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A STUDY ON MIGRATION OF POPULATIONS AND  
STABILITY OF ECOSYSTEMS

by

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the requirements for the degree of Doctor of  
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## Summary

An ecosystem is a complex system composed of many species subject to various interactions. The number of individuals in a population fluctuates annually or generation to generation. There are two aspects in variations of numbers of individuals. It is known that some populations exhibit large fluctuations, in the form of periodic oscillations or irregular outbreaks. However, in many populations, fluctuations are not so severe and the numbers of individuals keep nearly constant levels. Therefore, the numbers of individuals may be regulated by some physical or biological factors. An ecosystem seems to be a fairly stable system, since its compositions exhibit persistent characteristics. One of the fundamental subjects in population ecology is to study the way of regulating numbers of individuals and stabilizing ecosystems. Particularly, we will pay our attention to the effects of migration of populations and spatial distribution patterns on the stability of ecosystems. In this paper, four mathematical models are presented in order to study relations between migration of populations and stability of ecosystems.

The first model is on the effects of the population pressure in a population which grows exponentially in a fertile area surrounded by hostile areas. It is shown that a population dispersing in a density-dependent manner by the population pressure effect can establish a stationary

distribution, without regard to the property of boundaries of the region. It is also verified that the population forms a stationary distribution also in a habitat of a limited size, while a randomly diffusing population goes to either extinction or explosion, depending on the size of the region.

Secondly, we will consider spatial distributions of two competing populations, either of which becomes extinct in the absence of migration. We will show that these populations can coexist with spatially segregated distributions in a heterogeneous environment, even if one of the two species is far inferior to the other with respect to the ability of migration.

The third problem is on asymptotic behaviour of densities of prey and predator with interactions of the Lotka-Volterra type. We will show that the densities tend to exhibit respective spatially synchronized oscillations in a homogeneous environment, and that random diffusion cannot serve as a mechanism to produce stable spatially heterogeneous distribution patterns.

Finally, we consider the effects of emigration in a prey-predator system in which population densities exhibit stable cyclic oscillations with large amplitudes. We will show that emigration of predator to an unsuitable region for growth of the population is a factor to enhance stability of the system, since it diminishes the amplitudes of oscillations and save the population densities from

extreme decrease.

Therefore, migration of a population can be an important mechanism to regulate the number of individuals and to stabilize an ecosystem in a heterogeneous environment. There remains need for further investigation as for the role of migration in a homogeneous environment, since the effects of migration on the dynamics of population densities with stable periodic oscillations have not been studied. It will also be a future problem to investigate in what ecological situations heterogeneity of the environment plays a fundamental role, since it has been known in some simple model ecosystems that spatially heterogeneous distribution patterns arise even in a homogeneous environment.

## Chapter I. General Introduction

An ecosystem is a complex system composed of many species which interact each other and with the natural environment. It is of critical importance to determine relevant variables in order to study such a complex system. In studying an ecosystem, there may be a wide choice of variables, for example, the number of various species, the number of individuals in a population, or the energy in different trophic levels. Population ecology is a field of ecology, mainly concerned with the numbers of individuals in populations, turning our attention to a population or a few populations in a complex ecosystem. It should be noted that the word "population" means a collection of individuals of a species in a region, although it originally means the number of the people in a city or in a country, in demography. We can understand importance to study the numbers of individuals, if we imagine red tide or outbreaks of pest insects, which are serious social problems.

It is known that populations of many species keep nearly constant numbers of individuals, although the numbers of individuals fluctuate annually or generation to generation. Therefore, the numbers of individuals may be regulated by some physical or biological factors and an

ecosystem may be a fairly stable system, since its compositions exhibit persistent characteristics. Thus, regulation of the number of individuals and stability of an ecosystem are fundamental subjects in population ecology. Many factors, for example, climatic factors such as temperature and humidity, diseases, biotic potential of the population itself, or interactions with other species, may be related with the problem. It is a typical question in population ecology what the most important factor is to determine the number of individuals.

The population density is also used frequently, since a thousand individuals of pest insects per are do much more damage to crops than a thousand individuals per hectare. To understand or to predict variations of the population density, we must know their dynamics. However, it is very difficult to determine from observations what the most important factor is on regulation of the population densities and stability of an ecosystem, since an ecosystem is a very complex composite of many species and various interactions. Therefore, a mathematical model formulated from some simple assumptions of ecological relevance serves as a method to understand general ideas. In principle, we can describe the dynamics in terms of ordinary differential equations or difference equations, if we know the growth rate, or natality and mortality as a function of population densities and environmental parameters, and sometimes of time. Such an

approach has been developed since the pioneering works by Lotka(1925) and Volterra(1931), and it has made some contributions to understanding of relations between types of interactions and stability of an ecosystem. One may refer some review articles, for example, May(1973) and Maynard Smith(1974), on details of classical models.

However, the description in terms of the population density might be an oversimplification, since there exist some internal structures, for example, age structures and size distributions, in populations. Particularly, we should note that, in the majority of classical models, only temporal variations of a population are considered and spatial variations are not considered. In general, a natural environment is fluctuating both temporally and spatially, and a population is perhaps making efficient use of heterogeneity of the environment. A population has more or less a dispersing ability and extends the distribution. Spatial distribution patterns also affect stability of an ecosystem. For example, local extinction of a population does not lead to extinction of the whole population of a species if the population is distributed in a large area, and competition between similar species may be relaxed if they are spatially segregated. Migration of a population may be an important mechanism to make efficient use of the heterogeneous environment and it may sometimes lead to persistence of a population in a fluctuating environment.

It is the purpose of this paper to study relations between migration of a population and stability of an ecosystem, by formulating and analyzing some mathematical models. Here, we should turn our attention to the concept of stability in ecology. It differs slightly from the mathematical definition. In mathematical usage, briefly saying, stability of a state means an ability of the system to recover from disturbances. Suppose that the density of a population exhibits a cyclic oscillation in an ecosystem. Then, the system is sometimes considered to be ecologically unstable, even if the oscillation is mathematically stable. For, at the minimum density of the oscillation, the population density becomes very low and the population may be exposed to danger of extinction, since the population experience much damage by fluctuations of environments and also chance of mating may decrease. The difference in concepts of stability may also be ascribed to limitation of mathematical models, since the mathematical models tend to deal with continuous variables, although the ecological unit is an individual. In practice, ecological stability means the persistence of a population, or mild fluctuations near the suitable population density. We will use the term both mathematically and ecologically, but this will give rise to no confusion.

Finally, mathematical frameworks of this study should be explained. Spatio-temporal variations of populations

can be understood, if we know the rate of temporal variations at any unit area in a region. The rate of variations in a small area is determined by interactions of a population with the environment and the other populations and migration through the area. The rate of migration may be suitably described in terms of the population flux through a unit area. Let  $u_i(x, t)$  be the population density of the  $i$ -th species at position  $x$  and time  $t$  and  $j_i$  be the population flux of the  $i$ -th species, which may depend on population densities. Then, our fundamental equations are formulated as follows;

$$\frac{\partial u_i}{\partial t} = f_i(u_1, \dots, u_N; \mu_1, \dots, \mu_m) - \nabla j_i, \quad (1)$$

$$i=1, \dots, N,$$

where  $f_i$  is the rate of increase (or decrease) by interactions which depends on the densities of  $N$  populations and environmental parameters  $\mu_1, \dots, \mu_m$ , and sometimes on position  $x$  and time  $t$ . One may refer, for example, to Mimura (1979), on details of derivations of the equations (1). If we specify  $f_i$  and  $j_i$  in the equations (1) from some ecological assumptions, a model can be constructed.

The population flux is often assumed to be in proportion to gradient of the population density, that is,

$$j_i = - D_i(u_1, \dots, u_N) \nabla u_i, \quad (2)$$

$$i=1, \dots, N,$$

which mean that a population migrate from a crowded area to a sparse area, if  $D_i$  is positive. When  $D_i$  is constant, the equations (2) represent diffusion, which is considered to

random motion of individuals, by the analogy of molecular diffusion in the inorganic world. If  $D_i$  is an increasing function of population densities, it is called the population pressure effect, since the dispersive force becomes stronger as the population densities become larger.

The above approach was initiated by Skellam(1951), and many models have been proposed for the recent decade(for example, Segel & Jackson,1972, Haderler, an der Heiden & Rothe, 1974, Gurney & Nisbet,1975, Segel & Levin,1976, Rosen,1977, Gurtin & MacCamy,1977, Shigesada, Kawasaki & Teramoto,1978, Mimura, Nishiura & Yamaguti,1979, Kawasaki & Teramoto,1979). The equations (1) with the equations (2) are often called reaction(or interaction)-diffusion equations and they have been extensively studied not only in ecology but also as models of chemical reactions, morphogenesis and nerve conduction(for example, Turing,1952, Nagumo, Arimoto & Yoshizawa,1962, Gierer & Meinhardt,1972, Nicolis & Prigogine, 1977, Maginu,1978). Therefore, in our framework, to investigate the role of migration is reduced to a study of reaction-diffusion equations. The readers may refer the good survey by A.Okubo(Okubo,1975) on other aspects of diffusion phenomena in an ecosystem.

It should be noted that the equations (1) describe variations of population densities in a continuous environment. However, an environment is sometimes considered

as a patchy one composed of discrete patches, for example, islands or rocks in an intertidal zone. It is also important to study the effects of migration in a patchy environment. If we assume random motion of individuals or diffusion of populations, the fundamental equations are formulated, in the case of a patchy environment, as follows;

$$\frac{du_i^j}{dt} = f_i^j(u_1^1, \dots, u_N^k; \mu_1, \dots, \mu_m) - D_i \{ (u_i^j - u_i^{j-1}) + (u_i^j - u_i^{j+1}) \},$$

$$i=1, \dots, N, \quad j=1, \dots, k, \quad (3)$$

where  $u_i^j$  is the density of the  $i$ -th species in the  $j$ -th patch and we have assumed that  $k$  patches are linearly arranged and that diffusion coefficients are spatially constant (Levin, 1974). We will use both the continuous version and the discrete version of the reaction-diffusion equations.

In the following chapters, we will formulate and analyze four mathematical models, each of which corresponds to a particular ecological situation. Details on specific ecological situations and mathematical assumptions will be explained in the beginning of each chapter. The author is afraid that there may be some duplications and some confusion in expressions and notations, since this paper is a collection of four papers by the author. However, the content of Chapter III is a result of a joint work by the author and Professor Masayasu Mimura of Konan University. The author has taken

care that contributions by M.Mimura are not included in this paper as far as possible.

## Chapter II. Density-Dependent Dispersal and Spatial Distributions of a Population

### 1. Introduction

Recently some authors (Gurney & Nisbet, 1975, Shigesada, Kawasaki & Teramoto, 1979) have shown that some dispersive forces with non-linear dependence on population densities enhance stability of an ecological system.

However, there are two problems which have been paid little attention. The first is concerned with the size of a habitat. Kierstead & Slobodkin (1953) considered the growth of a phytoplankton population in a mass of water surrounded by water which is unsuitable for survival of the population. They showed that there is a critical minimum size for plankton blooms and that a population in a habitat with a size smaller than that goes to extinction. Similar models for various types of growth and for prey-predator systems have been studied (See McMurtrie, 1978, for reviews). On the other hand, it is known that populations of some mobile species grow explosively and serious overgrazing occurs when the populations are confined in some limited areas by a geographical condition or an artificial enclosure (Odum, 1971). In such a case, there may be a critical size such that a popula-

tion in a habitat with a size larger than that can establish a stationary distribution, whereas a population in a habitat with a size smaller than that grows explosively. We will say that regulation of the population number is effective if the population neither goes to extinction nor grows explosively. Thus our first problem is to find a critical minimum size for effective regulation.

The second is on the property of the boundary. With regard to the property of the boundary, many authors assumed reflecting boundaries or absorbing boundaries (for example, Segel & Jackson, 1972, Haderler, an der Heiden & Rothe, 1974, McMurtrie, 1977). Some stationary distributions obtained as such are highly depending on the boundary conditions. However, in some cases it may be more natural that interactions between a dispersing population and a heterogeneous environment determine a stationary distribution of the population which does not depend on boundary conditions. In such a stationary distribution, there may be a boundary where both the population density and the flow of the density are zero. We will call this a "natural boundary". We will show that a stationary distribution with natural boundaries is formed by density-dependent dispersal in a heterogeneous environment, without regard to the property of boundaries.

In view of the above two problems, we will study the models by Gurney & Nisbet (1975), since the models are very simple and useful to study the relations between the types of animal dispersal and the above problems. In the next section, we will introduce the models by Gurney & Nisbet (1975). Then we will

consider the problems of the natural boundary and of the critical minimum size for effective regulation.

## 2. Gurney-Nisbet Model

We introduce three models by Gurney & Nisbet(1975). We consider a single mobile species existing in a heterogeneous environment. The population is growing with a local growth rate  $G(x)$  which does not depend on the population density and dispersing with a local population current density  $j(x,t)$ , where  $x$  and  $t$  represent position and time respectively. Then the population density  $u(x,t)$  satisfies the equation

$$\frac{\partial u}{\partial t} = G(x)u - \nabla j(x,t) \quad . \quad (1)$$

Gurney & Nisbet(1975) proposed three models for the local population current density, according as motion of individuals depends on the population density  $u$  or do not. These are

(a) the random motion model

$$j = - D\nabla u,$$

(b) the biased random motion model

$$j = - d\nabla u - \mu u\nabla u \quad ,$$

and

(c) the directed motion model

$$j = -\lambda u\nabla u \quad ,$$

where  $D, d, \mu$  and  $\lambda$  are positive constants. The model (a) is obtained from the assumption of random motion of individuals and called diffusion. They obtained the models (c) and

(b) respectively from the microscopic assumptions 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 & Nisbet, 1975, 1976, for details). The models (b) and (c) may also be considered as some kinds of the diffusion model with coefficients depending on the population density. We will call them density-dependent dispersal models.

Gurney & Nisbet (1975) made an assumption on the growth rate  $G(x)$  that the environment is a largely hostile ( $G(x) < 0$ ) "universe" containing a single region of viable habitat ( $G(x) > 0$ ) (Fig. 1). They considered the equations in an infinite region

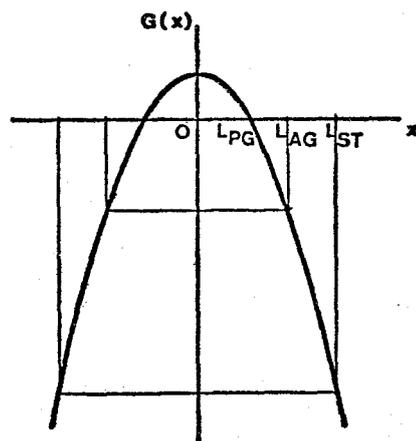


Fig. 1 Spatial dependence of a growth rate  $G(x)$ .  $x=L_{PG}$  is a position where  $G(x)=0$ . The spatial average of the growth rate  $G(x)$  over  $(-L_{AG}, +L_{AG})$  is zero.  $x=L_{ST}$  is a position of a natural boundary in a stationary distribution.

with the boundary condition that

$$u(x,t) \rightarrow 0, \text{ as } |x| \rightarrow +\infty,$$

and have shown that a population which goes to extinction or grows explosively when dispersing randomly can establish a stationary distribution when dispersing density-dependently.

In the following sections, we will consider the models in view of the problems of the natural boundaries and of explosive growth in a habitat with a limited size. We will pay our main attention to the directed motion model, since we are interested in the role of density-dependent dispersal on stability of an ecosystem.

### 3. A Stationary Solution with Natural Boundaries

In the following two sections, we consider the directed motion model

$$\frac{\partial u}{\partial t} = G(x)u + \lambda \nabla(u \nabla u) . \quad (2)$$

For the present, we will restrict ourselves to the case that the domain is a one-dimensional interval  $(-L, +L)$ , where  $L$  is an adjustable parameter that determines the size of a domain. We make similar assumptions on  $G(x)$  as those by Gurney & Nisbet (1975), that is,  $G(x)$  is positive only in a small bounded domain and otherwise  $G(x)$  is negative (Fig.1). For simplicity, we make a further assumption that  $G(x)$  is an even function, that is,  $G(-x) = G(x)$ . We will also use a special form

$$G(x) = A - Bx^2, \quad (3)$$

which was used by Gurney & Nisbet (1975) for their numerical calculations. We need the specific assumption (3) only when we prove existence of a stationary distribution. Otherwise we need not use it except for numerical calculations.

The stationary problem of the equation (2) can be described as

$$\frac{d^2}{dx^2} u_s(x)^2 = -\frac{2}{\lambda} G(x) u_s(x). \quad (4)$$

When  $G(x)$  satisfies the equation (3), we can find a very simple solution of the equation (4). If we assume that a polynomial of  $n$ -th order satisfies the equation (4) and put it into (4), then we can obtain a solution  $\bar{u}(x)$  of a fourth order polynomial by comparison of orders and coefficients;

$$\bar{u}(x) = \frac{B}{28\lambda} (x - L_{ST})^2 (x + L_{ST})^2, \quad (5)$$

where  $L_{ST} = \sqrt{7A/B}$ . The solution (5) is not a desirable one because  $\bar{u}(x) \rightarrow \infty$  as  $|x| \rightarrow \infty$ . However, we can construct a new solution of  $C^1$  class from  $\bar{u}(x)$  and a trivial solution  $u_0(x) = 0$ . The solution thus obtained is

$$u_s(x) = \begin{cases} \frac{B}{28\lambda} (x - L_{ST})^2 (x + L_{ST})^2, & |x| \leq L_{ST}, \\ 0 & |x| > L_{ST}. \end{cases} \quad (6)$$

Apparently from the construction,

$$u_s(\pm L_{ST}) = \frac{du_s}{dx}(\pm L_{ST}) = 0, \quad (7)$$

and the stationary solution (6) represents a stationary distribution with natural boundaries at  $x = \pm L_{ST}$ . When we consider the equation (2) or (4) in the domain containing the interval  $(-L_{ST}, +L_{ST})$ , the solution (6) satisfies both zero flux and zero fixed boundary conditions. Unfortunately we have been unable to solve the equation (4) for other forms of  $G(x)$ . However some numerical calculations show that a stationary solution with natural boundaries exists for a wider class of the growth rate  $G(x)$  which satisfies the assumption at the beginning of this section. Thus, we assume existence of a stationary solution  $u_s(x)$  with natural boundaries at  $x = \pm L_{ST}$  for any growth rates which satisfy the assumption.

