eminently stable) the probability cloud is highly dispersed with a significant likelihood that one or both species of population may vanish. In such case, the deterministic model clearly is irrelevant.

For models with deterministic environmental parameters, we have a stable neighborhood of the equilibrium point if and only if all eigenvalues of the community matrix lie in the left-hand half of the complex plane: (Fig.5.2(a)). for the corresponding model with stochastic parameters, this condition is necessary, but insufficient, for the existence of a relatively compact equilibrium probability cloud for the population. It is required, in addition, that the stability provide by the interactions, which is measured by the real part of the community matrix eigenvalues, be sufficiently great to counteract the diffusive effects of the random fluctuations. Thus the eigenvalues must all lie to the left of the imaginary axes by an amount measured roughly by the degree of environment variance: (Fig. 5.2(b)).

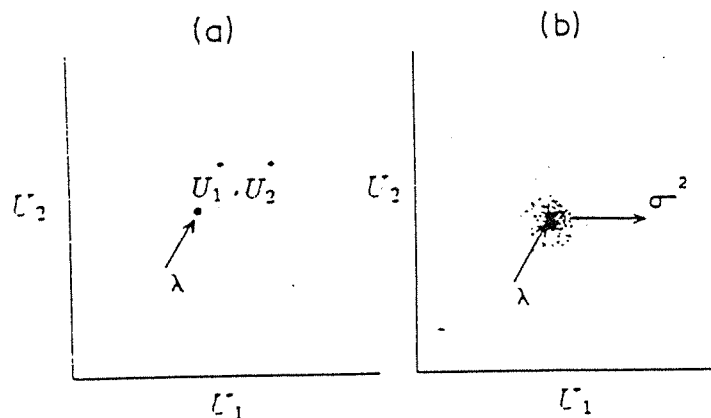


FIGURE 5.1. Schematic representation of the character of an equilibrium two-species community in (a) a deterministic and (b) a stochastic environment. In (a) we have a stable equilibrium point, corresponding to populations U_1^* and U_2^* ; the community dynamics, as measured by the eigenvalues λ of the community matrix, return the system to its equilibrium point if it is perturbed. For the corresponding stochastic environment of (b), the equilibrium community is described by some time-independent probability distribution: this probability cloud is in tension between the stabilizing influences of the interaction dynamics (again measured by the eigenvalues λ), which act to compact the cloud, and the destabilizing environmental fluctuations (measured by σ^2), which act to disperse the cloud.

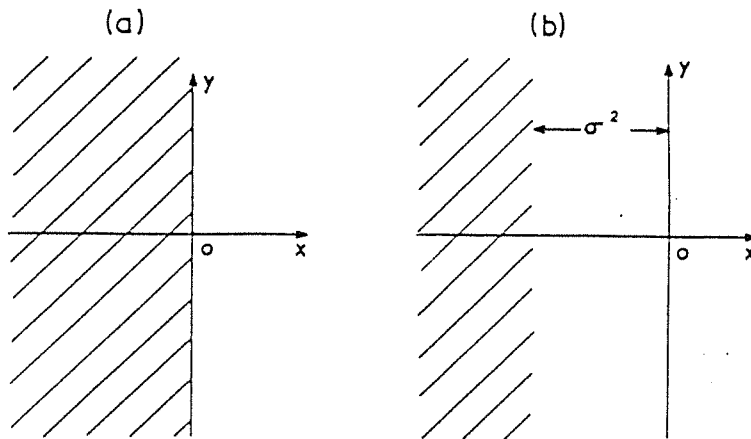


FIGURE 5.2. The eigenvalues λ of the community matrix A may be represented as points (x, y) in the complex plane. In the deterministic case, (a), the criterion for an equilibrium community to be stable with respect to small disturbances is that all such eigenvalues have negative real parts, i.e. lie in the hatched area of (a). For a stochastic environment, (b), with a variance characterized by σ^2 , it is necessary for the eigenvalues to lie far enough into the left-half plane for their stabilization to countervail against the diffusive effects of the random fluctuations, i.e. they need to lie in the hatched area of (b).

As we have seen, also in the simplest space independent model of population dynamics, if the environment is randomly fluctuating, so that one or more of the parameters in this general equation are stochastic variable, we need to reformulate the mathematics in the terms of the probability distribution function $f(u, t)$. In interesting and general case when the variability is "white noise", the partial differential equation for the probability distribution is called, depending on the author's background, the Fokker-Planck, or the Kolmogorov, or simply the diffusion equation:

$$\frac{\partial f(u, t)}{\partial t} = \frac{\partial}{\partial u} (M(u)f(u, t)) + \frac{1}{2} \frac{\partial^2}{\partial u^2} (V(u)f(u, t)). \quad (5.1)$$

Here $M(u)$ is defined as the mean value, and $V(u)$ as the variance, of the population density $F(u)$

$$M(u) = \langle F(u) \rangle$$

$$V(u) = \langle (F(u) - M)^2 \rangle$$

These averages are taken over all the stochastic parameters in the function F .

With some populations the random fluctuations are small, and for many purposes it is sufficient to construct a model, which is called deterministic. The most important property of deterministic models is that, if we know the history of the population up to the present time, we can predict its exact value at any future time, while a stochastic model is only able to predict the probability that at a given time, the population will be of a particular size.

Wherever an assumption of randomness is made in a stochastic model, it implies neglect (often reflecting ignorance), of some of details of the systems being modelled. However, at present it is useful to note that the transition to a probabilistic approach is valid when considering large numbers of statistically independent factors. One such situation arises if the external factors which cause population fluctuations are uncorrelated in time; we then use a mathematical idealisation known as "white noise" which enormously simplifies the analysis.

In this work we will not deal with the stochasticity, or randomly fluctuating environment but we will focus our attention on the periodically perturbation of the environmental external factors. Recently (May, 1987) states that a central task for population biologists is to disentangle, from the superimposed fluctuations caused by environmental noise and other chance events, the underlying mechanisms that regulate natural population so that no one species of plant or animal increases without bound. Such studies lead us to consider simple equations that might describe the dynamics of natural populations if the environmental noise and the heterogeneity could be stripped away. A clear understanding of the dynamics of these simple deterministic, but nonlinear, models then serves as a point of departure for evaluating the effects of various kind of complications associated with environmental unpredictability and heterogeneity. Interactions with other species mean that populations are usually governed by higher-order systems of equations. These complications are, of course compounded by environmental noise and spatial heterogeneity. Thus, although broad patterns may be understandable (four-year cycles in many populations of small mammals in extremely seasonal environments may be an example), most work on the dynamics of natural populations is concerned just with trying to tease out density-

dependent signals from a confusing background of density-independent noise, rather than with nonlinear details of the density-dependent signal as such.

Ultimately, environment noise does not act on populations as such, but on their constituent individuals. Thus we really need to derive deterministic models for the dynamics of populations from assumptions about the behaviour of individuals, so that the parameters in the population model derive from the biology of individuals. The effect of environmental variations can then be introduced in the proper way, through their effects on individuals (May, 1987).

6. DESCRIPTION OF THE NEW MODEL

Consider a model which take into account the effects of periodic external factors and let assume that dispersal is more governed by intra and interspecific pressures between species, rather by random motion, i.e density-dependent dispersal of species which move to avoid crowding. Therefore, we neglect random motion . Then, we consider the Namba's model, as exposed in the (chapter 4)

$$\frac{\partial u_1}{\partial t} = d_1 \frac{\partial^2}{\partial x^2} [u_1 + \alpha_1 u_2] u_1 + G_1(x) u_1 \quad (6.1a)$$

$$\frac{\partial u_2}{\partial t} = d_2 \frac{\partial^2}{\partial x^2} [u_2 + \alpha_2 u_1] u_2 + G_2(x) u_2, \quad (6.1b)$$

and substitute $G_i(x)$ functions by $G_i(x, t)$ which is time dependent , thus we can write the following system of equations:

$$\frac{\partial u_1}{\partial t} = d_1 \frac{\partial^2}{\partial x^2} [(u_1 + \alpha u_2) u_1] + G_1(x, t) u_1 \quad (6.2a)$$

$$\frac{\partial u_2}{\partial t} = d_2 \frac{\partial^2}{\partial x^2} [(u_2 + \alpha u_1) u_2] + G_2(x, t) u_2. \quad (6.2b)$$