We now investigate stability of the stationary solution  $u_s(x)$ . Gurney & Nisbet (1975) have shown stability of a everywhere positive stationary solution of the equation (2) against small amplitude fluctuations  $\varepsilon(x,t)$ , making use of a Lyapunov functional of  $\varepsilon$ . Since our stationary solution is not everywhere positive, we must modify the functional.

Let

$$u(x,t) = u_s(x) + \varepsilon(x,t),$$

then the fluctuation  $\varepsilon(x,t)$  satisfies

$$\frac{\partial \varepsilon}{\partial t} = G(x)\varepsilon + \lambda u_s \nabla^2 \varepsilon + \lambda \varepsilon \nabla^2 u_s + 2\lambda \nabla u_s \nabla \varepsilon, \quad (8)$$

to first order in  $\epsilon$ . We define a positive definite functional

$$V = \frac{1}{2} \int_{|x| < L_{ST}} u_s(x) \epsilon(x,t)^2 dx + \frac{1}{2} \int_{|x| > L_{ST}} \epsilon(x,t)^2 dx. \quad (9)$$

By virtue of the equations (8) and (4),

$$\frac{dV}{dt} = -\lambda \int_{|x| < L_{ST}} [u_s^2 (\nabla \epsilon)^2 + \epsilon^2 (\nabla u_s)^2] dx + \int_{|x| > L_{ST}} G(x) \epsilon^2 dx, \quad (10)$$

since  $u_s(x)=0$  for  $|x|>L_{ST}$ . Note that we need not use boundary conditions to obtain the equation (10).  $dV/dt$  is negative-definite, since clearly  $G(x)<0$  when  $|x| >L_{ST}$ . The equations (9) and (10) mean that the "mean square fluctuation" decreases with time. Thus the stationary solution  $u_s(x)$  is stable against small amplitude fluctuations. As we couldn't analytically prove stability against large amplitude perturbations, we solved the equation (2) numerically in an interval  $(-L_{ST}, +L_{ST})$  with zero flux boundary conditions, using an explicit method. A few examples are shown in Fig.2. The fat line is the stationary distribution. Dashed lines indicate that a solution with the initial distribution ( $t=0$ ) converges to the stationary solution as time goes on. Three thin lines are examples of initial distributions with which solutions converge to the stationary solution. Thus

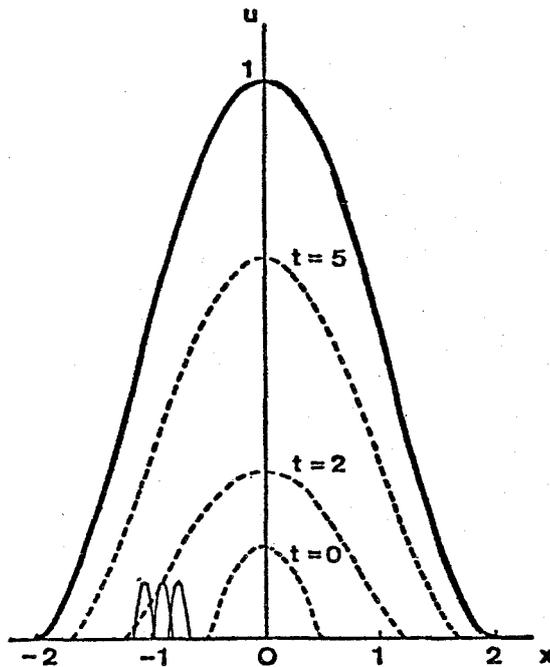


Fig.2 A stationary distribution of a population exhibiting directed motion ( $G(x) = A - Bx^2$ ,  $A=1$ ,  $B=7/4$ ,  $\lambda=1$ , and  $L_{ST}=2$ .) The fat line is the stationary distribution. Dashed lines indicate that a solution with the initial distribution ( $t=0$ ) converges to the stationary solution as time goes on. Three thin lines are examples of initial distributions with which solutions converge to the stationary solution.

we can conclude that the stationary solution  $u_s(x)$  is also stable against large amplitude fluctuations.

#### 4. Size of a Habitat and Explosive Growth

In this section, we consider the problem of the critical minimum size for effective regulation. We investigate behaviour

of solutions of the equation (2) in the domain  $(-L,+L)$ , as  $L$  being a changing parameter. We assume reflecting boundaries, which correspond to the condition that a population is confined in a limited habitat.

For further analysis, we define two quantities  $L_{PG}$  and  $L_{AG}$  which depend only on  $G(x)$ , by

$$G(\pm L_{PG}) = 0 , \tag{11}$$

$$\frac{1}{2L_{AG}} \int_{-L_{AG}}^{+L_{AG}} G(x) dx = 0 .$$

The interval  $(-L_{PG},+L_{PG})$  is the region where the growth rate  $G(x)$  is positive, which is called the region of net growth by Gurney & Nisbet (1975).  $2L_{AG}$  is the size of a domain where the spatial average of the growth rate is zero, and if  $L$  is larger (resp. smaller) than  $L_{AG}$ , the spatial average of the growth rate in the interval  $(-L,+L)$  is negative (positive). As is shown later,  $L_{PG} < L_{AG} < L_{ST}$  hold in general, where  $L_{ST}$  is the position of a natural boundary in a stationary solution. In the special case when  $G(x)$  satisfies the equation (3),

$$L_{PG} = \sqrt{A/B} , L_{AG} = \sqrt{3A/B} , L_{ST} = \sqrt{7A/B} .$$

We consider the equation (2), distinguishing three cases depending on the size of a region.

(i)  $L \leq L_{PG}$

As  $G(x)$  is positive at any point in the domain  $(-L,+L)$ , any solution except the trivial solution  $u_0(x) = 0$  diverges to infinity as  $t \rightarrow +\infty$ . It is verified by the equation

$$\frac{d}{dt} \int_{-L}^{+L} u \, dx = \int_{-L}^{+L} G(x)u \, dx > 0 .$$

$$(ii) L_{PG} < L \leq L_{AG}$$

Though  $G(x)$  is negative in the domain  $|x| \in (L_{PG}, L_{AG})$ , any solution with a positive initial distribution diverges to infinity as  $t \rightarrow +\infty$ , since

$$\begin{aligned} \frac{d}{dt} \int_{-L}^{+L} \log u \, dx &= \lambda \int_{-L}^{+L} \frac{1}{u} \left( \frac{\partial u}{\partial x} \right)^2 dx + \int_{-L}^{+L} G(x) dx \\ &> 0 \end{aligned}$$

Thus a positive stationary solution cannot exist in a domain smaller than  $(-L_{AG}, +L_{AG})$ .

From the equation (4), if  $u_s(x)$  is zero at  $x=x_0$ ,  $du_s/dx$  is also zero at the point and by an integration

$$\frac{du_s}{dx} + \int_0^x \frac{1}{u_s} \left( \frac{du_s}{dx} \right)^2 dx = - \frac{1}{\lambda} \int_0^x G(x) dx$$

hold. Thus if  $u_s(x_0)=0$ ,  $\int_0^{x_0} G(x) dx < 0$  must hold. This means that  $L_{ST}$ , the position of the natural boundary, must be larger than  $L_{AG}$ , and a stationary solution which vanishes in some interval cannot exist either in a domain  $(-L,+L)$  with  $L$  smaller than  $L_{AG}$ .

$$(iii) L_{AG} < L < L_{ST}$$

In this case, as we couldn't obtain any analytical result,

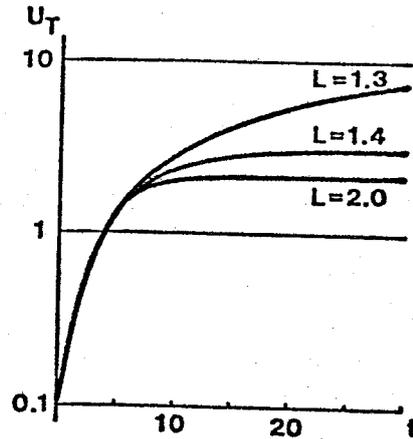


Fig.3 Time development of the total population number  $U_T$  of a population exhibiting directed motion in a domain  $(-L,+L)$  with  $L$  being an adjustable parameter. Other parameters are same as in Fig.2.

we solved the equation (2) numerically. Results are shown in Figs.3 and 4. The total population number  $U_T (= \int_{-L}^{+L} u \, dx )$  converges to a limit for  $L=1.4 (>L_{AG})$  as well as for  $L=2.0 (=L_{ST})$  and  $U_T$  diverges to infinity for  $L=1.3 (<L_{AG})$  as is shown analytically(Fig.3). Fig.4 shows stable stationary solutions for  $L=2.0, 1.6, 1.4$  and  $1.35$ . We obtained stable stationary solutions for  $L \geq 1.35 > L_{AG} \approx 1.31$ , and we may consider that there exist a stable stationary solution for any  $L$  larger than  $L_{AG}$ . A population whose dispersal is completely density-dependent grows explosively only when the spatial average of the growth rate is positive. Therefore, the critical minimum size for effective regulation coincides with the size of a region in which the spatial average of the growth rate is zero.

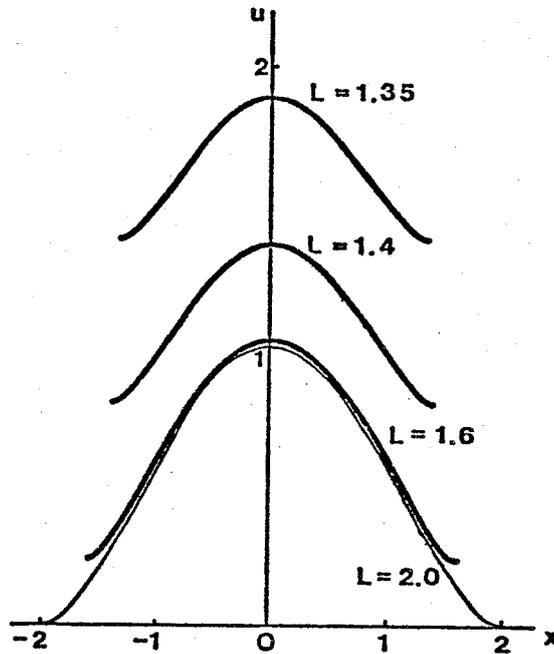


Fig.4 Stationary distributions of populations exhibiting directed motion. Details are same as in Fig.3.

##### 5. Random Motion Model and Biased Random Motion Model

We consider the relations between the size of a region and behaviour of solutions in other two models (a) and (b) by Gurney & Nisbet(1975). The equations describing these models are

(a) the Random Motion Model

$$\frac{\partial u}{\partial t} = G(x)u + DV^2u, \quad (12)$$

and

(b) the Biased Random Motion Model

$$\frac{\partial u}{\partial t} = G(x)u + d\nabla^2 u + \mu\nabla(u\nabla u) \quad (13)$$

We consider these equations in a domain  $(-L,+L)$  with zero flux boundary conditions, with the same assumptions on  $G(x)$  as before. Similarly as in the previous section, we can prove that any positive solution of the equations (12) and (13) diverges to infinity if the spatial average of the growth rate is positive, that is  $L \leq L_{AG}$ . When  $L > L_{AG}$ , we investigated behaviour of solutions by numerical calculations. We consider only the case when a randomly diffusing population goes to extinction in an infinite region, since we are interested in explosive growth of a population in a habitat with a limited size. Gurney & Nisbet (1975) called such a population a random motion decreaser.

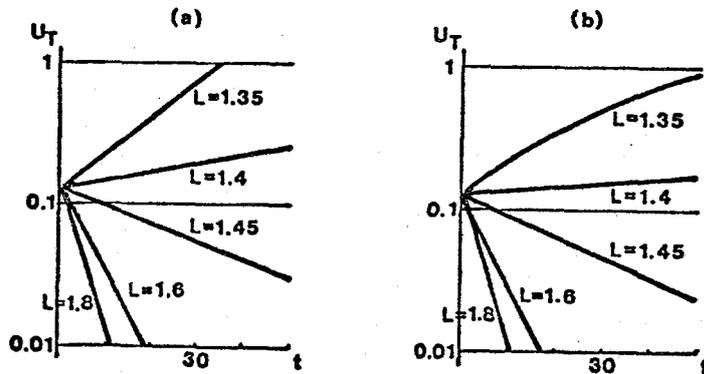


Fig.5 Time development of the total population number  $U_T$  of populations exhibiting (a) random motion and (b) biased random motion.  $G(x)=A-Bx^2$ ,  $A=1$ ,  $B=7/4$ ,  $D=d=1$ ,  $\mu=1$ , and  $L_{AG} \approx 1.31$ .

The condition for a population to be a random motion decreaser is given by  $A < \sqrt{BD}$  when  $G(x)=A-Bx^2$ . Parameters are chosen so as to satisfy the condition. Time development of the total population number is shown in Fig.5. In the random motion model, a solution diverges to infinity even when the spatial average of the growth rate is negative ( $L=1.35, 1.4$ ). In these cases, solutions of the biased random motion model converge to certain limits. In the biased random motion model, a solution diverges to infinity only when the spatial average of the growth rate is positive. But if the size of a region is too large,

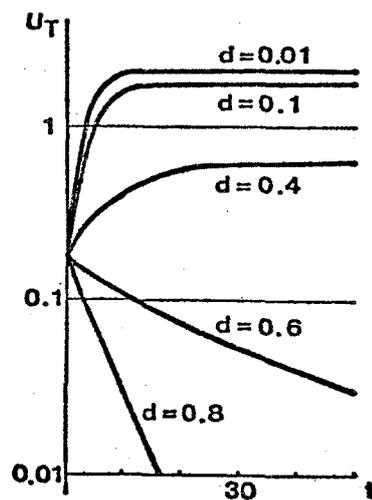


Fig.6 Dependence of growth of a population exhibiting biased random motion on the diffusion coefficient  $d$ . The population is confined in a region  $(-L,+L)$  with  $L=2.0$ , except in the case with  $d=0.01$ . When  $d=0.01$ ,  $L=2.5$ . Other parameters are same as in Fig.5 and  $\mu$  is fixed at 1.0.

the population goes to extinction. Dependence of solutions of the biased random motion model on the diffusion coefficient  $d$  is shown in Fig.6. Here,  $L=2.0$  except the case with  $d=0.01$ , and  $\mu$  is fixed at 1.0. Even when the size of a region is so large that solutions with large  $d$  converge to the trivial solution  $u_0(x)=0$ , there are stable stationary solutions if effects of random dispersal are sufficiently small. The biased random motion offers an effective mechanism for regulation if effects of random dispersal are not too large. However, a stationary distribution in the model does not have a natural boundary.

## 6. Discussion

In the previous consideration, we put some restrictions. Firstly we assume that the environment is one-dimensional. When the environment is two dimensional, above conclusions also hold. Especially when the growth rate depends only on the axial component  $r$  of polar coordinates  $(r, \theta)$  and  $G(r)=A-Br^2$ , a stationary solution with a natural boundary is analytically obtained in the directed motion model;

$$u_s(r) = \begin{cases} \frac{B}{32\lambda} (r-2\sqrt{A/B})^2 (r+2\sqrt{A/B})^2, & |r| \leq 2\sqrt{A/B}, \\ 0, & |r| > 2\sqrt{A/B}. \end{cases}$$

The second is that a stationary solution with natural boundaries exists only when dispersal is completely density-dependent. In the natural environment, even if a population is dispersing in a highly density-dependent manner, there may be some random factors. However, when the random effect is small (the case with a small diffusion coefficient in the biased random motion model), we can scarcely distinguish the solution from the one with  $d=0$  (Fig. 6,  $d=0.01$ ) and the size of a region where the stationary solution with small  $d$  is positive does not depend on the boundary conditions. Therefore when dispersal is highly density-dependent and the random effect is very small, we may suppose in practice that a natural boundary is formed.

Density-dependent dispersal is an effective mechanism for regulation not only when the size of a habitat is so large that a randomly diffusing population goes to extinction, but also when the habitat is limited in a small region and a randomly diffusing population grows explosively. A population dispersing in a highly density-dependent manner can establish a stationary distribution with natural boundaries in a heterogeneous environment, without regard to the property of the boundaries of the region. Though our conclusions are only in terms of mathematical considerations without experimental evidences, we may point out that density-dependent dispersal plays an important role for regulation of the population number and formation of the spatial distribution pattern.

## Chapter III. Spatial Distributions of Competing Populations

### 1. Introduction

In the natural environment, populations of many species exist and experience the struggle for existence. According to the competitive exclusion principle, (i) if two noninterbreeding populations have similar needs and habits (ecological niche) and (ii) if they live in the same habitat, then either of the two populations becomes extinct (Hardin, 1960). It was predicted theoretically by the Lotka-Volterra competition equations (Lotka, 1925, Volterra, 1931) and was examined experimentally by Gause (1934a, 1934b). On the other hand, populations competing with populations of other species relax the interspecific competition by various types of niche diversification, or by evolving some forms of ecological separation in foods, in time or in space. For example, in Gause's classical experiment (Gause, 1934b, cited from Crombie, 1947), *Paramecium caudatum* and *P. bursaria* are able to survive together in a mixed culture because they feed in different parts in the suspension. Lack (1969) reported that, in the middle of Europe, six species of *Parus* coexist, segregated partly by habitat and partly by feeding stations and size of prey.

Coexistence of two species by means of spatial segregation has been also of theoretical interest (Levins & Culver, 1971, Horn & MacArthur, 1972, Levin, 1974, Gopalsamy, 1977a, 1977b, Shigesada, Kawasaki & Teramoto, 1979, Mimura & Kawasaki, 1979). Levin (1974) considered a spatially discrete version of reaction-diffusion equations as a model for two competing species dispersing between two patches of the same property. He showed that they can coexist in some cases, with spatially heterogeneous distributions, although either of the two species becomes extinct in a single patch. However, if the initial numbers of one of the species are smaller in both patches, then it goes to extinction, although Mimura & Kawasaki (1979) showed that, if cross-population pressures are introduced into Levin's model, the stability condition and the restriction on the initial data for assuring coexistence and spatial segregation can be weakened. Shigesada et al. (1979) proposed an excellent model taking account of dispersive forces including population pressures and environmental potential forces. They showed, by computer simulations, that coexistence of two similar and competing species, which can not coexist in the absence of dispersal, is realized if the environmental heterogeneity and the nonlinear dispersive forces are introduced. However, they assumed that the environmental heterogeneity modifies only the dispersive forces and does not alter the growth rates and the competitive interactions. The growth rates and the ranks of competitive ability also varies as the environmental conditions change (Park, 1954) and some inferior competitors can survive in heterogeneous environments, because of their wider tolerance to the environmental conditions (Connell, 1961, Miller, 1964).