Instead of $G_i(x, t)$, (Gurney and Nisbet, 1975) used a special form $G_i(x)$ which do not depend explicitly on time t and made the following assumption. The environment which is a favorable habitat for the growth of the population is surrounded by a hostile universe. Thus, $G(x) > 0$ for $x \in \Omega$ and $G(x) < 0$ for the largely hostile universe. They considered the equations in an infinite region with the boundary condition

$$u(x, t) \longrightarrow 0, \quad \text{as } |x| \longrightarrow \infty.$$

Now, we restrict ourselves to the case where the domain is a one dimensional interval $(-L, L)$, and L is an adjustable parameter that determines the size of a domain. $G(x)$, is positive only in this bounded domain, otherwise $G(x)$ is negative. For simplicity, (Gurney and Nisbet, 1975) made a further assumption that $G(x)$ is an event function. The above

properties were discussed originally by (Namba, 1975), particularly, when the growth rates $G_i(x)$ of the i -th species takes a specific quadratic form,

$$G_i(x) = r_i \left[1 - \left(\frac{x}{x_i} \right)^2 \right]. \quad (6.3)$$

We will make further assumption about $G(x)$, which in this model is considered as a simple exponential growth rate (Malthusian parameter birth minus death rates). In the real world birth and death rates clearly depend on external environment parameters such as temperature and humidity which vary with time t . Therefore, $G(x)$ in this case will depend explicitly on time through the external parameter $\phi(t)$.

We assume that, the heterogeneous space is affected by external factors (seasonal climatic variations). In macroscopic point of view, it is well known that the climate changes periodically (diurnal, annual and seasonal cycles are the good examples of periodic variations). To incorporate environmental variability into the models, we assume that some time-dependent external factors $\phi(t)$ influences the growth rate of the population. This means that, in a varying environment the population growth rate fluctuates in response to the driving term $\phi(t)$. The effect of this is to introduce driven into the partial differential equations that describe the spatio-temporal development of the population densities distributions. Nevertheless, we may still hope to make some progress in predicting the spatio-temporal pattern of environmentally driven fluctuation in the cases where demographic fluctuations are negligible. Historically, most strategic studies of the effects of environmentally variability on population dynamics have proceeded by a heuristic approach in which one or more of the parameters in a deterministic equation are permitted to wobble and the resulting population fluctuations studied [26]. This approach is useful (and indeed is the source of most existing insights on the consequences of variable environments) but it has severe limitations which become most apparent when question of extinction arises. Because of these difficulties, also (Nisbet and Gurney, 1982) approach the question of environmentally driven fluctuation rather cautiously through successive modifications of the basic formalism of birth and death processes. Following their approach, but neglecting environmental stochasticity, we consider a general model of two interacting species distributed over a one dimensional space with densities $u_1(x, t)$, $u_2(x, t)$ respectively. Both

species are assumed to have population growth rate G_1 and G_2 which depend only on space x , time t , a single environment parameter $\phi(t)$, and disperse because of intra and interspecific pressures. Thus we can express the growth rate as a function of space x and environmental external factors which itself depends on time t :

$$G\left(r(\phi(t)), x\right).$$

We assume a sinusoidal variation of the growth rate with respect to the periodically variability of climate. Therefore,

$$G_i(x, t) = r_0[1 + \phi(t)]\left[1 - \left(\frac{x}{x_i}\right)^2\right], \quad (6.4)$$

where $\phi(t) = b \cos \omega t$, is the external environmental factors, b the amplitude of periodical oscillations, and ω is the angular frequency. Then,

$$G_i(x, t) = r_0(1 + b \cos \omega t)\left[1 - \left(\frac{x}{x_i}\right)^2\right]. \quad (6.5)$$

This means that the growth rate $G_i(x, t)$ is affected by the periodic changes of climate. We recall that, the population u_1 and u_2 have the same favorable region of growth. Therefore the amplitude b , the angular frequency ω and the time t over which the growth of population is observed will be the same for each population. We assume also that the periodic effects of the environment affect the growth rate of different species differently. In the natural environment there exist many species who share the same region and can grow in it. Usually, they coexist and their growth rates can be affected differently by the variation of climate or weather. Therefore, we can assume in our model that, the climatic variations have a strong effect on one of the species only. The growth rate of the second species is assumed unaffected by the climatic changes. Then, according to (6.5) and the above assumptions the system (6.2) becomes:

$$\frac{\partial u_1}{\partial t} = d_1 \frac{\partial^2}{\partial x^2} [(u_1 + \alpha_1 u_2)u_1] + r_1(1 + b \cos \omega t)\left[1 - \left(\frac{x}{x_1}\right)^2\right] u_1 \quad (6.6a)$$

$$\frac{\partial u_2}{\partial t} = d_2 \frac{\partial^2}{\partial x^2} [(u_2 + \alpha_2 u_1)u_2] + r_2\left[1 - \left(\frac{x}{x_2}\right)^2\right] u_2. \quad (6.6b)$$

Finally we complete our model by assuming some positive initial distribution, that is

$$u_i(x, 0) > 0 \quad \text{for} \quad -L < x < L,$$

and we define the initial population as a function of space; $u_i(x, 0) = k_i(x)$, thus,

$$k_i(x) = \begin{cases} x + w_i, & \text{if } -s_i < x < p_i: \\ -x + w_i, & \text{if } p_i < x < s_i: \\ 0, & \text{otherwise,} \end{cases} \quad (6.7)$$

where w_i , p_i are constant and $s_i \ll L$, (see Fig. 6.1). Note that this is only a convenient assumption for the initial population which is used only in the numerical analysis of model, and there are no reasons to assume (6.7)

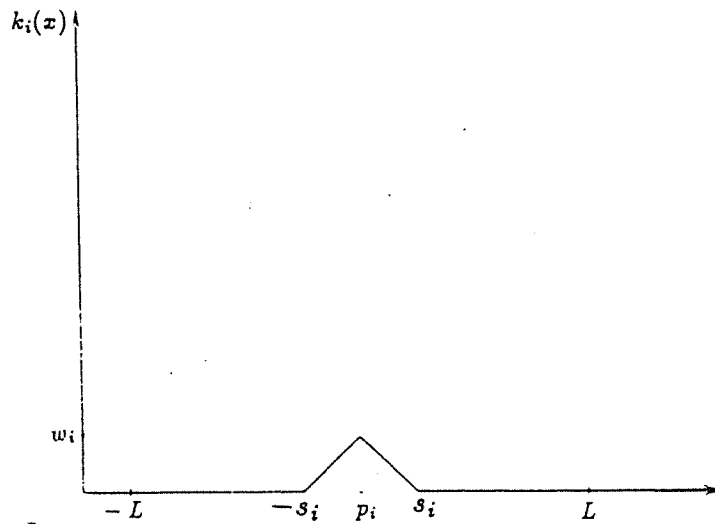


Fig.6.1 Example of initial population density $k_i(x)$

7. ANALYSIS OF THE NEW MODEL BEHAVIOR

Let $u_1(x, t)$ and $u_2(x, t)$ be defined on the domain $[-L, L] \times [0, T]$ in which there exist a non-negative solution of the system (6.6). To complete the formulation of the model, we shall assume that, the densities u_1 and u_2 satisfy the following initial conditions:

$$u_1(x, 0) = k_1(x) \quad \text{and} \quad u_2(x, 0) = k_2(x), \quad (6.1)$$

with

$$|x| \leq L, \quad (7.2)$$

i.e $k_1(x)$ and $k_2(x)$ are bounded continuous non negative functions, representing the initial population densities, which we will use for the numerical calculations. For simplicity, we consider the following boundary conditions:

$$u_1(L, T) = 0, \quad u_2(L, T) = 0 \quad (7.3a)$$

$$u_1(-L, T) = 0, \quad u_2(-L, T) = 0 \quad (7.3b)$$

$$\frac{\partial u_1}{\partial x} = 0 = \frac{\partial u_2}{\partial x} \quad \text{at} \quad \pm L. \quad (7.4).$$