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 (Lack, 1969, Miller, 1964). In this paper, we will deal with competition between populations whose habitats are partly overlapping. We will consider the distributions of populations in the overlapping region, where two competing populations are dispersing with different dispersive rates. Our interest is to study which species is the superior competitor either the species dispersing faster which tends to extend the distribution rapidly, or the species with the faster growth rate, or do they coexist in the overlapping region.

## 2. Model

We consider populations of two species  $S_1$  and  $S_2$ , and assume that the environment  $R$  is divided into three subregions  $R_i$  ( $i=1,2,3.$ ) (Fig.1). The subregions  $R_1$  and  $R_2$  are respectively the exclusive territories of the species  $S_1$  and  $S_2$ , with the equilibrium densities  $U^*$  and  $V^*$ , because of the environmental conditions and the differences of physiological tolerance of two species. Thus, we fix densities of two populations at  $U^*$  and 0 in  $R_1$  and at 0 and  $V^*$  in  $R_2$ . The two populations are competing and diffusing in the subregion  $R_3$ . We assume that the local population dynamics is the Lotka-Volterra type and either of

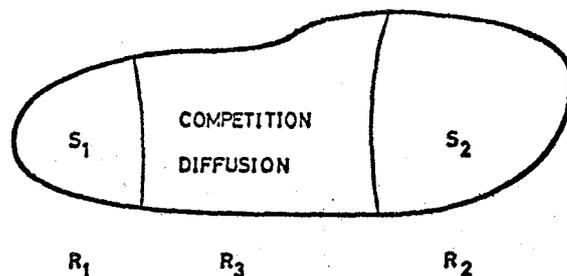


Fig.1. The environment consisting of subregions  $R_1, R_2$  and  $R_3$ .  $R_1$  and  $R_2$  are respectively exclusive territories of species  $S_1$  and  $S_2$ . In  $R_3$ , populations of two species compete and diffuse.

the two species becomes extinct, depending on the initial population densities, although each species can maintain their equilibrium densities  $U^*$  and  $V^*$  in the absence of the other species. Thus, distributions of the populations in the subregion  $R_3$  are determined by competition and diffusion in the region and immigration from the "population baths",  $R_1$  and  $R_2$ . We will consider the simple case where the region  $R_3$  is a one dimensional interval. We suppose that  $U(s, \tau)$  and  $V(s, \tau)$  are respectively population densities of the species  $S_1$  and  $S_2$ , at position  $s$  and time  $\tau$ . Then,  $U$  and  $V$  satisfy the following equations;

$$\begin{aligned} \frac{\partial U}{\partial \tau} &= D_1 \frac{\partial^2 U}{\partial s^2} + (\epsilon_1 - \alpha_{11}U - \alpha_{12}V)U, \\ \frac{\partial V}{\partial \tau} &= D_2 \frac{\partial^2 V}{\partial s^2} + (\epsilon_2 - \alpha_{21}U - \alpha_{22}V)V, \end{aligned} \tag{1}$$

where  $D_i, \epsilon_i$  and  $\alpha_{ij}$  ( $i, j=1, 2$ ) are non-negative constants. We can reduce the numbers of parameters without loss of generality, transforming the variables and parameters by

$$u = (\alpha_{11}/\epsilon_2)U, \quad v = (\alpha_{22}/\epsilon_2)V, \quad t = \epsilon_2\tau, \quad x = \sqrt{\epsilon_2/D_2} s, \quad (2)$$

$$d = D_1/D_2, \quad a = \epsilon_1/\epsilon_2, \quad b_1 = \alpha_{12}/\alpha_{22}, \quad b_2 = \alpha_{21}/\alpha_{11}.$$

Then, we obtain

$$\frac{\partial u}{\partial t} = d \frac{\partial^2 u}{\partial x^2} + f(u, v)u, \quad (3)$$

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} + g(u, v)v,$$

where

$$\begin{aligned} f(u, v)u &= (a - u - b_1 v)u, \\ g(u, v)v &= (1 - v - b_2 u)v. \end{aligned} \quad (4)$$

We will consider the equations (3) in

$$(x, t) \in (0, L) \times \mathbb{R}^+ \quad (5)$$

with boundary conditions

$$\begin{aligned} u(0, t) &= u^*, & u(L, t) &= 0, \\ v(0, t) &= 0, & v(L, t) &= v^*, \end{aligned} \quad (6)$$

where  $u^*=a$  and  $v^*=1$  are the equilibrium population densities which satisfy

$$f(u^*, 0) = 0, \quad g(0, v^*) = 0. \quad (7)$$

Here we make two assumptions;

$$(A1) \quad 1/b_2 < a < b_1,$$

and

(A2)  $d = \epsilon^2$  ( $\epsilon > 0$ ) is sufficiently small.

The assumption (A1) means that either of the two species goes to extinction depending on the initial population densities, in the absence of dispersal (Fig.2). The assumption (A2) is made for mathematical simplicity, for dealing with a typical case when diffusions of the two species are extremely different, i.e.  $0 \leq d \ll 1$ .

In the first place, we consider the asymptotic behaviour of solutions of the equations (3) with  $d=0$ , so that we deal with its stationary problem.

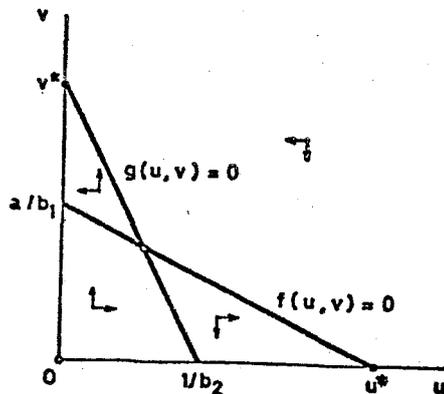


Fig.2. Isoclines of  $f(u, v) = 0$  and  $g(u, v) = 0$  and vector field  $(f(u, v)u, g(u, v)v)$ .

### 3. Stationary Problem ( $d=0$ )

When  $d=0$ , the stationary problem of the equations (3) can be written as

$$\begin{aligned} f(\hat{u}, \hat{v}) \hat{u} &= 0, \\ \frac{d^2 \hat{v}}{dx^2} + g(\hat{u}, \hat{v}) \hat{v} &= 0, \end{aligned} \tag{8}$$

with boundary conditions

$$\hat{v}(0) = 0, \quad \hat{v}(L) = v^*. \tag{9}$$

From the first equation of (8), we can solve  $\hat{u}$  as a function of  $\hat{v}$ . In the phase plane  $(u, v)$ , there are two branches where  $f(u, v)u=0$  is satisfied (Fig.3). The first is  $u=h_0(v) \equiv 0$ , and the second is  $u=h_1(v) = a - b_1 v$ . From the boundary conditions (9), both branches must be used to solve the first of (8). Therefore, we

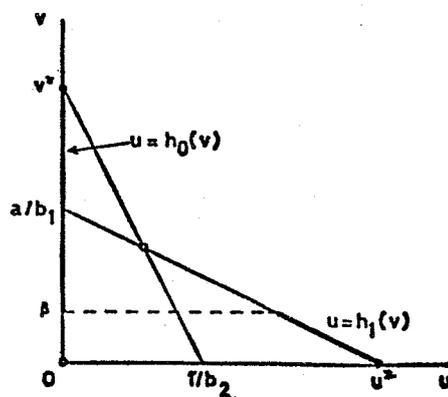


Fig.3. Branches  $u=h_0(v)$  and  $u=h_1(v)$  satisfying  $f(u, v)u=0$  and a patching value  $\beta$  ( $0 \leq \beta \leq a/b_1$ ).

assume that there is a patching value  $\beta$  ( $0 \leq \beta \leq a/b_1$ ) such that

$$\hat{u} = h(\hat{v}) = \begin{cases} h_1(\hat{v}) = a - b_1 \hat{v}, & 0 \leq \hat{v} < \beta, \\ h_0(\hat{v}) \equiv 0, & \beta < \hat{v} \leq v^*, \end{cases} \quad (10)$$

although  $\hat{u}=h(\hat{v})$  is defined in an intricate way such that several patching values are used. Then, the following problem is formulated;

$$\frac{d^2 \hat{v}}{dx^2} + G(\hat{v}) = 0, \quad (11)$$

where

$$G(v) = g(h(v), v)v = \begin{cases} g(h_1(v), v)v = [-(ab_2-1) + (b_1b_2-1)v]v, & 0 \leq v < \beta, \\ g(h_0(v), v)v = (1-v)v, & \beta < v \leq v^*. \end{cases} \quad (12)$$

Here, we note that  $G(v)$  has a discontinuity of the first kind at the point  $v=\beta$ , except for the value  $\beta=a/b_1$  (Fig.4). As is shown in Appendix A1, the problem (11), (12) and (9), and hence the

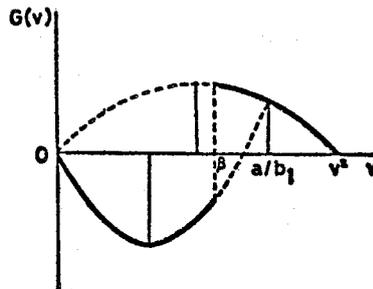


Fig.4.  $G(v)$  with a discontinuity at  $v=\beta$ .

problem (8) and (9a) can be solved. The results are summarized as follows;

(i) There exists a solution  $(\hat{u}(x;\beta), \hat{v}(x;\beta))$  for any  $\beta$  ( $0 \leq \beta \leq a/b_1$ ), where  $\hat{u}(x;\beta) = h(\hat{v}(x;\beta))$  (Fig. 5).

(ii) Define a patching point  $\ell(\beta)$  as a function of  $\beta$ , from the relation  $\hat{v}(\ell;\beta) = \beta$ .

(a)  $\ell(\beta)$  is a monotone increasing function of  $\beta$ , and takes the maximum value at  $\beta = a/b_1$ , where the solution  $(\hat{u}(x;a/b_1), \hat{v}(x;a/b_1))$  is continuous.

(b1) If  $\delta = a^3 b_2 / b_1^2 < 1$ , the maximum length  $\ell(a/b_1)$  is bounded independently of  $L$ ,

and

(b2) if  $\delta = a^3 b_2 / b_1^2 \geq 1$ , the maximum length  $\ell(a/b_1)$  is a monotone increasing function of  $L$  and approaches to infinity as  $L$  goes to infinity.

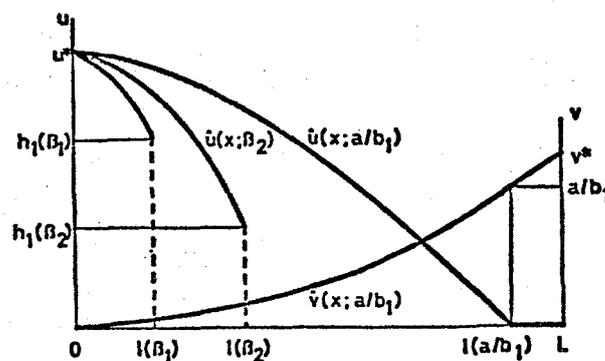


Fig.5. Stationary solutions  $(\hat{u}(x;\beta), \hat{v}(x;\beta))$  when  $d=0$

We can see that there exists remarkable heterogeneity in the solution  $\hat{u}(x;\beta)$ , where  $\hat{u}(x;\beta)$  is positive only in the domain  $(0, \ell(\beta))$  and  $\hat{u}(x;\beta)=0$  in  $(\ell(\beta), L)$  (Fig.5 ). From an ecological point of view,  $(0, \ell(\beta))$  is the region where the species  $S_1$  with the smaller diffusion coefficient can survive and  $(\ell(\beta), L)$  is the dead region of  $S_1$ , although the other species  $S_2$  is living in the whole region. From (b1) and (b2), we find that the size of the region where the species  $s_1$  can survive crucially depends on the parameter  $\delta$ . Later, we will consider this point more precisely.

#### 4. Singular Perturbation Analysis

We have obtained a  $\beta$ -family of solutions of (8) with spatial discontinuities in  $u$ , where the value of  $u$  makes a sudden jump from the branch  $u=h_1(v)$  to the one  $u=h_0(v)$  at  $x=\ell(\beta)$ . The next problem is to study the stationary problem of (3) with  $\varepsilon^2 \neq 0$ . One can expect the existence of an internal transition layer in the vicinity of  $x=\ell(\beta)$ . Therefore, in order to study this problem, we will use singular perturbation techniques (see, for example, Fife, 1976, or Murray, 1977). Supposing that stationary solutions of (3) are expected such that  $\varepsilon^2 \partial^2 u / \partial x^2 = O(1)$  near  $x=\ell(\beta)$ , we stretch the variable  $x$  by the transformation

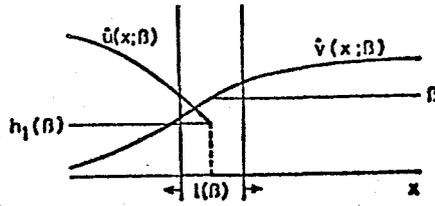


Fig.6. An internal transition layer and stretch of the coordinate.

$$\xi = \frac{x - l(\beta)}{\varepsilon} \quad (13)$$

in the neighbourhood of  $x=l(\beta)$  (Fig.6). Since  $v$  does not have a large spatial gradient there, we may assume that  $v$  is independent of  $x$  and takes the constant value  $\beta$  near the distinguished surface. Therefore, the first of the equations (3) can be rewritten in the form,

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial \xi^2} + f(u, \beta)u. \quad (14)$$

The solution of (14) is the zeroth approximation to the inner solution in the transition layer and  $\hat{u}(x; \beta)$  obtained previously is the zeroth approximation to the outer solution. Thus, the boundary conditions at  $\xi = \pm\infty$  for (14) are imposed as follows;

$$\lim_{\xi \rightarrow -\infty} u(\xi, t) = h_1(\beta), \quad \lim_{\xi \rightarrow +\infty} u(\xi, t) = h_0(\beta), \quad (15)$$

which will match the outer solution. Note that the equation (14)

is the logistic equation with the diffusion term and that  $f(u, \beta)u = 0$  is satisfied if and only if  $u = h_0(\beta)$  or  $u = h_1(\beta)$ . The problem (14) and (15) is the classical one which was already studied by Fisher (1937) and Kolmogoroff, Petrovsky & Piskunoff (1937). It is well known that it has travelling wave solutions  $u(\xi - ct; \beta)$  with velocities  $c(\beta) \geq 2\sqrt{a - b_1\beta} > 0$  for fixed  $\beta$ , if  $\beta < a/b_1$ . It should be noted that the velocities of the travelling wave fronts are positive and of order  $\varepsilon$  with respect to the original coordinate  $x$ , when  $\beta$  is fixed.

We can confirm from numerical evidences that the equations (3) have a stationary solution  $(u_\varepsilon(x), v_\varepsilon(x))$  with a parameter  $d = \varepsilon^2 > 0$ , such that

$$\lim_{\varepsilon \rightarrow 0} u_\varepsilon(x) = \hat{u}(x; a/b_1), \text{ almost everywhere in } (0, L)$$

and

$$\lim_{\varepsilon \rightarrow 0} v_\varepsilon(x) = \hat{v}(x; a/b_1), \text{ uniformly in } (0, L).$$

## 5. Pattern Formation

We study a time-dependent solution of (3) from the previous analysis and some numerical calculations (Fig. 7). In the first stage, a solution with sufficiently smooth initial data satisfies approximately the equations (3) with  $d=0$ , and approaches a stationary solution  $(\hat{u}(x; \beta), \hat{v}(x; \beta))$  for some  $\beta$ , depending on the initial data (Fig. 8). The large spatial gradient develops in  $u$  in the neighbourhood of  $x = \ell(\beta)$  and  $v$  becomes

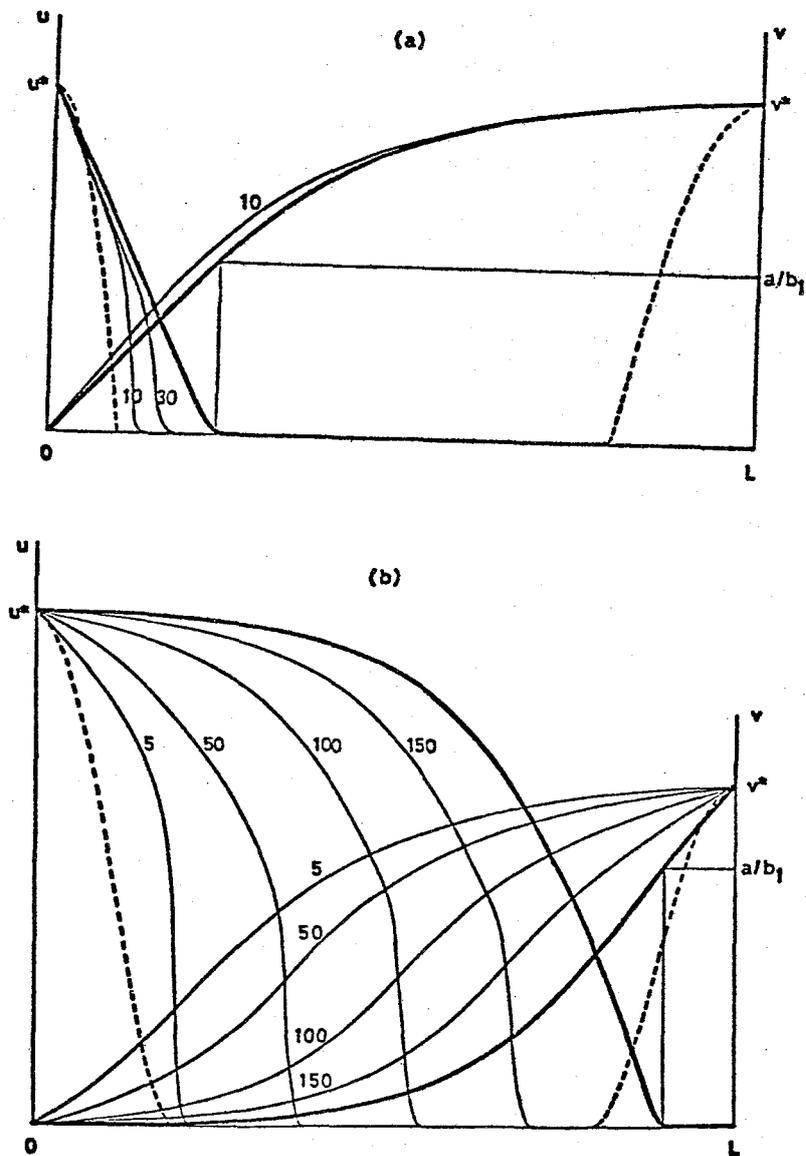


Fig.7. Stationary solutions (fat lines) and development of solutions (thin lines) with the initial distributions (broken lines), when (a)  $\delta=1/2 < 1$  ( $a=1, b_1=b_2=2$ ) and (b)  $\delta=27/16 > 1$  ( $a=3/2, b_1=b_2=2$ ).  $L=5.0$  and  $\epsilon=0.01$  both in (a) and in (b). The numbers beside thin lines indicate time.