Using similar condition and assumption as in Namba's model, we arrive to the following inequalities for the system (6.6):

$$G_i(x, t) > 0, \quad \text{with} \quad |x| < x_i.$$

Thus

$$r_1(1 + b \cos \omega t) \left[1 - \left(\frac{x}{x_1} \right)^2 \right] > 0, \quad (7.7)$$

and

$$r_2 \left[1 - \left(\frac{x}{x_2} \right)^2 \right] > 0, \quad (7.8)$$

$$r_1 > 0, \quad |b| < 1, \quad r_2 > 0. \quad (7.9)$$

For $b = 0$, the model (6.6) reduces to

$$\frac{\partial u_1}{\partial t} = d_1 \frac{\partial^2}{\partial x^2} [(u_1 + \alpha u_2)u_1] + r_1 \left[1 - \left(\frac{x}{x_1} \right)^2 \right] u_1 \quad (7.10a)$$

$$\frac{\partial u_2}{\partial t} = d_2 \frac{\partial^2}{\partial x^2} [(u_2 + \alpha u_1)u_2] + r_2 \left[1 - \left(\frac{x}{x_2} \right)^2 \right] u_2, \quad (7.10b)$$

which is the Namba's model. Because of mathematical difficulties and according to the sufficient condition (4.14), the system (7.10) was solved numerically. The numerical analysis leads to two different cases depending whether $\alpha_1 \alpha_2 > 1$ or not. That is, when interspecific repulsive effects are stronger than intraspecific ones. In the inverse case, one has $\alpha_1 \alpha_2 < 1$.

Using the same assumptions and conditions as Namba we will analyse numerically the model (6.6). We focus our attention to the case in which all the species survive and coexist together in a limited and favorable region, i.e., the positive stationary solution. We repeated the work of Namba (see Fig.7.1 and Fig.7.3). These are the cases in which the conditions $\alpha_1 \alpha_2 < 1$ and $\alpha_1 \alpha_2 > 1$ respectively are satisfied. To be sure for the nonextinction of the populations in the given region, we will assume that the case in which the population is confined near the border will be neglected. We choose the positive stationary solution because we are more interested for the case of persistence of the both populations. The Fig.7.1 shows the spatio-temporal distribution of u_1 and u_2 , with different initial data, and in the absence of external environment factors. Fig.7.2, shows the effects of external factors on the demographic parameters of population species u_1 which consequently exhibits periodically fluctuations in time. This confirms the assumption made by Nicolson that, "any periodic change of climate tends to impose its period ...". While u_2 is affected indirectly through a nonlinear interactions between species, and therefore exhibits also periodically fluctuations. This provides a good tool to understand that the intra and interspecific forces play a central role in the distribution of population species both in space and in time.

The cases for which $\alpha_1 \alpha_2 > 1$ is satisfied are showed in Fig.7.3. In these cases the initial data for u_1 and u_2 are equal. The Fig.7.3 shows the coexistence of the species

u_1 and u_2 in the absence of external fluctuations. In Fig.7.4, u_1 is strongly affected by external factors, while u_2 remains unaffected. However, under these conditions the situation seems to be similar to the previous in Fig.7.2. Therefore a number of general points can be drawn from an examination of the numerical analysis of our model (5.6), which is the interconnection between spatio-temporal distribution of the population species, dispersing to avoid crowding and their response to periodically variations of climate:

(a) u_1 increases attain a maximum value, which could be his maximum number in the absence of the environment fluctuations, while u_2 decreases to a certain value in response to these fluctuations. It is clear from the Fig.7.2 and Fig.7.4 that the oscillations of u_1 and u_2 are not synchronized and that u_2 practically is affected because of nonlinear interactions with u_1 .

(b) If the angular frequency ω is to hight and tends to infinity, then the populations cannot change fast enough to respond to the rapid changes in the environment and the population oscillations are much more smaller and some time are not observed for the hight living organisms.