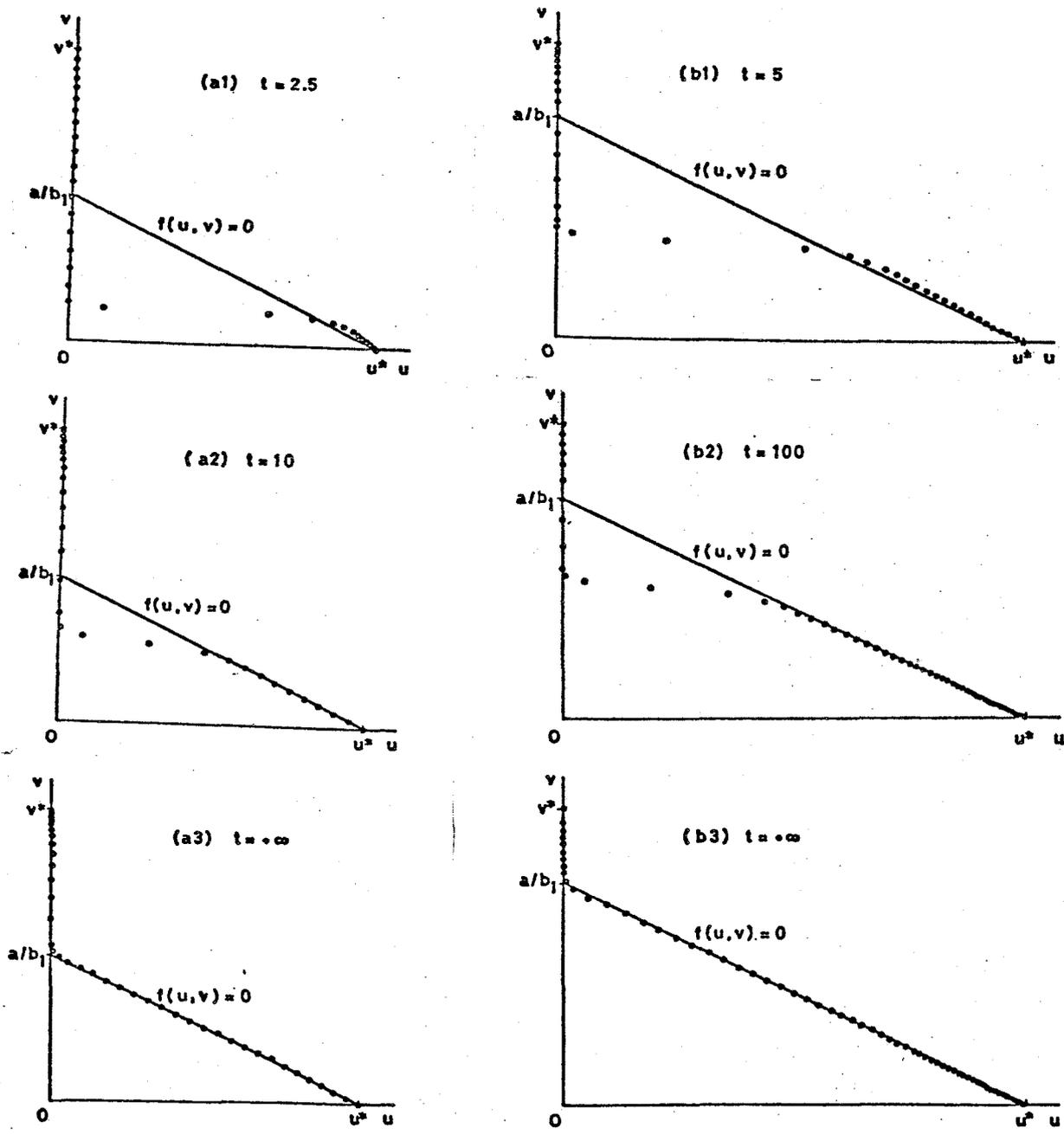


Fig.8. Phase plane portraits of solutions  $(u(x,t), v(x,t))$  at (a1)  $t=2.5$ , (a2)  $t=10$  and (a3)  $t=+\infty$  (steady state), in the case shown in Fig.7a, and also at (b1)  $t=5$ , (b2)  $t=100$  and (b3)  $t=+\infty$  (steady state), in the case shown in Fig.7b.

positive at any point in the domain  $(0, L)$ , because of its fast diffusion. Then, the surface where the transition from the one state  $u=h_1(v)$  to the other  $u=h_0(v)$  occurs, moves in such a manner that  $u$  will increase and approaches the value  $h_1(\beta)$ , slowly with the velocity of order  $\epsilon$ . While the surface is moving slowly, the function  $v(x, t)$  is adjusting to this motion and a new surface  $x=\ell(\beta')$  with slightly larger  $\beta'$  is formed (see Figs. 7 and 8). The value of  $u$  near the surface decreases slightly because  $h_1(\beta)$  is a decreasing function of  $\beta$ . The surface where transition occurs move successively and finally the solution approaches the stationary solution  $(u_\epsilon(x), v_\epsilon(x))$ . In the stationary solution, The size of the region  $(0, \ell_\epsilon)$  where  $u$  takes values larger than  $\epsilon$  has the following properties;

$$(a) \quad \ell_\epsilon = \ell(a/b_1) + O(\epsilon),$$

and

(b1)' if  $\delta = a^3 b_2 / b_1^2 < 1$ ,  $\ell_\epsilon$  is bounded independently of the size of the whole region  $(0, L)$ ,

(b2)' if  $\delta \geq 1$ , it increases monotonously and approaches to infinity as  $L$  goes to infinity.

From an ecological point of view, the species with the far smaller dispersive rate can survive only in a part of the region. However, when the intrinsic growth rate  $a$  of the species  $S_1$  is sufficiently larger than that of the species  $S_2$ , or when the individuals of the species  $S_1$  suppress the growth of the population of the species  $S_2$  more than the latter do the former ( $b_2 > b_1$ ), the slowly dispersing species  $S_1$  can occupy a fairly large area, in proportion to the size of the whole region.

## 6. The Case with Several Patching Points

In section 3, we have considered a solution with a single patching value, of the reduced stationary problem (8) and (9). In this section, we will briefly discuss the case with several patching values, since mathematically interesting phenomena will arise and also it offers an example to show stability of the stationary solution  $(u_\varepsilon(x), v_\varepsilon(x))$  of the equations (3).

Similarly as before, if we assume three patching values  $\beta_1, \beta_2,$  and  $\beta_3$  (Fig.9), we can solve  $\hat{u}$  as a function of  $\hat{v}$  from the first of the equations (8) as

$$\hat{u} = h'(\hat{v}) = \begin{cases} h_1(\hat{v}), & 0 \leq \hat{v} < \beta_1, \\ h_0(\hat{v}), & \beta_1 < \hat{v} < \beta_2, \\ h_1(\hat{v}), & \beta_2 < \hat{v} < \beta_3, \\ h_0(\hat{v}), & \beta_3 < \hat{v} \leq v^*. \end{cases} \quad (15)$$

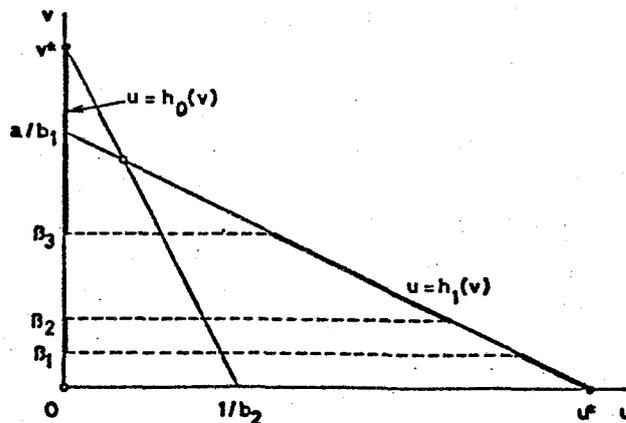


Fig.9. Branches  $u=h_0(v)$  and  $u=h_1(v)$  and three patching values  $\beta_1, \beta_2$  and  $\beta_3$  ( $0 \leq \beta_1 < \beta_2 < \beta_3 < a/b_1$ ).

Then, the following problem is formulated;

$$\frac{d^2 \hat{v}}{dx^2} + G'(\hat{v}) = 0, \quad (16)$$

where

$$G'(v) = g(h'(v), v)v, \\ = \begin{cases} g(h_1(v), v)v, & 0 \leq v < \beta_1, \\ g(h_0(v), v)v, & \beta_1 < v < \beta_2, \\ g(h_1(v), v)v, & \beta_2 < v < \beta_3, \\ g(h_0(v), v)v, & \beta_3 < v \leq v^*. \end{cases} \quad (17)$$

$G'(v)$  has a discontinuities at the points  $v=\beta_1, \beta_2,$  and  $\beta_3$  (Fig.10).

We can solve the problem (16), (17) and (9), and hence the problem (8) and (9), for any  $\beta_1, \beta_2$  and  $\beta_3$ , although the proof is omitted, since it is similar as in the case with a single patching point (Appendix A) and lengthy. A solution is shown in Fig.11, where  $\ell_1, \ell_2,$  and  $\ell_3$  are patching points defined by  $v(\ell_1)=\beta_1, v(\ell_2)=\beta_2$  and  $v(\ell_3)=\beta_3$ .

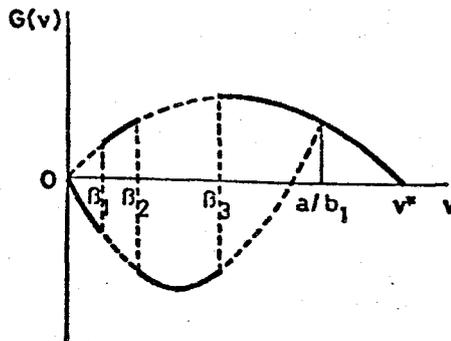


Fig.10.  $G''(v)$  with discontinuities at  $v=\beta_1, \beta_2$  and  $\beta_3$ .

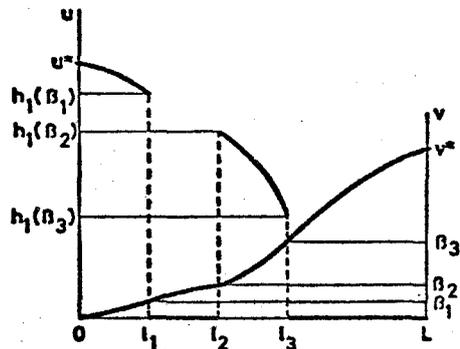


Fig.11. A stationary solution  $(\hat{u}(x), \hat{v}(x))$  with three patching points, when  $d=0$ .

We have obtained a family of solutions of the equations (8) with spatial discontinuities in  $u$  at three points. As in section 4, the singular perturbation technique can be used to analyze the equations (3) with  $\epsilon \neq 0$ , since the solutions are expected to possess strong spatial gradients. The procedure is same as before, and we can show existence of travelling wave solutions in the neighbourhoods of  $x=l_1$ ,  $x=l_2$  and  $x=l_3$ . We should note that the sign of the velocity of a travelling wave solution is determined by which state,  $u=h_0(v)$  or  $u=h_1(v)$ , is dominant (Fife, 1976). Therefore, velocities of wave fronts are negative in the neighbourhood of  $x=l_2$  and positive in the neighbourhoods of  $x=l_1$  and  $x=l_3$ , since the state  $u=h_1(v)$  is dominant.

Then, we compare the absolute values of velocities of wave fronts  $\Gamma_1, \Gamma_2$  and  $\Gamma_3$  respectively in the neighbourhoods of  $x=l_1, x=l_2$  and  $x=l_3$ . Let  $c_1(\beta_1), c_2(\beta_2)$  and  $c_3(\beta_3)$  be minima of absolute values of velocities of wave fronts  $\Gamma_1, \Gamma_2$  and  $\Gamma_3$ , respectively. Then,

$$\begin{aligned} c_1(\beta_1) &= 2 \sqrt{a-b_1\beta_1}, \\ c_2(\beta_2) &= 2 \sqrt{a-b_1\beta_2}, \\ c_3(\beta_3) &= 2 \sqrt{a-b_1\beta_3}, \end{aligned} \tag{18}$$

and

$$c_1(\beta_1) > c_2(\beta_2) > c_3(\beta_3), \tag{19}$$

since  $\beta_1 < \beta_2 < \beta_3$ . It may be important to consider minimum velocities, since it is known that solutions of the equations (14) with a wide class of initial data asymptotically approach to the travelling wave solution with the minimum velocity (see, for example, Kametaka, 1977).

From the above analysis, we can expect pattern formations as follows. Similarly as before, a solution with smooth initial data develops large spatial gradients at some points, in the first stage. Then, the surface where the transitions occur move so as to increase the value of  $u$ , and the function  $v(x,t)$  changes adjusting to the motion. However, in this case, the surfaces  $\Gamma_1$  and  $\Gamma_2$  move in the opposite directions and they will collide at some instance. The collision is expected to occur before the surface  $\Gamma_3$  reaches  $l_\epsilon$ , since velocities of  $\Gamma_1$  and  $\Gamma_2$  are faster than the velocity of  $\Gamma_3$ .

in terms of the minimum velocities, although we cannot prove that the minimum velocities are realized. After the collision of wave fronts  $\Gamma_1$  and  $\Gamma_2$  occurs, the solution exhibit similar behaviours as those considered in the previous section, since there remains only one wave fronts  $\Gamma_3$ . Therefore, we can expect collision and absorption of waves.

To test these ideas, we have done a numerical study (see Fig.12 and also Fig.13). It can be seen, in Fig.12, that

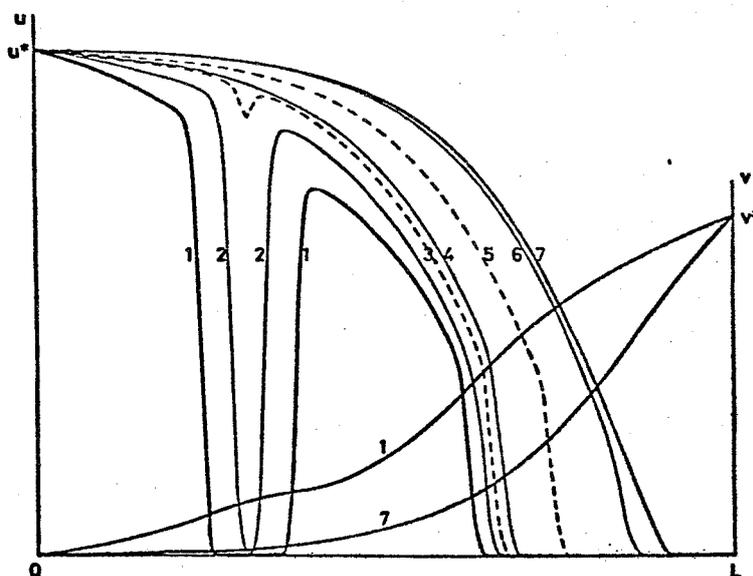


Fig.12. Time development of a solution. Details are same as in Fig.7b, except the initial data. The numbers beside lines indicate the time course; (1)  $t=7.5$ , (2)  $t=15$ , (3)  $t=20$ , (4)  $t=25$ , (5)  $t=50$ , (6)  $t=100$  and (7)  $t=150$ .

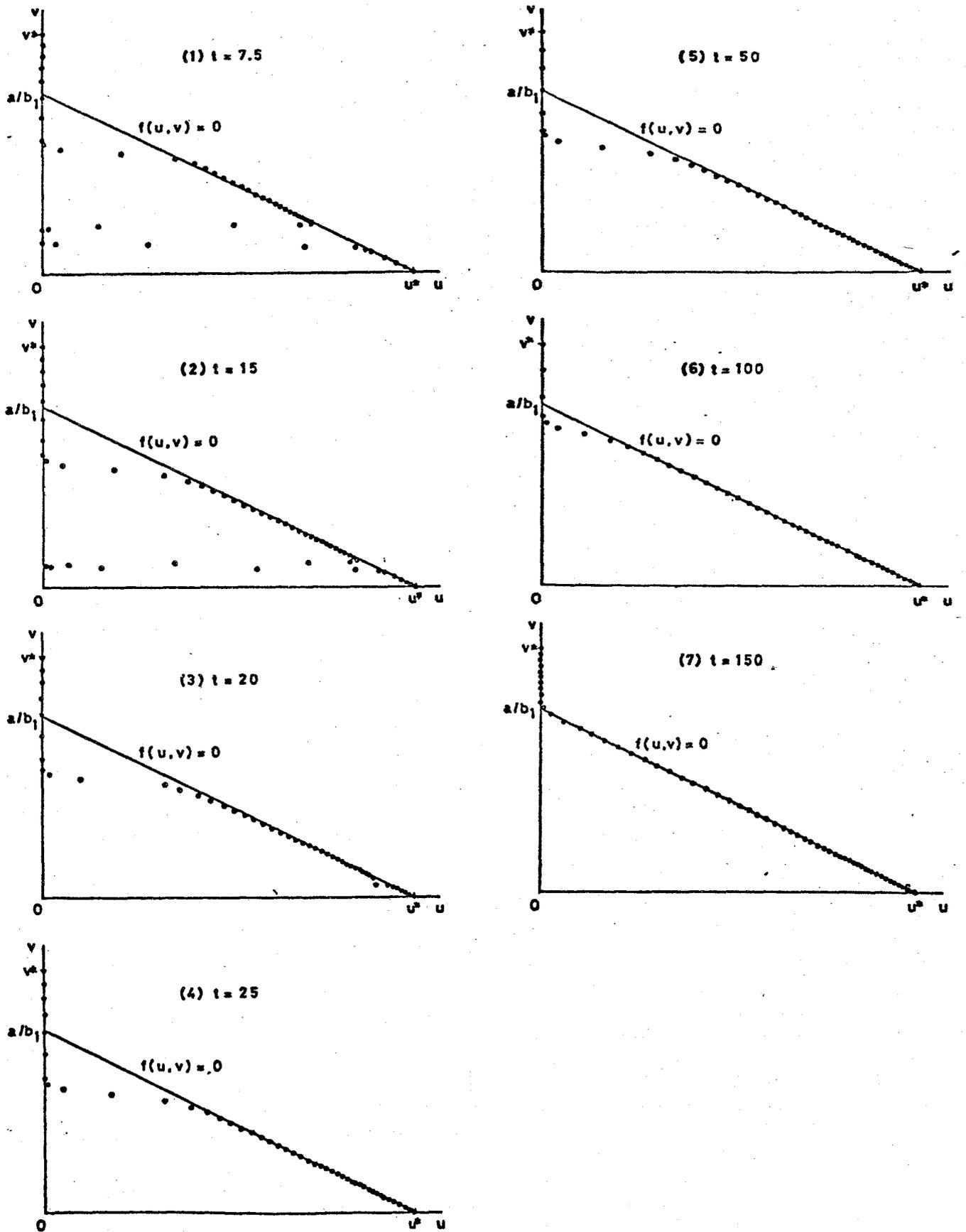


Fig.13. Phase plane portraits of the solution, in the case shown in Fig.12.

large spatial gradients have developed at three points, at  $t=7.5$ . Then, these surfaces move and collision of two surfaces occurs, as was expected. The solution asymptotically approaches to the stationary solution, similarly as was shown in Figs. 7 and 8. We should note that, at any  $t$ , the solution  $(u(x,t), v(x,t))$  approximately satisfies the stationary problem (8) and (9) with  $d=0$  (Fig. 13). Therefore, above statements have been verified from the numerical evidence.