(c) We assume that b satisfies the condition (7.9). For b near 1 and if the angular frequency ω is small we can expect some period in which there are no population at all in the considered space. This is the case of strong oscillations which deal on a long period. In the real ecosystem this phenomenon arises very often, that is, in the natural world, there exist some period when a given population species disappear almost completely in a given space because of the hostility of climate or weather, and appear when the period is favorable for their life.

$\alpha_1 = 0.24$ $r_1 = 0.8$ $z_1 = 1$ $d_1 = 1$
 $\alpha_2 = 1.7$ $r_2 = 2.5$ $z_2 = 1$ $d_2 = 1$
 $p_1 = 0.0$ $s_1 = 0.1$ $w_1 = 0.09$
 $p_2 = 0.0$ $s_2 = 0.2$ $w_2 = 0.5$
 $b = 0.0$ $\omega = 0.6$ $t = 40$

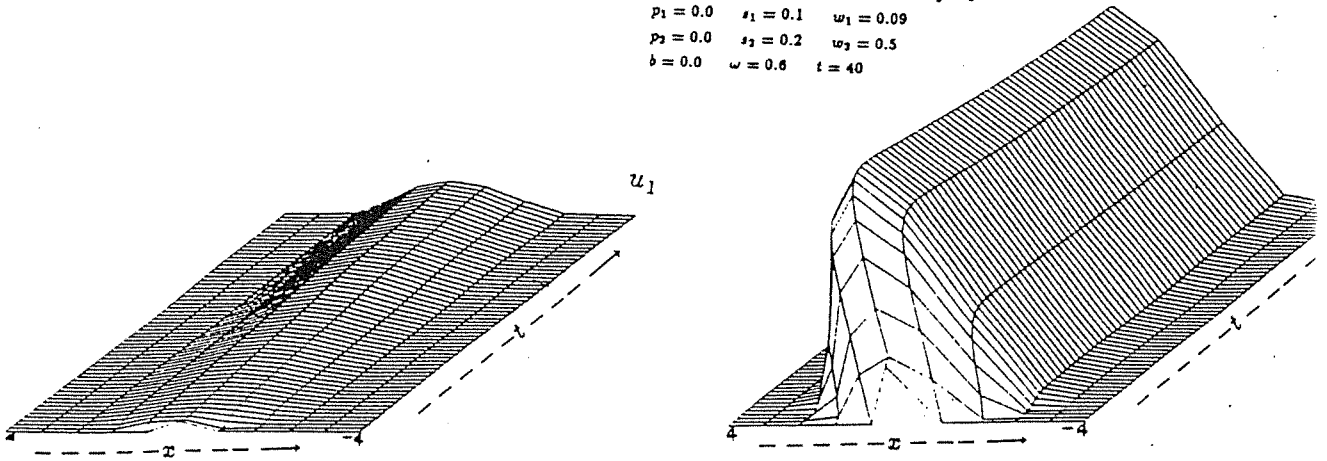


Fig.7.1 The permanent coexistence of two species u_1 and u_2 ,
 with different initial data $k_1(x) < k_2(x)$. This is the case in which the
 condition $\alpha_1\alpha_2 < 1$ is satisfied

$\alpha_1 = 0.24$ $r_1 = 0.8$ $z_1 = 1$ $d_1 = 1$
 $\alpha_2 = 1.7$ $r_2 = 2.5$ $z_2 = 1$ $d_2 = 1$
 $p_1 = 0.0$ $s_1 = 0.1$ $w_1 = 0.09$
 $p_2 = 0.0$ $s_2 = 0.2$ $w_2 = 0.5$
 $b = 0.7$ $\omega = 0.6$ $t = 40$