## 7. Discussion

We have considered spatial distributions of two competing populations with quite difference in their diffusive velocities, when their habitats are partly overlapping. At the first insight, it seems that the fastly diffusing species  $S_2$  surpasses the species  $S_1$  by the founder effect, because of the ability of rapid invasion. However, the slowly moving species  $S_1$  can survive in certain subregions, without regard to its intrinsic growth rate or its competitive ability. The parameters affect the size of the regions where the species  $S_1$  can survive in the stationary distribution. The markedly qualitative change occurs at  $\delta = a^3 b_2 / b_1^2 = 1$  ( $\delta = [\alpha_{21} \alpha_{22}^2 / (\alpha_{11} \alpha_{12}^2)] \cdot \varepsilon_1^3 / \varepsilon_2^3$  in terms of the original parameters) and the populations of the species  $S_1$  can occupy a

fairly large area if  $\delta \geq 1$ . Especially, when the overlapping region is an infinite region, it is known that the slowly moving species  $S_1$  can extend the distribution infinitely if  $\delta \geq 1$  (Namba & Mimura, 1980). The condition  $\delta \geq 1$  means that the species  $S_1$  is the slightly superior competitor in the following sense;  $S_1$  has the greater growth rate ( $\epsilon_1 > \epsilon_2$ ), or the population of  $S_1$  suppresses the growth of the population of  $S_2$  more than the latter do the former ( $\alpha_{21} > \alpha_{12}$ ), or the intraspecific competition is milder in the species  $S_1$  ( $\alpha_{11} < \alpha_{22}$ ). This indicates mathematically that, in the absence of dispersal, solutions with a wider class of initial values approach the stationary solution  $(u^*, 0)$ , where the species  $S_2$  is extinct (Fig. 2) (Namba & Mimura, 1980).

The second point we would like to emphasize is that, in the stationary distributions, populations of two species exhibit spatial segregation. Thus, competition between two populations is largely reduced. Coexistence of two competitive populations with spatially segregated distributions is realized simply by random dispersal in a heterogeneous environment, such as considered in this paper, though it is known that spatial segregation is realized if population pressures are introduced (Shigesada et al., 1979, Mimura & Kawasaki, 1979). Although Levin (1974) has shown that coexistence of populations, which cannot coexist in the absence of dispersal, is possible in a homogeneous environment, when random diffusion is taken into consideration, the stationary distribution obtained there is stable only locally and some restrictions must be imposed

on the initial distributions for the populations to coexist. It is verified by some numerical calculations that our stationary distributions are globally stable. And the way of approaches to the stationary distributions is very interesting (Fig.7). It is known that one species competing with the other species extends its distribution, slowly at the expense of habitats of the other species, when the environmental conditions permit its existence (Miller, 1964). Though we can't compare the details, since our model is too simple, the model may have some relevance to such situations.

Chapter IV. Asymptotic Behaviour of Solutions of the  
Diffusive Lotka-Volterra Equations

1. Introduction

The diffusive Lotka-Volterra equations have been studied extensively (Haderer, an der Heiden and Rothe, 1974, Dubois, 1975, Jorné and Carmi, 1977). The system of equations has its origin in the famous Lotka-Volterra equations which describe the population dynamics of prey and predator on the assumption of uniform distributions of populations. The Lotka-Volterra equations with crowding effects both in the prey population and in the predator population are

$$\frac{du}{dt} = (a - Ku - bv)u, \quad (1)$$

$$\frac{dv}{dt} = (-c - Lv + du)v,$$

where  $u$  and  $v$  are densities of the prey population and the predator population respectively and all the parameters are non-negative constants.  $K$  and  $L$  are coefficients of crowding effects or intraspecific competition. Here we assume that  $K < ad/c$  so that the system (1) may have a positive stationary solution  $(u^*, v^*)$ , where  $u^* = (La + bc)/(KL + bd)$  and  $v^* = (ad - cK)/(KL +$

bd). It is well-known that, when there are no crowding effects ( $K=L=0$ ), solutions of the system (1) exhibit sustaining oscillations, and that when there exist some crowding effects ( $K \neq 0$  or  $L \neq 0$ ), the stationary solution  $(u^*, v^*)$  is globally stable. Taking account of effects of dispersal in a continuous environment, the diffusive Lotka-Volterra equations are formulated by adding diffusion terms to the system (1);

$$\frac{\partial u}{\partial t} = (a - Ku - bv)u + d_1 \nabla^2 u, \tag{2}$$

$$\frac{\partial v}{\partial t} = (-c - Lv + du)v + d_2 \nabla^2 v,$$

where the diffusion coefficients  $d_1$  and  $d_2$  are both non-negative constants.

Steele (1974) proposed the system (2) without crowding effects ( $K=L=0$ ) to explain the patchy distribution of planktonic populations in a turbulent sea. He considered the system with zero flux boundary conditions and conjectured that spatial inhomogeneities would appear by the balance of non-linear interactions and diffusion effects. Murray (1975) considered the same problem as Steele's on the assumption of same diffusion coefficients,  $d_1=d_2=d$ , and showed that spatial inhomogeneities would disappear asymptotically. In other words, he denied Steele's conjecture.

Since then, various authors have shown asymptotical spatial homogeneity of solutions of the system (2). When crowding effects exist ( $K \neq 0$  or  $L \neq 0$ ), global stability of the spatially homogeneous equilibrium solution has been shown

(Leung, 1978, Hastings, 1978). When there exist no crowding effects ( $K=L=0$ ), some authors gave sufficient conditions for stability of the spatially homogeneous equilibrium solution of (2) with equilibrium boundary conditions (Rothe, 1976, Mimura and Nishida, 1978) and for convergence to spatially homogeneous but temporally oscillating solutions in the case of zero flux boundary conditions (Williams and Chow, 1978, Mimura, 1979). But they restricted their attention to the case of same diffusion coefficients,  $d_1=d_2=d$ , or to the case of one-dimensional space, or to the case with some restrictions on the initial data. The reason is that we must have an a priori bound for solutions of the equations (2) to use their method and it is very difficult to obtain it, since the corresponding spatially homogeneous system (1) has infinitely many closed orbits.

Some authors considered effects of dispersal in a patchy environment (Levin, 1974, Segel and Levin, 1976, Kawasaki and Teramoto, 1979). An environment is sometimes consisting of discrete patches and in a continuous environment artificial division into patches is also taken place for sampling by an investigator. Thus when we consider a model taking account of effects of dispersal, a spatially discrete model should also be considered. Hastings (1978) considered the spatially discrete version of (2) with crowding effects and showed that the spatially homogeneous equilibrium solution is stable. In this paper, we will also consider the spatially discrete version of (2).

We will show that all the solutions become spatially homogeneous asymptotically without regard to crowding effects. Our results are analogous to those by Rothe(1976) and Mimura and Nishida(1978) in the spatially continuous model. However, we will put no restrictions on diffusion coefficients, dimension of space and initial values. Especially, diffusion coefficients for one of the two species may be identically zero. The reason is that we will need only a Liapunov function and will not need an a priori bound, since we deal with the system of ordinary differential equations rather than the system of partial differential equations.

## 2. Model

We consider a patchy environment which consists of  $N$  compartments(Fig.1). We assume that, in the absence of dispersal of populations between compartments, population dynamics of prey and predator can be described by the Lotka-Volterra equations (1) in any compartment. Adding diffusion terms to the system (1), the following system of ordinary differential equations with  $2N$  variables is obtained(Hastings,1978);

$$\frac{du_i}{dt} = (a - Ku_i - bv_i)u_i - \sum_{j=1}^N D_{ij}^u (u_i - u_j), \quad (3)$$

$$\frac{dv_i}{dt} = (-c - Lv_i + du_i)v_i - \sum_{j=1}^N D_{ij}^v (v_i - v_j),$$

$$i=1, \dots, N,$$

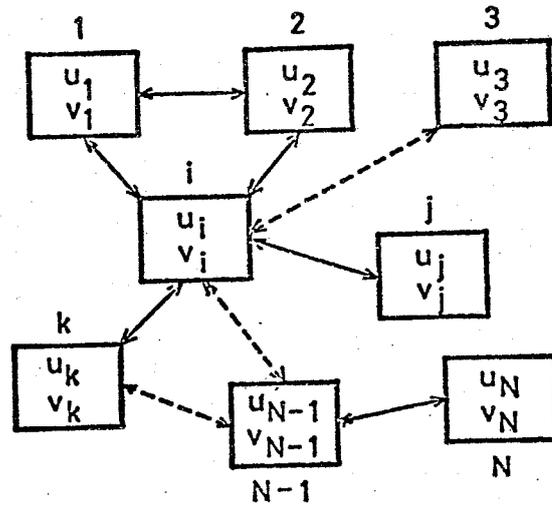


Fig.1 A patchy environment consisting of  $N$  compartments.  $u_i$  and  $v_i$  are respectively population densities of prey and predator in the  $i$ -th compartment. An array means that the  $i$ -th compartment and the  $j$ -th are connected, that is, individuals of prey or predator can move between these compartments. A dashed array means that there are some other compartments between those compartments.

where  $u_i$  and  $v_i$  are respectively population densities of prey and predator in the  $i$ -th compartment and  $D_{ij}^u$  and  $D_{ij}^v$  are non-negative diffusion coefficients.  $D_{ij}^u > 0$  (resp.  $D_{ij}^v > 0$ ) means that individuals of prey (predator) species can randomly move between the  $i$ -th compartment and the  $j$ -th. When at least one of the diffusion coefficients  $D_{ij}^u$  or  $D_{ij}^v$  is positive, we will say that the  $i$ -th compartment and the  $j$ -th are connected.

Here we make two assumptions;

$$(A1) D_{ij}^u = D_{ji}^u \quad \text{and} \quad D_{ij}^v = D_{ji}^v \quad \text{for any } i, j.$$

(A2) There are no isolated compartments which are not connected with any other compartments, and no isolated groups of compartments.

We define two subsets of the set of indices  $\{1, \dots, N\}$ , depending on diffusion coefficients. The first is

$$S = \{i \mid i \in \{1, \dots, N\} \text{ and for any } i \text{ in } S, \text{ there exists an integer } j \text{ in } S, \text{ such that } D_{ij}^u > 0.\},$$

and the second is

$$T = \{i \mid i \in \{1, \dots, N\} \text{ and for any } i \text{ in } T, \text{ there exists an integer } j \text{ in } T, \text{ such that } D_{ij}^v > 0.\}.$$

$S$  (resp.  $T$ ) may be divided into disjoint subsets  $S_1, \dots, S_m$  ( $T_1, \dots, T_n$ ).  $S_k$  for  $k$  in  $\{1, \dots, m\}$  is defined as

$$\text{for any } i, j \text{ in } S_k, \text{ there exists a sequence of distinct integers } p_1, \dots, p_s, \text{ such that } D_{ip_1}^u > 0, D_{p_1 p_2}^u > 0, \dots, D_{p_s j}^u > 0.$$

Similarly  $T_k$  is defined for  $k$  in  $\{1, \dots, n\}$  as

$$\text{for any } i, j \text{ in } T_k, \text{ there exists a sequence of distinct integers } q_1, \dots, q_t, \text{ such that } D_{iq_1}^v > 0, D_{q_1 q_2}^v > 0, \dots, D_{q_t j}^v > 0.$$

The set of compartments whose indices are in  $S_i$  (resp.  $T_i$ ) is a local region where individuals of prey (predator) species can move, and the set of compartments whose indices are in  $S$  (resp.  $T$ ) is the whole region where the population of prey (predator) species can move. For example, if an environment

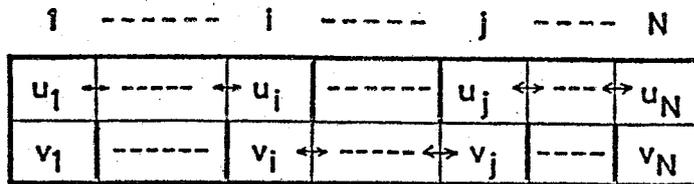


Fig.2 An example of regions where populations of prey or predator can diffuse. A fat line means a barrier for the population. An array means that a population can diffuse across the boundary.

is such as in Fig.2, then

$$S_1 = \{1, \dots, i\},$$

$$S_2 = \{j, \dots, N\},$$

and

$$S = S_1 \cup S_2 = \{1, \dots, i, j, \dots, N\},$$

and

$$T = \{i, \dots, j\}.$$

From the assumption (A2), next Lemma immediately follows.

Lemma Assume (A1) and (A2). Then, either of the following two cases hold;

(i) S is empty and T coincides with the set {1, ..., N}

or vice versa.

(ii) Both S and T are not empty and at least one integer belongs both to S and to T. If there are some disjoint subsets,  $S_1, \dots, S_m$ , in S and  $T_1, \dots, T_n$ , in T, then for each  $S_i$  (resp.  $T_i$ ) there exists at least a set  $T_j(S_i)$  such that one integer belongs both to  $S_i(T_i)$  and to  $T_j(S_j)$ .

Note that S (resp. T) is empty means that diffusion coefficients for prey (predator) species are identically zero.

We consider the system (3) in the positive orthant  $\Omega$  in  $2N$ -dimensional phase space.  $\Omega$  is explicitly written as

$\Omega = \{ (u_1, \dots, u_N, v_1, \dots, v_N) \mid u_i \in (0, +\infty), v_i \in (0, +\infty) \text{ for all } i \}$ .

We will use an abbreviated notation  $(u, v)$  for a point  $(u_1, \dots, u_N, v_1, \dots, v_N)$  in  $\Omega$ . Clearly the positive orthant  $\Omega$  is an invariant set of the system (3). The system (3) has only one spatially homogeneous equilibrium solution  $(u^*, v^*)$  in  $\Omega$ , where  $u_i = u^* = (La + bc) / (KL + bd)$  and  $v_i = v^* = (ad - cK) / (KL + bd)$  for any  $i$ .

We consider three types of boundary conditions.

(i) Equilibrium boundary condition.

$u_i = u^*$  or  $v_i = v^*$  for some  $i$ .

(ii) Periodic boundary condition.

There exist some circular relations in the connectivity of compartments, that is, there exists a sequence of distinct integers,  $p_1, \dots, p_c$ , such that

$$D_{p_i p_{i+1}}^k > 0, \text{ for } i \text{ in } \{1, \dots, c-1\},$$

and

$$D_{p_c p_1}^k > 0,$$

where the subscript  $k$  takes  $u$  or  $v$ .

(iii) Zero flux boundary condition.

We make no conditions on the connectivity and the values of state variables. Then the system consisting of  $N$  compartments is a closed system and there are no fluxes from and into the system.

Hastings (1978) showed global stability of the spatially homogeneous equilibrium solution of (3) with zero flux boundary conditions, when crowding effects exist. Therefore our main interest is in the case without crowding effects. Some authors (Jorne and Carmi, 1977, Hastings, 1978, Mimura and Nishida, 1978) dealt with a more general prey-predator system consisting of many species. However, since the essential feature of the problem can be appreciated in the simple two species system, we will deal with only the two species system.

### 3. Result

To study global behaviour of solutions of (3), we construct a Liapunov function  $V$  which has its origin in the conservative quantity of the equations (1) with  $K=L=0$ .

Let  $V(u,v)$  be

$$V(u,v) = \sum_{i=1}^N \{d[(u_i - u^*) - u^* \log u_i / u^*] + b[(v_i - v^*) - v^* \log v_i / v^*]\} . \quad (4)$$

Using (3) and rearranging, we obtain

$$\begin{aligned} \frac{dV}{dt} = & - \sum_{i=1}^N [dK(u_i - u^*)^2 + bL(v_i - v^*)^2] \\ & - \sum_{i>j} [du^* D_{ij}^u (u_i - u_j)^2 / (u_i u_j) + bv^* D_{ij}^v (v_i - v_j)^2 / (v_i v_j)] , \end{aligned} \quad (5)$$

where the sum  $\sum_{i>j}$  is taken for  $j \in \{1, \dots, N-1\}$  and for

$i > j$ , and we also used the assumption (A1). The function  $V$  is positive-definite, but  $dV/dt$  is not necessarily negative-definite. Thus the following theorem by La Salle and Lefshetz (1961) should be noted.