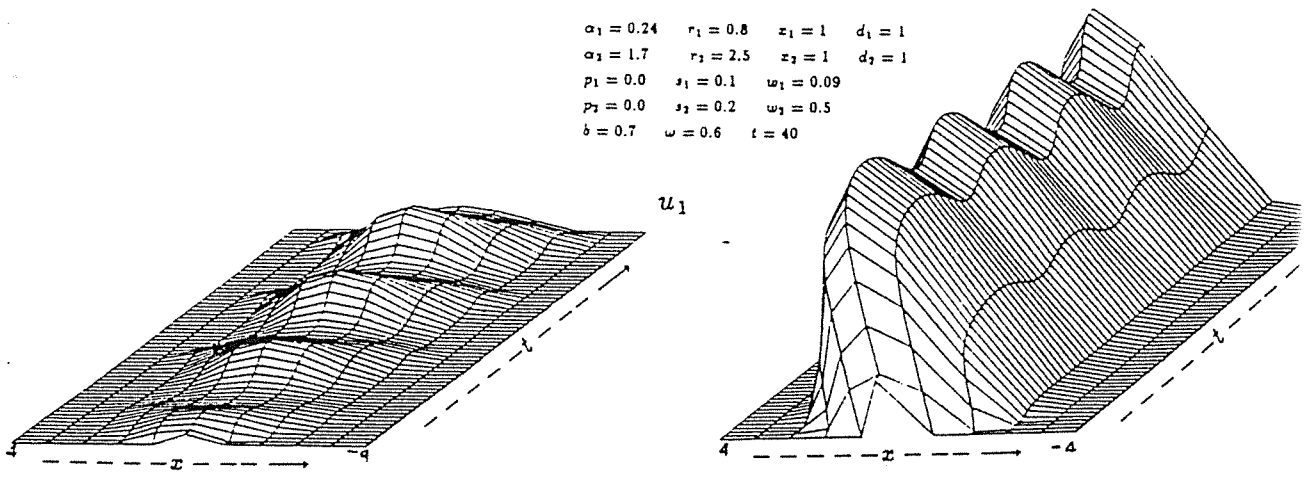


Fig.7.2 External factor effects of periodically varying environment on the coexistent species.

Note that u_2 is affected indirectly through the interspecific interferences with
 $\alpha_1\alpha_2 < 1$, and the initial data $k_1(x) < k_2(x)$

$\alpha_1 = 1.0$	$r_1 = 1.0$	$z_1 = 1$	$d_1 = 1$
$\alpha_2 = 2.0$	$r_2 = 1.5$	$z_2 = 1$	$d_2 = 1$
$p_1 = 0.0$	$s_1 = 0.2$	$w_1 = 0.4$	
$p_2 = 0.0$	$s_2 = 0.2$	$w_2 = 0.4$	
$b = 0.0$	$\omega = 1.6$	$t = 10$	

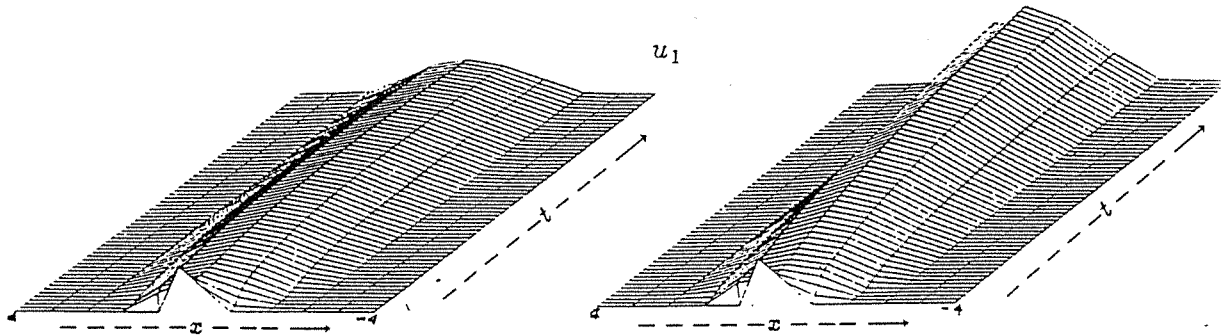


Fig.7.3 Coexistence of the species u_1 and u_2 in the case where $\alpha_1\alpha_2 > 1$ with the same initial data $k_1(x) = k_2(x)$