Theorem 1 (La Salle and Lefshetz)

Consider the autonomous system

$$\dot{x} = X(x), \quad X(0) = 0.$$

Let  $V(x)$  be a scalar function with continuous first partial derivatives. Let  $\Omega_r$  designate the domain of  $x$  where  $V(x) < r$ . Assume that  $\Omega_r$  is bounded and within  $\Omega_r$

$$\underline{V(x) > 0 \text{ for } x \neq 0, \text{ and } \dot{V}(x) \leq 0.}$$

Let  $R$  be the set of all points within  $\Omega_r$  where  $\dot{V}(x)=0$  and

$M$  be the largest invariant set in  $R$ . Then every solution  $x(t)$  in  $\Omega_r$  tends to  $M$  as  $t \rightarrow +\infty$ .

We distinguish two cases according as crowding effects do exist or do not.

(i)  $K \neq 0$  or  $L \neq 0$ .

If  $K \neq 0$ , the set  $R$  in Theorem 1 consists of all points which satisfy the relations

$$u_i = u^* \text{ for all } i$$

and

$$v_i = v_j \text{ for any } i, j \text{ in } T_k, k=1, \dots, n.$$

From the first equation of (3), next relations must be also satisfied at all points in the largest invariant set  $M$  in  $R$ ;

$$0 = \frac{du^*}{dt} = (a - Ku^* - bv_i)u^* \text{ for any } i.$$

Therefore  $v_i=v^*$  must also hold for any  $i$  and  $M$  consists of only the spatially homogeneous equilibrium solution  $(u^*,v^*)$ . Global stability of  $(u^*,v^*)$  is a direct consequence of Theorem 1. On the other hand, if  $L \neq 0$ , similar arguments hold.

(ii)  $K=L=0$ .

In this case, we consider two subclasses depending on boundary conditions.

(a) Equilibrium boundary condition.

Suppose that the value of  $u_1$  is fixed at  $u^*$  and that  $1$  is in  $S_1$ . From the equation (5) all points in  $R$  must satisfy the relations

$$u_i = u^*, \text{ for any } i \text{ in } S_1,$$

$$u_i = u_j, \text{ for any } i, j \text{ in } S_k, k=2, \dots, m,$$

and

$$v_i = v_j, \text{ for any } i, j \text{ in } T_k, k=1, \dots, n.$$

If  $i$  is in  $S_1$ ,  $v_i=v^*$  must also hold in the invariant set  $M$  in  $R$  as before. From the equations (3)

$$\frac{du_i}{dt} = (a - Ku_i - bv_i)u_i$$

must take the same value for any  $i$  in each  $S_k$  and

$$\frac{dv_i}{dt} = (-c - Lv_i + du_i)v_i$$

must take the same value for any  $i$  in each  $T_k$ .

Thus, in the invariant set  $M$

$$u_i = u_j \text{ and } v_i = v_j$$

must be satisfied for any  $i, j$  in each  $S_k$  and  $T_k$ . It follows from Lemma that  $u_i = u^*$  and  $v_i = v^*$  for all  $i$  in the invariant set  $M$ , which means global stability of the spatially homogeneous equilibrium solution  $(u^*, v^*)$ .

(b) Periodic and zero flux boundary conditions.

All points in  $R$  must satisfy the relations

$$u_i = u_j, \text{ for any } i, j \text{ in } S_k, k=1, \dots, m,$$

and

$$v_i = v_j, \text{ for any } i, j \text{ in } T_k, k=1, \dots, n.$$

By similar arguments as those in (a), all points in the invariant set  $M$  must satisfy the relations

$$u_i = u_j \text{ and } v_i = v_j$$

for any  $i, j$ .

Thus,

$$M = \{(u, v) \mid u_i = u(t), v_i = v(t) \text{ for any } i \text{ and } u(t) \text{ and } v(t) \text{ satisfy the system (1) with } K=L=0.\}$$

By Theorem 1, we can conclude that any solution must converge to a spatially homogeneous and temporally oscillating solution. This means asymptotical spatial homogeneity of solutions of the system (3).

Our results are summarized as follows.

Theorem 2      Assume (A1) and (A2). Then any solution of the system (3) becomes spatially homogeneous asymptotically and

(i) if either  $K \neq 0$  or  $L \neq 0$ , or  $K=L=0$  and at least one boundary condition fixes  $u_i$  or  $v_i$  at its equilibrium value, then the spatially homogeneous equilibrium solution  $(u^*, v^*)$  is globally stable.

(ii) If  $K=L=0$  and the boundary conditions are periodic or zero flux, then asymptotical solutions are spatially homogeneous and temporally oscillating, though they depend on initial values.

Remark      Note that above conclusions are valid for any positive initial values and that diffusion coefficients of one of two species may identically vanish.

#### 4. Discussion

We could conclude that any solution of the system (3) is spatially homogeneous asymptotically without restrictions on diffusion coefficients, dimension of space and initial values. However, those asymptotical solutions are temporally oscillating and dispersal of populations of prey and predator interacting according to the Lotka-Volterra equations cannot

stabilize the system in a homogeneous environment. Kawasaki and Teramoto(1979) considered a spatially discrete version of the diffusive Lotka-Volterra equations in a heterogeneous environment and showed that solutions converge to a spatially heterogeneous stationary solution. In the previous section, we assumed positive initial values. When some initial values are zero and diffusion coefficients of either species are zero between some compartments,behaviour of solutions is very different (Kawasaki and Teramoto,1979). For example,if  $u_1(0)=0$  and  $D_{1j}^u=0$  for all  $j$ ,then  $u_1(t)=0$  for  $t > 0$  and the solution will never become spatially homogeneous. This may offer a new interesting problem for us.

## Chapter V. Emigration of a Population and Stability of a Prey-Predator System

### 1. Introduction.

It is known that population densities of some species undergo large fluctuations in simple ecosystems consisting of a few species, especially in communities in the Arctic Circle or in artificially forested woods (Odum, 1971). Some populations exhibit periodic oscillations and others do irregular outbreaks. *Lepus americanus* and its predator *Lynx canadensis* (MacLulich, 1937), and lemmings and foxes which eat lemmings (Elton, 1924) are famous species whose densities oscillate periodically. Populations of some insects, for example, the grey larch budmoth *Zeirophera diniana* (G.) in the European Alps (Baltensweiler, 1964, Auer, 1971) and the blackheaded budworm *Acleris variana* (Fern.) in Canada (Morris, 1959), also exhibit cyclic oscillations. The spruce budworm *Choristoneura fumiferana* (Clem.) in Canada experience rather irregular outbreaks (Pilon & Blais, 1961).

Mass migrations at peak densities are one of the characteristic phenomena which are known in such populations (Baltensweiler, 1964, Pilon & Blais, 1961). Lemmings in Norway (Elton, 1942, cited from Odum, 1971) may be the most famous example. Owls in North America which eat lemmings also make southward migrations, and cyclic invasions of owls to the

United States which correlate with cyclic regressions of lemming populations, have been observed (Shelford, 1943, Gross, 1947, the latter is cited from Odum, 1971). Such emigrations from the crowded habitats have definite directions and few individuals return to their habitats. Regions invaded by the populations are not so fit for growth of the populations as their habitats (Odum, 1971).

It is an ecologically interesting problem to study what role emigration plays on stability of an ecosystem in which population densities oscillate periodically. Odum (1971) said that emigration from crowded regions is a factor of crash, or sudden decrease of population densities. However, if the population does not disperse from the crowded habitats, lack of foods becomes severer and crash of the populations may occur. On the other hand, many theoretical workers (for example, Comins & Blatt, 1974, Shigesada, Kawasaki & Teramoto, 1978, Kawasaki & Teramoto, 1979) have suggested that animal dispersal and heterogeneity of the environment enhance stability of some ecosystems. Therefore, we will study, in this paper, the role of emigration in populations whose densities oscillate periodically.

## 2. Model

We consider populations of two species, prey and predator, or plant and herbivorous animal. For simplicity, we will call them prey and predator in both cases. Periodic oscillations of densities of prey and predator was predicted theoretically by the Lotka-Volterra equations (Lotka, 1925, Volterra,

1931). However, many questions have been proposed on possibility that observed cyclic oscillations are simply due to interactions of prey and predator (Cole, 1951, Ito & Kiritani, 1971). On the other hand, it is known in laboratory experiments that, in a simple two species systems of prey and predator (Luckinbill, 1973), and of host and parasite (Utida, 1957), population densities oscillate periodically, even if the environmental conditions are kept physically constant. It is also suggested that cyclic oscillations of population densities of *Lepus americanus* and *Lynx canadensis* may be explained by interactions of prey and predator (Ito, 1978). Therefore, we will consider the case when periodic oscillations are due to interactions of prey and predator.

We assume that interactions of prey and predator are of Holling type (Holling, 1959), instead of Lotka-Volterra type. The first reason is that the former is derived from more realistic assumptions and the second is that amplitudes of periodic solutions of the Lotka-Volterra equations crucially depend on initial population densities. We also assume that dynamics of the prey population is described by the logistic equation in the absence of predator. As is shown later, we can prove, from the above assumptions, that densities of prey and predator oscillate periodically. We will consider the case where only individuals of predator can migrate from the habitat  $R_1$  to the other region  $R_2$ , especially when the population density is high in the habitat  $R_1$  (Fig. 1). The region  $R_2$  is not suitable for growth of the population, since it cannot make use of its

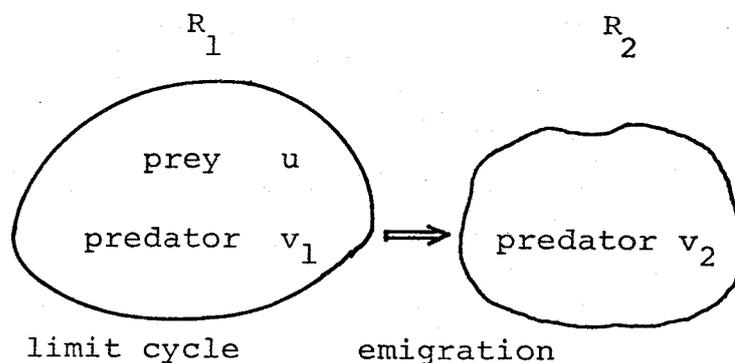


Fig.1. An environment where populations of prey and predator live.

main prey. Thus, the growth rate of the population in  $R_2$  is negative, although some individuals can live in the region. Further, we assume that emigration is described by diffusion, that is, individuals of the population move randomly, and the rate of emigration is in proportion to the difference of densities in two regions, since there is no evidence to show that emigration is restricted in a period at the peak density and there are no available data on relations between population densities and rates of emigration. For example, lemmings do seasonal migrations even at low densities, and at high densities emigration is not so extensive as was previously considered (Ito & Kiritani, 1971). Therefore, we assume random motion of individuals, which may be the simplest assumption.

Let  $u, v_1$  and  $v_2$  be population densities of prey in  $R_1$  and of predator in  $R_1$  and  $R_2$ , respectively (Fig.1). Then, from

the above assumptions, we can formulate the equations satisfied by  $u, v_1$  and  $v_2$ ;

$$\begin{aligned}\frac{du}{dt} &= (a - Ku - \frac{bv_1}{eu+1})u, \\ \frac{dv_1}{dt} &= (-c + \frac{du}{eu+1})v_1 - D_v(v_1 - v_2), \\ \frac{dv_2}{dt} &= -cv_2 - D_v(v_2 - v_1),\end{aligned}\tag{1}$$

where parameters  $a, b, c, d, e, K$  and  $D_v$  are non-negative constants. We have assumed that death rates of predator in  $R_1$  and  $R_2$  are same.

We are interested in the case when the equations (1) with  $D_v=0$  have a stable limit cycle. Our problem is how stability of the system changes when emigration of predator is taken into consideration. In the next section, we will investigate the equations (1) with  $D_v=0$ , as a preliminary study.

### 3. Stability of a Prey-Predator System without Emigration

When  $D_v=0$ , the equations (1) can be reduced to

$$\begin{aligned}\frac{du}{dt} &= (a - Ku - \frac{bv_1}{eu+1})u, \\ \frac{dv_1}{dt} &= (-c + \frac{du}{eu+1})v_1,\end{aligned}\tag{2}$$

since  $v_2$  asymptotically becomes zero, independently of  $u$  and  $v_1$ . Investigating isoclines  $du/dt=0$  and  $dv_1/dt=0$  in the phase plane  $(u, v_1)$  (Fig.2), we can distinguish following two cases depending on the value of  $\bar{u}=c/(d-ce)$ ;

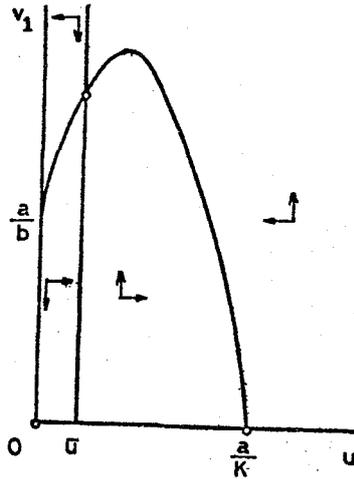


Fig.2. Isoclines  $du/dt=0$  and  $dv_1/dt=0$ , and directions of the vector field, when  $ae-K>0$  and  $0<\bar{u}<u_0=(ae-K)/2eK$ .

(1) When  $\bar{u} \geq a/K$ , the equations (2) have two critical points, the origin  $(0,0)$  and  $(a/K,0)$ .

(2) When  $0 < \bar{u} < a/K$ , or  $a(d-ce) - cK > 0$ , the equations (2) have three critical points, the origin  $(0,0)$ ,  $(a/K,0)$  and  $(\bar{u}, \bar{v}_1)$ , where  $\bar{u} = c/(d-ce)$  and  $\bar{v}_1 = (a - K\bar{u})(e\bar{u} + 1)/b$ .

From an ecological point of view, the origin is a steady state where both species are extinct, and the population of predator is also extinct at the steady state  $(a/K,0)$ . By linear stability analysis, we can confirm that the origin is unstable in both cases. Then, we study stability of the critical point  $(a/K,0)$ . Linearizing the equations (2) near  $(a/K,0)$ , eigenvalues of the coefficient matrix are

$$\lambda = -a, \frac{a(d-ce) - cK}{ae+K}. \quad (4)$$

Comparing the eigenvalues and the condition for the critical point  $(u, v_1)$  to exist with positive values, we can see that,

[I] if the critical point  $(\bar{u}, \bar{v}_1)$  does not exist,

the critical point  $(a/K, 0)$  is stable,

and that

[II] if the former exist, the latter is unstable.

Above arguments show that, when we consider  $\bar{u}$  as a bifurcation parameter, the critical point  $(a/K, 0)$  loses stability at  $\bar{u}=a/K$ , and that a new critical point  $(\bar{u}, \bar{v}_1)$  will bifurcates (Fig.3a)

Then, we examine linear stability of the critical point  $(\bar{u}, \bar{v}_1)$ . The eigenequation of the coefficient matrix of the linearized equations near  $(\bar{u}, \bar{v}_1)$  is

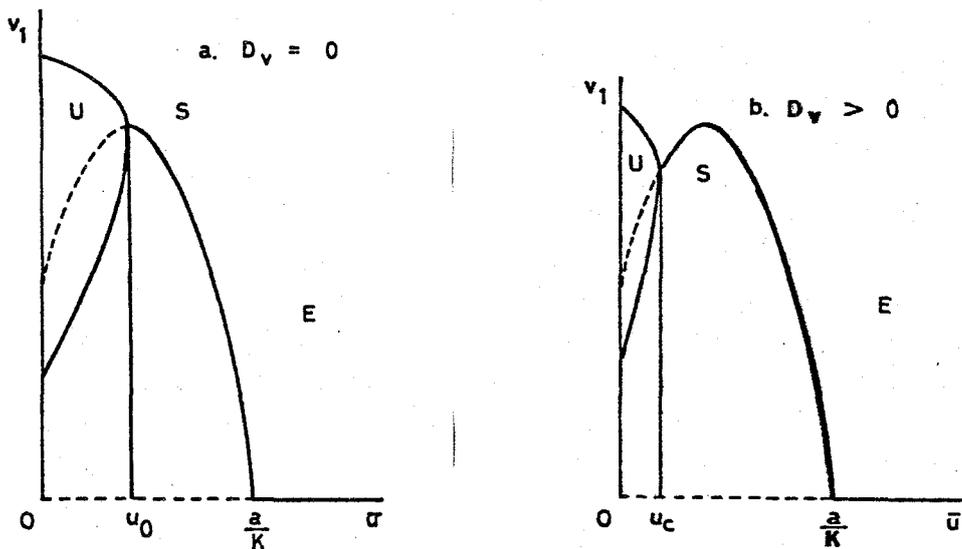


Fig.3. Schematic bifurcation diagrams when (a)  $D_v=0$  and (b)  $D_v>0$ . Amplitudes of  $v_1$  in stable stationary solutions or stable limit cycles are shown.

$$\lambda^2 - \frac{ae-K-2eK\bar{u}}{e\bar{u}+1} \bar{u} \lambda + \frac{d\bar{u}(a-K\bar{u})}{(e\bar{u}+1)^2} = 0. \quad (5)$$

If  $ae-K < 0$ , the critical point  $(\bar{u}, \bar{v}_1)$  is stable, since  $d\bar{u}(a-K\bar{u})/(e\bar{u}+1)^2 > 0$  and  $[(ae-K)-2eK\bar{u}]\bar{u}/(e\bar{u}+1) < 0$ . When  $ae-K \geq 0$ , the eigenvalues become pure imaginary at

$$\bar{u} = u_0 = \frac{ae-K}{2eK}, \quad (6)$$

and they have negative real parts if  $\bar{u} > u_0$  and have positive real parts if  $\bar{u} < u_0$ . Therefore, Hopf bifurcation occurs at  $\bar{u} = u_0$ , and periodic solutions bifurcate from the stationary solution  $(\bar{u}, \bar{v}_1)$  (see, for example, Marsden & McCracken, 1976). We can also show that the bifurcation is supercritical, and that stable periodic solutions exist in the parameter region where the stationary solution  $(\bar{u}, \bar{v}_1)$  is unstable ( $\bar{u} < u_0$ ) (see, Appendix B). An example of a stable limit cycle is shown in Fig.4.

Above results are summarized as follows (see. also Fig.3a);

(E) If  $\bar{u} \geq a/K$ , or  $0 < d \leq c(ae+K)/a$ , the critical point  $(a/K, 0)$  is stable and the population of predator goes to extinction.

(S) If  $a/K > \bar{u} > u_0$ , or  $c(ae+K)/a < d < ce(ae+K)/(ae-K)$ , the critical point  $(\bar{u}, \bar{v}_1)$  is stable, and densities of prey and predator approach positive stationary values.