$\alpha_1 = 1.0$	$r_1 = 1.0$	$z_1 = 1$	$d_1 = 1$
$\alpha_2 = 2.0$	$r_2 = 1.5$	$z_2 = 1$	$d_2 = 1$
$p_1 = 0.0$	$s_1 = 0.2$	$w_1 = 0.4$	
$p_2 = 0.0$	$s_2 = 0.2$	$w_2 = 0.4$	
$b = 0.9$	$\omega = 1.6$	$t = 10$	

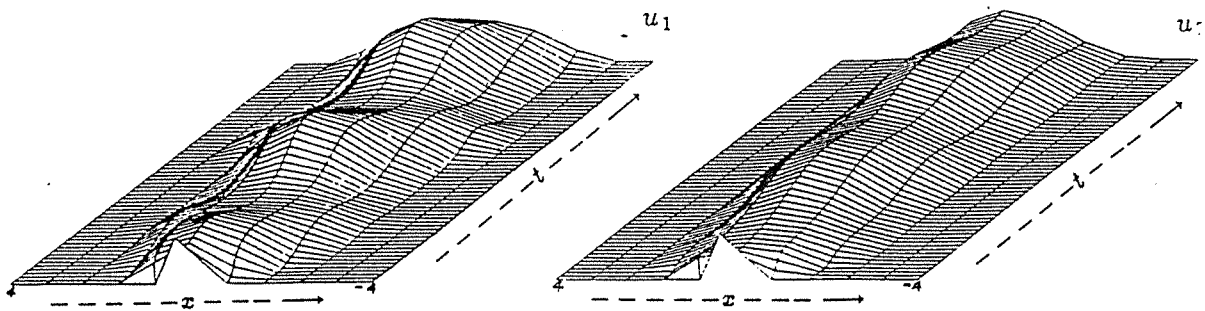


Fig.7.4 External factors effects of periodically varying environment for the case $\alpha_1\alpha_2 > 1$ with the same initial data $k_1(x) = k_2(x)$

8. DISCUSSION

We have considered the effects of periodic environmental constraints on the spatio-temporal distribution of population species in a favorable habitat surrounded by largely hostile region. The population species are assumed to be governed by a nonlinear interactions between species, that force them to disperse in a considered space, to avoid crowding. It is also assumed that population species persist together in the same favorable region. In the real world, all population, natural or artificial, are affected to some extent by external perturbations [10] and, birth and death rates clearly depend on external parameters such as temperature and humidity. Therefore the effects of environmental variation can be introduced in the proper way, through the demographic parameters.

From these assumptions, periodic environmental variations were introduced in the nonlinear interaction-diffusion model. Furthermore, it was assumed that the periodic environmental variations affected only one of population species u_1 and the other u_2 remained unaffected.

In the previous works, see for example Shigesada and al. 1978, Namba and Mimura 1980, Gurney and Nisbet 1975, it has been emphasized that two competing populations can coexist by virtue of dispersal and environment heterogeneity, even if local coexistence is impossible when no migration occurs. However, (Namba, 1989) has shown that density-dependent dispersal in a heterogeneous environment some times results in extinction of one of two populations, although no one of them become extinct in the absence of the other population. Therefore, mutual repulsive interactions that exclude other individuals may cause an inevitable damage if the effects are too strong, and migration in a heterogeneous environment is not always a stabilizing agent

Nevertheless, we may still hope to make some progress in predicting the spatio-temporal distribution of population species and their coexistence in a fluctuating environment for the cases where demographic fluctuations are negligible. Thus, we have shown that the introduction of this kind of periodic environmental variation in the demographic parameter provide the distribution of population species in the time and confirm the assumption made by Nicolson about the influence of the period of climate changes on the ecosystem.

These effects also provide a good tool to assume that intra and interspecific forces between species play a central role in the distribution of population not only in space, but also in time. These results are not surprising in the natural ecosystem where, in some regions, the life and the abundance of some population species appear to be periodically, and coincide with climatic variations. Good weather can stimulate growth in body size and reproduction, and bad weather can cause death.

It seems to me that for further studies, a more general model can be constructed if one assumes a very large space which is divided into two or more regions so that to allow migration of species from one region to another when the period is hostile. Thus the population flux at the border of the regions should not vanish, rather can vary on time.

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