(U) If  $u_0 > \bar{u} > 0$ , or  $ce(ae+K)/(ae-K) < d$ , the critical point  $(\bar{u}, \bar{v}_1)$  is also unstable and a stable limit cycle exists, and densities of two populations oscillate periodically.

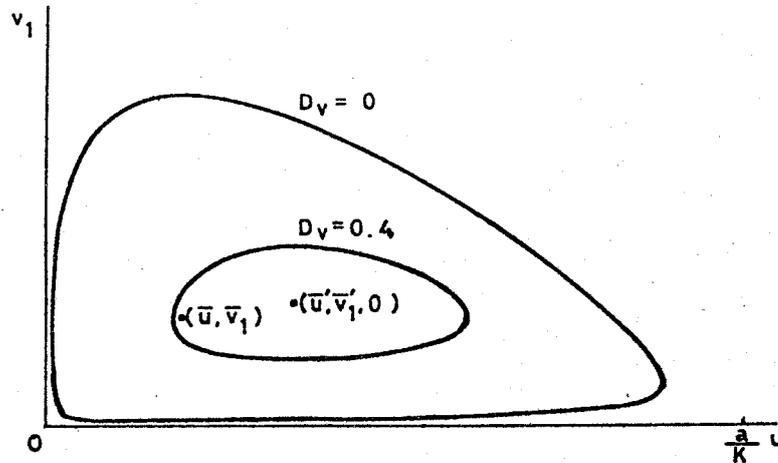


Fig.4. Projections of limit cycles on the plane  $(u, v_1)$  ( $a=b=c=d=1, e=1/2$  and  $K=1/10$ ).

Thus, if the predation rate is too large, that is, predation is too effective, the steady state where two populations coexist becomes unstable, and densities of two populations oscillate periodically, although the population of predator becomes extinct if the predation rate is too small. We should note that we can prove global stability of the critical points  $(a/K, 0)$  and  $(u, v_1)$ , when they are linearly stable, by constructing Liapunoff functions (Appendix C). We can also prove existence of large amplitude periodic solutions by applying Poincare-Bendixson Theorem, although those proved by the bifurcation theory are only small amplitude ones in the neighbourhood of the bifurcation point (Appendix D).

#### 4. Emigration and Stability of the System

In the previous section, we have shown that the equations (1) with  $D_v = 0$  have stable periodic solutions when  $ae-K > 0$  and  $\bar{u} < u_0$  are satisfied. Our next problem is how stability changes when emigration of predator is taking into consideration. Hereafter, we will consider only the case with  $ae-K > 0$ .

Let

$$\bar{u}' = \frac{c(c+2D_v)}{c(d-ce) + (d-2ce)D_v} \quad (7)$$

be a bifurcation parameter. Note that  $\bar{u}'$  is a monotone increasing function of  $D_v$  and that  $\bar{u}'$  coincides with  $\bar{u}$  when  $D_v=0$ . Similarly as before, the following two cases should be distinguished depending on the value of  $\bar{u}'$ ;

(1) when  $\bar{u}' \geq a/K$ , the equations (1) have two critical points, the origin  $(0,0,0)$  and  $(a/K,0,0)$ .

(2) When  $0 < \bar{u}' < a/K$ , the equations (1) have three critical points, the origin  $(0,0,0)$ ,  $(a/K,0,0)$  and  $(\bar{u}', \bar{v}_1', \bar{v}_2')$ , where

$$\begin{aligned} \bar{u}' &= \frac{c(c+2D_v)}{c(d-ce) + (d-2ce)D_v}, \\ \bar{v}_1' &= (a-K\bar{u}') (e\bar{u}'+1)/b, \\ \bar{v}_2' &= \frac{D_v}{c+D_v} \bar{v}_1'. \end{aligned} \quad (8)$$

The origin is unstable in both cases. As in the previous section, we study linear stability of the critical point  $(a/K,0,0)$ . The eigenequation of the coefficient matrix of linearized equations in the neighbourhood of the point is

$$(\lambda+a) \left\{ \lambda^2 + \frac{2c(ae+K) - ad + 2(ae+K)D_v}{ae+K} \lambda - \frac{a[c(d-ce) + (d-2ce)D_v] - cK(c+2D_v)}{ae+K} \right\} = 0. \quad (9)$$

If

$$a[c(d-ce) + (d-2ce)D_v] - cK(c+2D_v) < 0, \quad (10)$$

or  $\bar{u}' > a/K$ , the critical point is stable and it is unstable if the inequality of (10) is reversed. Therefore,

[I] if the critical point  $(\bar{u}', \bar{v}_1', \bar{v}_2')$  does not exist, the critical point  $(a/K, 0, 0)$  is stable,

and

[II] if the former exist, the latter is unstable.

Thus, there occurs a bifurcation phenomenon at  $\bar{u}' = a/K$ , and the critical point  $(\bar{u}', \bar{v}_1', \bar{v}_2')$  bifurcates from the branch  $(a/K, 0, 0)$  (Fig. 3b). We should note that global stability of  $(a/K, 0, 0)$  can be also shown when  $\bar{u}' > a/K$  (Appendix C).

Our final problem is at what point periodic solutions bifurcate when the value of  $\bar{u}'$  varies. When we linearize the equations (1) near the critical point  $(\bar{u}', \bar{v}_1', \bar{v}_2')$ , the eigen-equation of the coefficient matrix is

$$\lambda^3 + A \lambda^2 + B \lambda + C = 0, \quad (11)$$

where

$$A = \frac{2eK\bar{u}' - (ae-K)}{e\bar{u}' + 1} \bar{u}' + c + D_v + \frac{D_v^2}{c + D_v},$$

$$B = \frac{2eK\bar{u}' - (ae-K)}{e\bar{u}' + 1} \bar{u}' \left( c + D_v + \frac{D_v^2}{c + D_v} \right)^2 + \frac{a - K\bar{u}'}{e\bar{u}' + 1} \cdot \frac{c(c + 2D_v)}{c + D_v}, \quad (12)$$

and

$$C = \frac{a - K\bar{u}'}{e\bar{u}'+1} c(c+2D_V) .$$

According to the criterion by Routh and Hurwitz (see, for example, Cesari, 1971), if all of the inequalities

$$A > 0, C > 0, AB - C > 0, \quad (13)$$

are satisfied, all the solutions of (11) have negative real parts and the critical point  $(\bar{u}', \bar{v}_1', \bar{v}_2')$  is linearly stable. If at least one of the inequalities (13) is not satisfied, then the critical point is unstable. By the condition  $u' < a/K$ ,  $C$  is always positive. From the equations (12)

$$\begin{aligned} AB - C = & \frac{2eK\bar{u}' - (ae - K)}{e\bar{u}'+1} \bar{u}' \left\{ \frac{2eK\bar{u}' - (ae - K)}{e\bar{u}'+1} \bar{u}' \left( c + D_V + \frac{D_V^2}{c + D_V} \right) \right. \\ & \left. + \left( c + D_V + \frac{D_V^2}{c + D_V} \right)^2 + \frac{a - K\bar{u}'}{e\bar{u}'+1} \cdot \frac{c(c + 2D_V)}{c + D_V} \right\} \\ & + \frac{a - K\bar{u}'}{e\bar{u}'+1} \cdot \frac{cD_V^2(c + 2D_V)}{(c + D_V)^2} . \end{aligned} \quad (14)$$

When  $ae - K > 0$ , there exists a unique  $u_c$  and  $AB - C$  becomes zero at

$$u' = u_c < u_0, \quad (15)$$

and then  $A$  and  $B$  are positive, at least when  $D_V$  is small.

Therefore, the equations (11) have two pure imaginary roots and one real root having negative real part, and the critical point  $(\bar{u}', \bar{v}_1', \bar{v}_2')$  is stable if  $\bar{u}' > u_c$  and unstable if  $\bar{u}' < u_c$ . Thus, a Hopf bifurcation occurs at  $\bar{u}' = u_c$  and periodic solutions bifurcate. We have also verified from numerical evidences that the bifurcation is supercritical and that periodic solutions are stable.

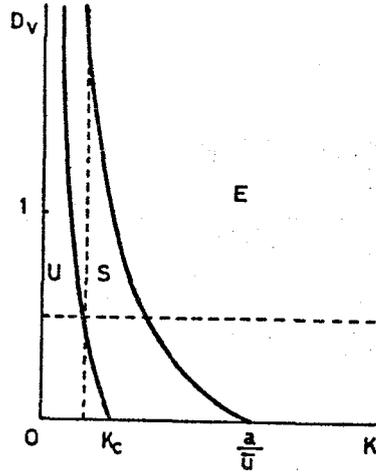


Fig.5. Stable regions of stationary solutions in the parameter space  $(K, D_v)$ . The region E is the stable region of  $(a/K, 0, 0)$  and the region S is the stable region of  $(\bar{u}', \bar{v}_1', \bar{v}_2')$ . In the region U, both solutions are unstable and there exists a stable limit cycle ( $a=b=c=d=1$  and  $e=1/2$ ).

In summary (Fig.3b),

(E) if  $\bar{u}' > a/K$ , the critical point  $(a/K, 0, 0)$  is stable and the populations of predator become extinct.

(S) If  $a/K > \bar{u}' > u_c$ , the critical point  $(\bar{u}', \bar{v}_1', \bar{v}_2')$  is stable and densities of prey and predator approach positive stationary values.

(U) If  $\bar{u}' < u_c$ , both critical points are unstable and there exists a stable limit cycle. Thus, densities of two species oscillate periodically.

Although, behaviour of solutions of the equations (1)

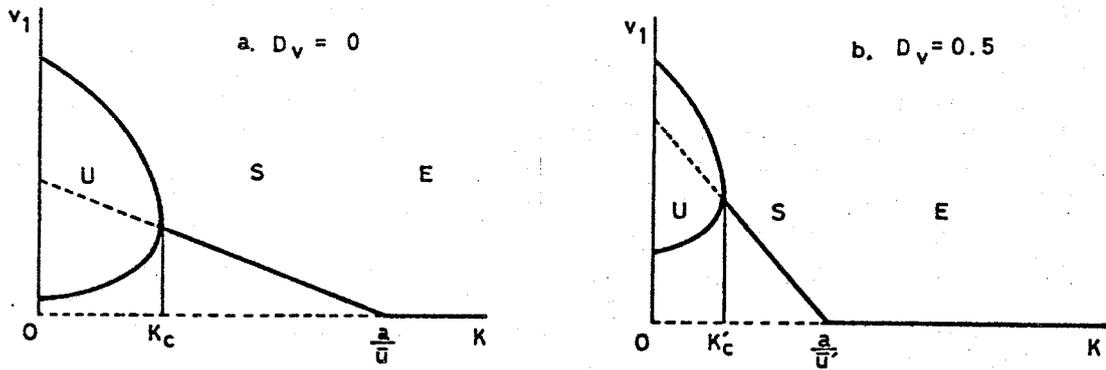


Fig.6. Schematic bifurcation diagrams as  $K$  being a parameter on the lines (a)  $D_V=0$  and (b)  $D_V=1/2$  (see also Fig.5).

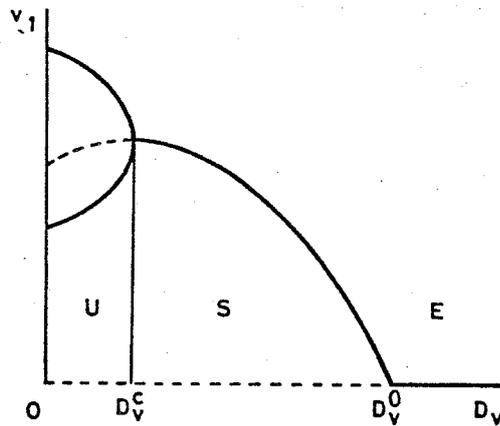


Fig.7. Schematic bifurcation diagrams as  $D_V$  being a parameter on the line  $K=1/10$ . Details are same as in Fig.5.

has been understood, it is not so easy to see the relation between stability and the rate of movement (or the value of  $D_v$ ) from the above analysis. Then, we investigate the relation between stability and the value of  $D_v$ , by dividing the parameter space  $(K, D_v)$ , depending on stability of the critical points (Fig.5). In Fig.5, the letters, E, S, and U attached to three regions correspond to the headings of the previous summary. Fig.6 is bifurcation diagrams which show amplitudes of  $v_1$  in stationary solutions and periodic solutions, as  $K$  being a parameter on the lines (a)  $D_v=0$  and (b)  $D_v=1/2$ . in Fig.5. We can see that, in the interval  $K_c' < K < K_c$ , periodic oscillations are stopped by introducing emigration of predator. The stabilizing effect of emigration can be most clearly seen from Fig.7, which is a bifurcation diagram as  $D_v$  being a parameter on the line  $K=1/10$  in Fig.5. Amplitudes of periodic solutions decreases as the value of  $D_v$  increases, and the critical point  $(\bar{u}', \bar{v}_1', \bar{v}_2')$  becomes stable if  $D_v$  exceeds the critical value  $D_v^c$ , although the critical point  $(a/K, 0, 0)$  which corresponds to the steady state where predator is extinct becomes stable if  $D_v$  is too large.

## 5. Discussion

We have considered a mathematical model to study the role of emigration to an unsuitable region for growth of a population. We have shown that amplitudes of cyclic oscillations can be reduced by emigration. From an ecological point of view, in the absence of emigration, the population

densities exhibit cyclic oscillations with large amplitudes and the populations experience crashes. Therefore, they are exposed to danger of extinction at low densities, by some stochastic factors such as decrease of chance of mating. Since decrease of amplitudes of oscillations means increase of the minimum density, the population can escape extinction if the population of predator makes emigration. Therefore, emigration enhances chance of persistence of populations and it is a stabilizing factor and not a factor of crash. On the other hand, it has been sometimes said that emigration of excessive individuals is a cause of crash of a population (Odum, 1971). It is difficult to compare results of our theoretical model and field observations, since our model is very simple, and in field observations we cannot compare the case with emigration and without emigration. However, we believe that emigration is at least a part of important factors for regulation of populations whose densities experience large fluctuations (Ito & Kiritani, 1971).

There may exist some objections against our model, especially to the assumption that emigration is described by simple diffusion. However, there are no available data on clear relations between densities of populations and numbers of emigrating individuals. Therefore, we should use the simplest assumption which serves as a model for a wider situation. We believe that random motion of individuals is such an assumption. However, we can consider effects of alternative assumptions on emigration. For example, we can imagine the case where the rate

of emigration depends only on the density of predator in its habitat. Then, the middle of the equations (1) becomes

$$\frac{dv_1}{dt} = \left(-c + \frac{du}{eu+1}\right) v_1 - J(v_1), \quad (16)$$

if we assume that the rate of emigration is described by  $J(v_1)$ . We consider effects of two assumptions on  $J(v_1)$ . The first is that  $J(v_1)$  is directly proportional to  $v_1$ , that is,  $J(v_1) = Dv_1$ . In this case, apparently emigration of predator stabilizes the system, since introduction of emigration is identical to increase of the death rate  $c$ . The second is the case where there is a threshold, that is,  $J(v_1) = kH(v_1 - v_1^c)$ , where  $H'(x) = 0$  if  $x < 0$  and  $H(x) = x$  if  $x > 0$ . If  $v_1^c$  is smaller than the maximum density in the oscillation, emigration serves as a stabilizing factor also in this case, although the critical point  $(\bar{u}, \bar{v}_1)$  is unstable without regard to the value of  $k$ , if  $v_1^c > \bar{v}_1$ .

Therefore, the stabilizing role of emigration does not depend on details of types of emigration, although there may exist more alternative assumptions. We may conclude that emigration of predator is a stabilizing agent in a prey-predator system in which population densities exhibit cyclic oscillations. We hope further development of researches for relations between population densities and rates of emigration.

## Chapter VI. Final Discussion

We have considered four mathematical models to study the effects of migration, or the relation between migration of populations and stability of ecosystems. We have shown that migration of a population is a stabilizing factor in a heterogeneous environment. Two competitive populations, either of which becomes extinct in the absence of migration, can coexist in a heterogeneous environment, if random diffusion of the two populations is introduced (Chapter III). In a prey-predator system in which densities of two populations exhibit periodic oscillations with large amplitudes, emigration of predator decreases the amplitudes and chance of extinction of two populations may be reduced, since their densities does not decrease extremely low (Chapter V). However, we should note that random motion of individuals sometimes leads to extinction of the population, if the rate of migration is too large (Chapters II and V). A population which grows or decays exponentially at any point in a habitat can establish a stationary distribution, if the population is dispersing according to dispersive forces including the population pressure (Chapter II). The population can form a stationary distribution also in a limited area, even if a randomly diffusing population grows explosively.

The idea that migration of a population enhances stability of an ecosystem has been also suggested by some authors (Comins & Blatt, 1974, Shigesada, Kawasaki & Teramoto, 1978, Kawasaki & Teramoto, 1979). Therefore, we may conclude that migration of a population is an important mechanism to regulate the number of individuals in a population and that it stabilizes an ecosystem in a spatially heterogeneous environment.

In a spatially homogeneous environment, population densities of prey and predator exhibit synchronized oscillations and random migration cannot stabilize the system in an ecological sense. One of the reasons may be that the Lotka-Volterra equations without crowding effects are structurally unstable, and that they lack ecological reality. Therefore, we must consider the effects of migration in the case when there exists a stable limit cycle. The effects of diffusion on the dynamics of biochemical oscillators have been also studied (see, for example, Nicolis & Prigogine, 1977) and it has been shown that the synchronized oscillation can be unstable and that a nonuniform steady state or an asynchronous oscillation can arise, when diffusion of one species is slow enough (Ashkenazi & Othmer, 1978). However, such a model has not been studied in ecology and we are in need of a future study, before drawing conclusions.

It is known, as the Turing idea (Turing, 1952), that a spatially constant stationary solution can be unstable, and that a new stable spatially heterogeneous stationary solution

bifurcates, in biochemical activator-inhibitor systems (Gierer & Meinhardt, 1972, Auchmuty & Nicolis, 1975, Herschkowitz-Kauffman, 1975) and in prey-predator systems (Mimura & Murray, 1978, Mimura, Nishiura & Yamaguti, 1979). Recently, Mimura and Kawasaki (1979) have shown that cross-diffusion instability occurs in a system composed of two competitive populations and that new stable states exhibiting segregation phenomena bifurcate. Therefore, diffusion and the population pressure are important mechanisms to produce heterogeneous spatial distribution patterns, in spatially homogeneous environments. Formation of spatial patterns in a homogeneous environment may be related with the potential ability to adapt a population to a heterogeneous environment (Mimura, personal communication). Therefore, it will be a future problem to study in what ecological situations spatial heterogeneity is of fundamental importance.

In conclusion, studies on effects of migration is far from complete and we need further refinement and extension of models. For example, effects of migration in two-dimensional environments, in three-species system, in fluctuating environments and in systems with time-delays in interactions, have been hardly studied. Further, we should give not only qualitative descriptions but also quantitative descriptions of particular ecological situations. Recently, Shigesada (1979) has demonstrated that results derived from a model taking account of the self-population pressure exhibit a good fit

with the data obtained from an experiment on dispersal of antlions by Morishita(1954). Such a work will become more important.

#### Acknowledgement

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## Appendices

A. Existence of a stationary solution when  $d=0$ , in Chapter III.

We consider the problem (11), (12) and (9). The equation (11) has the first integral

$$(\hat{d}\hat{v}/dx)^2 = \alpha - H(\hat{v}), \quad (\text{A1})$$

where

$$H(v) = 2 \int_0^v G(z) dz = \begin{cases} \frac{2}{3} (b_1 b_2 - 1) v^3 - (a b_2 - 1) v^2, & 0 \leq v \leq \beta, \\ -\frac{1}{3} (v-1)^2 (2v+1) + \phi(\beta), & \beta \leq v \leq v^*, \end{cases} \quad (\text{A2})$$

$$\phi(\beta) = \frac{1}{3} (2b_1 b_2 \beta^3 - 3 a b_2 \beta^2 + 1), \quad (\text{A3})$$

and

$$\alpha = (\hat{d}\hat{v}/dx(0))^2 \quad (\text{A4})$$

is an adjustable parameter to be determined later. As the right hand side of (A1) must be non-negative,  $\alpha$  must satisfy the conditions

$$\begin{aligned} \alpha &\geq 0, \\ \alpha &\geq \phi(\beta) \end{aligned} \quad (\text{A5})$$

(see Fig.A1). We can solve the equation (A1), using another adjustable parameter  $\ell$  which satisfies

$$\hat{v}(\ell) = \beta. \quad (\text{A6})$$

The implicit solution  $\hat{v}(x;\beta)$  is expressed as follows;

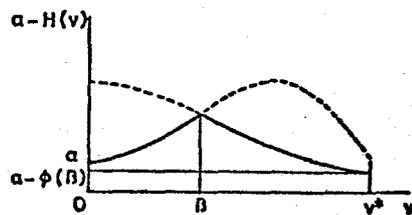


Fig.A1. Dependence of  $\alpha-H(v)$  on  $v$ .

$$\int_0^{\hat{v}} \left\{ -\frac{2}{3} (b_1 b_2 - 1) z^3 + (a b_2 - 1) z^2 + \alpha \right\}^{-\frac{1}{2}} dz = x, \quad 0 \leq x \leq \ell \quad (0 \leq \hat{v} \leq \beta) \quad (A7)$$

$$\int_{\hat{v}}^{v^*} \left\{ \frac{1}{3} (z-1)^2 (2z+1) + \alpha - \phi(\beta) \right\}^{-\frac{1}{2}} dz = L-x, \quad \ell \leq x \leq L \quad (\beta \leq \hat{v} \leq v^*).$$

For the solution actually to satisfy (A1) and (9a), the next relations

$$\int_0^{\beta} \left\{ -\frac{2}{3} (b_1 b_2 - 1) z^3 + (a b_2 - 1) z^2 + \alpha \right\}^{-\frac{1}{2}} dz = \ell, \quad (A8)$$

$$\int_{\beta}^{v^*} \left\{ \frac{1}{3} (z-1)^2 (2z+1) + \alpha - \phi(\beta) \right\}^{-\frac{1}{2}} dz = L-\ell,$$

must be satisfied. We define the functions  $\ell(\alpha; \beta)$  and  $R(\alpha; \beta)$  by the quantities of the left sides of the equations (A8) and let

$$L(\alpha; \beta) = \ell(\alpha; \beta) + R(\alpha; \beta). \quad (A9)$$

Then, the condition (A8) is reformulated as

$$L = L(\alpha; \beta). \quad (A10)$$

If we can determine  $\alpha$  as a function of  $\beta$ , from the relation (A10),  $\ell$  is also determined by the first of (A8) as a function of  $\beta$ , through the relation  $\alpha = \alpha(\beta)$ . We will use the following properties to prove that  $\alpha(\beta)$  is determined uniquely from the condition (A10);

(P1)  $L(\alpha; \beta)$  is a monotone decreasing function of  $\alpha$  for fixed  $\beta$  and approaches zero as  $\alpha$  goes to infinity.

(P2) If  $\phi(\beta) > 0$ , then

$$\lim_{\alpha \rightarrow \phi(\beta)} R(\alpha; \beta) = \lim_{\alpha \rightarrow \phi(\beta)} L(\alpha; \beta) = +\infty,$$

and if  $\phi(\beta) \leq 0$ , then

$$\lim_{\alpha \rightarrow 0} \ell(\alpha; \beta) = \lim_{\alpha \rightarrow 0} L(\alpha; \beta) = +\infty.$$

(P3) For fixed  $\alpha$ ,  $\ell(\alpha; \beta)$  is a monotone increasing function of  $\beta$  and  $L(\alpha; \beta)$  is a monotone decreasing function of  $\beta$ .

(P4)  $\phi(\beta)$  is a monotone decreasing function (Fig.A2) and

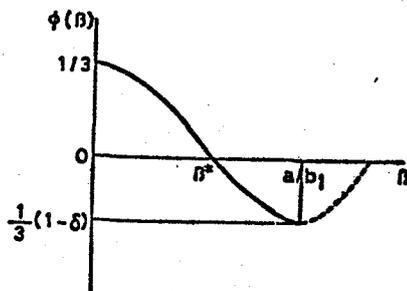


Fig.A2. Dependence of  $\phi(\beta)$  on  $\beta$ , when  $\delta > 1$ .

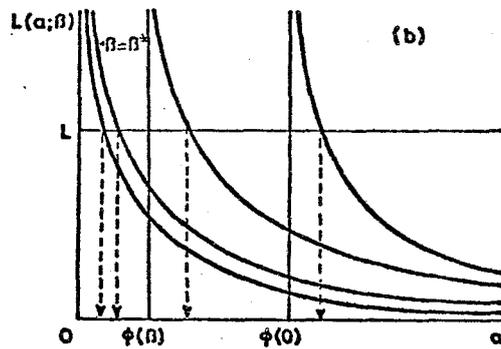
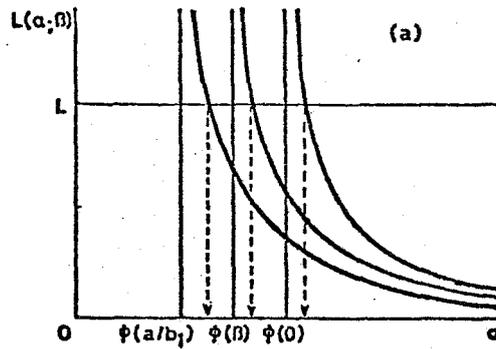


Fig.A3. The schematic representations of relations between  $\alpha$  and  $L(\alpha; \beta)$ , when (a)  $\delta < 1$  and (b)  $\delta \geq 1$ , and of determination of  $\alpha$ .

if  $\delta = a^3 b_2 / b_1^2 < 1$ ,  $\phi(\beta) > 0$  for any  $\beta$ .

If  $\delta \geq 1$ , there exists a unique  $\beta^*$  such that

$$\phi(\beta) > 0 \quad \text{for } 0 \leq \beta < \beta^*,$$

$$\text{and } \phi(\beta) < 0 \quad \text{for } \beta^* < \beta \leq a/b_1.$$

In view of the above properties, we can draw the relations between  $\alpha$  and  $L(\alpha; \beta)$  schematically as shown in Fig.A3,

distinguishing the two cases according as  $\delta < 1$  or  $\delta \geq 1$ . Therefore, if we fix  $L$ , the size of the region,  $\alpha$  is determined uniquely for any  $\beta$ . Then, we can determine  $\ell = \ell(\beta)$  by the first equation of (A8), and (A7) is a solution of the equation (A1), in terms of  $\alpha(\beta)$  and  $\ell(\beta)$ . By the above arguments, we could prove that the problem (A1) and (9a) has a unique solution for any  $\beta$ , and so the problem (11), (12) and (9a). With respect to the patching point, we can see that  $\ell(\beta)$  is a monotone increasing function and takes the maximum value when  $\beta = a/b_1$ , since  $\ell(\alpha; \beta)$  is monotone increasing as a function of  $\beta$ , and monotone decreasing as a function of  $\alpha$ , and  $\alpha = \alpha(\beta)$  is a monotone decreasing function of  $\beta$ . The maximum length  $\ell(a/b_1)$  has a qualitative difference depending on the value of  $\delta$ ;

(i) if  $\delta < 1$ ,  $\ell(a/b_1)$  is bounded without regard to the size of the region  $(0, L)$ ,

and

(ii) if  $\delta \geq 1$ , it is a monotone increasing function of  $L$  and goes to infinity as  $L \rightarrow +\infty$ .

B. Stability of bifurcating periodic solutions when  $D_V = 0$ ,  
in Chapter V.

In section 3, we have shown that there occurs a Hopf bifurcation at  $u=u_0$  (or  $d=c(ae+K)/a$ ) as  $u$  (or  $d$ ) being a bifurcation parameter. Here, we study stability of these periodic solutions (or closed orbits in the phase plane).

We consider a closed orbit  $\gamma$ . Let  $\alpha$  be a point on plane  $S$  which is transversal to the closed orbit  $\gamma$ . A trajectory which start  $\alpha$  at  $t=0$  may intersect with the plane  $S$  at some points as time goes on. Let  $\beta$  be the first of such points. Then, the Poincare map  $P$  is a map  $P(\alpha)=\beta$ . Let  $S$  be a half line defined by  $v_1=\bar{v}_1$  and  $u>\bar{u}$ , in our case. Then, we can consider a Poincare map  $P(u;\bar{u})$  depending on the parameter  $\bar{u}$ , since our closed orbits depends on the bifurcation parameter  $\bar{u}$ . A displacement map  $V$  is defined by

$$V(u;\bar{u}) = P(u;\bar{u}) - u.$$

Let  $g$  be

$$g = \frac{\partial^3 V}{\partial u^3}(u;\bar{u}).$$

Then, it is known (Marsden & McCracken, 1976) that

if  $g < 0$ , periodic solutions bifurcate in the region where the critical point is unstable, and that they are stable.

If  $g > 0$ , periodic solutions bifurcate in the region where the critical point is stable and that they are unstable.

In our case,

$$g = -6\pi \frac{beK(ae-K)}{c(ae+K)^2} < 0,$$

and it can be seen that the bifurcation is supercritical and that these periodic solutions are stable. We can also consider stability of periodic solutions as  $a, d$  or  $K$  being a bifurcation parameter.

C. Global stability of the critical points when  $D_V = 0$ ,  
in Chapter V.

In the following, we will show that the critical points of the equations (2) are globally stable, if they are linearly stable, by the Liapunoff's method. Liapunoff functions used below is due to Nakajima(1978).

(B1) Stability of  $(a/K, 0)$  when  $\bar{u} \geq a/K$

Let  $H_1(u, v_1)$  be a function

$$H_1(u, v_1) = bv_1 + (d-ce) \left[ (u-a/K) - (a/K) \log u/(a/K) \right].$$

$H_1(u, v_1)$  is positive-definite and it becomes zero if and only if  $u=a/K$  and  $v_1=0$ . From the equations (2),

$$\begin{aligned} \frac{dH_1}{dt} &= - \frac{d-ce}{eu+1} \left[ K \left( u - \frac{a}{K} \right)^2 (eu+1) + b \left( \bar{u} - \frac{a}{K} \right) v_1 \right] \\ &\leq 0, \end{aligned}$$

and the equality is satisfied if and only if  $u=a/K$  and  $v_1=0$ .

Therefore,  $H_1(u, v_1)$  is a Liapunoff function and global stability of the critical point is a direct consequence. The above analysis is easily extended to analysis of stability of the critical

point  $(a/K, 0, 0)$  of the equations (1), making use of a function

$$H_2(u, v_1, v_2) = bv_1 + b \frac{D_v}{c+D_v} v_2 + \frac{c(d-ce) + (d-2ce)D_v}{c+D_v} \left[ \left(u - \frac{a}{K}\right) - \frac{a}{K} \log \frac{u}{(a/K)} \right],$$

instead of  $H_1(u, v_1)$ .

### (B2) Stability of $(\bar{u}, \bar{v}_1)$

We consider stability of the critical point  $(\bar{u}, \bar{v}_1)$ , when  $ae-K > 0$  and  $\bar{u} > u_0$ . We define  $H(u, v_1)$  by

$$H(u, v_1) = v_1^p \left[ (u - \bar{u}) - \bar{u} \log \frac{u}{\bar{u}} \right] + \frac{c}{d-ce} \int_{\bar{v}_1}^{v_1} (s - \bar{v}_1) s^{p-1} ds,$$

where  $p$  is a parameter defined later.  $H(u, v_1)$  is also positive-definite and vanishes if and only if  $u = \bar{u}$  and  $v_1 = \bar{v}_1$ . By the equations (2)

$$\frac{dH}{dt} = \frac{v_1^p (u - \bar{u})}{e\bar{u} + 1} \left\{ (d-ce)p \left[ (u - \bar{u}) - \bar{u} \log \frac{u}{\bar{u}} \right] + (a-Ku)(e\bar{u} + 1) - (a-K\bar{u})(e\bar{u} + 1) \right\}.$$

We define  $f(u)$  by

$$f(u) = (d-ce)p \left[ (u - \bar{u}) - \bar{u} \log \frac{u}{\bar{u}} \right] + (a-Ku)(e\bar{u} + 1) - (a-K\bar{u})(e\bar{u} + 1).$$

Then,  $f(\bar{u}) = 0$ , and if we set

$$p = (ae-K)/(d-ce),$$

$f(u)$  is a monotone decreasing function. Therefore,

$$(u - \bar{u})f(u) \leq 0,$$

and the equality is satisfied if and only if  $u = \bar{u}$ . This means that

$$\frac{dH}{dt} \leq 0,$$

and that the above equality is satisfied if and **only** if  $u=\bar{u}$ .  
Therefore, global stability of  $(\bar{u}, \bar{v}_1)$  can be proved by the theorem by La Salle and Lefshetz (1961) (see section IV-3).

D. Existence of periodic solutions with large amplitudes when  $D_v=0$ , in Chapter V.

By the bifurcation theory, we can only prove existence of periodic solutions with small amplitudes, in the neighbourhood of the bifurcation point. In the following, we will show that a stable periodic solution always exists if the critical point  $(\bar{u}, \bar{v}_1)$  is linearly unstable, that is, if  $\bar{u} < u_0$ . Firstly, we define five curves in Fig.D1 as follows;

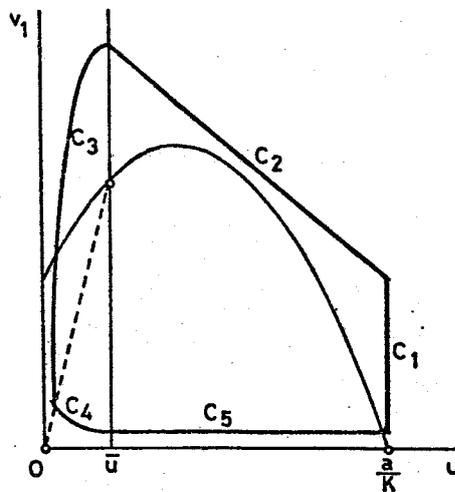


Fig.D1 An invariant set of the equations (2).

$$C_1; \quad u = a/K.$$

$$C_2; \quad K_1(u, v_1) = (d-ce) + bv_1 \\ = K_1^0.$$

$$C_3; \quad K_2(u, v_1) = (d-ce) [(u-\bar{u}) - \bar{u} \log(u/\bar{u})] + bv_1 \\ = K_2^0.$$

$$C_4; \quad K_3(u, v_1) = d[(u-\bar{u}) - \bar{u} \log(u/\bar{u})] \\ + b[(v_1-\bar{v}_1) - \bar{v}_1 \log(v_1/\bar{v}_1)] \\ = K_3^0.$$

$$C_5; \quad v_1 = v_1^0.$$

$K_1^0, K_2^0, K_3^0$  and  $v_1^0$  are adjustable parameters defined later.

Then, we investigate directions of the flow defined by the equations (2), on these curves. On the curve  $C_1$ ,

$$\frac{du}{dt} = - \frac{(ab/K)}{(ae/K)+1} v_1 < 0.$$

On the curve  $C_2$ ,

$$\frac{dK_1}{dt} = \frac{c}{eu+1} \left[ \frac{d-ce}{c} u(a-Ku)(eu+1) + (d-ce)u - K_1^0 \right].$$

Then, if the value of  $K_1^0$  is sufficiently large,

$$\frac{dK_1}{dt} < 0,$$

when  $\bar{u} < u < a/K$ .

On the curve  $C_3$ ,

$$\frac{dK_3}{dt} = d(u-\bar{u}) \{ K(\bar{u}-u) + \frac{be}{(e\bar{u}+1)(eu+1)} (\bar{v}_1 u - \bar{u} v_1) \} \\ \leq 0,$$

since  $u \leq \bar{u}$  and  $u \geq (\bar{u}/\bar{v}_1) v_1$ .

On the curve  $C_5$ ,

$$\frac{dv_1}{dt} = (d-ce)(u-\bar{u}) \frac{v_1^0}{eu+1} \geq 0,$$

since  $u \geq \bar{u}$ .

If we take sufficiently large  $K_1^0$ , other parameters  $K_2^0$ ,  $K_3^0$ , and  $v_1^0$  can be determined by continuity of those curves, and all of the above inequalities are satisfied. Therefore, we consider the region surrounded by these curves, the flow is in the inward direction on boundaries of the region. Thus, the region is an invariant set of the equations (2). So, it can be shown that if the only critical point  $(\bar{u}, \bar{v}_1)$  in the region is unstable, there exists at least a stable closed orbit, by the Poincare-Bendixson theorem (see, for example, Cesari, 1971).