

## EFFECT OF A SINGULAR PATCH ON POPULATION PERSISTENCE IN A MULTI-PATCH SYSTEM

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### ABSTRACT

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Environmental heterogeneity conditions the structure of population dynamics. In this paper, by means of a mathematical model we study the effects of a singular (different kind of) patch on the persistence of a population distributed over patches in a one-dimensional environment. It is assumed that there is migration between any two adjacent patches, and that there is a constant rate of leakage in the migration process. The population in the singular patch is assumed to have growth and emigration rates different from the corresponding rates in the other patches. By means of the eigenvalue estimation, it is quantitatively studied how population persistence is influenced by: (a) the location of the singular patch, (b) the difference in the growth and emigration rates from the corresponding rates in the other patches, and (c) the total number of patches in the system.

### INTRODUCTION

Populations in nature are influenced by environmental patchiness (Wiens, 1976); for example, the distribution of resources, geography, disturbance regime. Various theoretical studies on the effect of such patchy environments on population have been developed following a great deal of field research (see Levin, 1976a, b, 1986, for review). For example, Kierstead and Slobodkin (1953) and Okubo (1982) studied plankton patchiness, using diffusion equations (see also Okubo, 1980). They studied the persistence of a population within an isolated patch and established a critical patch size below which the population becomes extinct (see also Skellam, 1951).

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DeAngelis et al. (1979), Kawasaki and Teramoto (1979), Allen (1983a, b, 1987) and Vance (1984) analyzed the population dynamics in a patchy environment, making use of 'multi-patch' (spatially discrete) systems. Allen (1987) discussed the critical patch number with a spatially discretized reaction-diffusion model. On the other hand, with the same type of system, May (1974) and Levin (1976b), Zeigler (1977), Travis and Post (1979), Hirata (1980) and Post et al. (1983) studied community dynamics. Stochastic versions of such models have also been studied by many researchers (for example, Bailey, 1968; Renshaw, 1972; Richer-Dyn and Goel, 1972; Roff, 1974a, b, 1975).

The system corresponding to the case when patches have generally different parameters has been mathematically investigated by many researchers, for example, Chau (1985). Further, DeAngelis et al. (1979) studied the general conditions for the persistence of population in the context of ' $M$ -matrix'. But their results are either too complicated or too general to be of practical use for a detailed analysis of dependency of population persistence on parameters in a system.

In this paper, we shall study an aspect of the persistence of population in a multi-patch system containing a patch within which emigration and growth rates are different from the corresponding rates within the other patches. We shall call such a patch a 'singular' patch. The singularity of a patch may be regarded as an effect of disturbance in an ecological system, as was discussed by DeAngelis et al. (1985), or of constant harvest, or of some artificial environmental change. Cohen (1972) studied a general linear multi-patch system involving a continuously time-varying rate of leakage from each patch. He showed that the leakage from each patch has no influence on the distribution of substance in the system if and only if the rate of leakage is the same in all the patches. Thus, the existence of a singular patch in the system must influence the distribution of a population and its persistence. We shall study quantitatively how the existence of a singular patch influences the persistence of population in a linear multi-patch system. It will be shown that Allen's (1987) result is suitable but not necessary for our model, though it is applicable to any general multi-patch system.

Our purpose is to analyze one starting point of the theoretical study of the effect of spatial structure of environment on the population dynamics. The results can be seen to be applicable to other models of various contexts such as the multi-membrane system, island biogeography, and the theory of information flow.

#### THE MODEL

We consider a one-dimensional spatially discrete model based on the following assumptions (see Fig. 1):

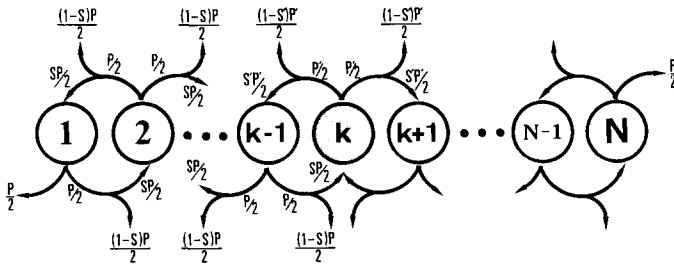


Fig. 1. Scheme of the system considered. The system contains  $N$  patches. The 1st and the  $N$ th patches are called the ‘edge’ patches. The  $k$ th patch is the ‘singular’ patch. Two subsystems can be defined on the right and left side of the singular patch. Arrows indicate the flows of population density. The detail explanation is given in the text.

- (1) There are  $N$  patches in one dimension.
- (2) Each patch is relatively isolated, but a single-species population migrates between any pair of adjacent patches.
- (3) A portion of the migrants leave the system at a constant rate and never return (‘leakage’). Another portion migrates evenly into each of the two nearest-neighbor patches except for the case of the two ‘edge’ patches (the 1st and the  $N$ th patch). Half of the migrants from each ‘edge’ patch leave the system and never return.
- (4) Within each patch, the population grows in a malthusian manner.
- (5) The population in the singular patch has rates of growth, emigration, and leakage different from those in the remaining patches, which have the same rates.

The leakage of migrants, regarded as a function of the risk of migration, may depend on the surrounding environment. Because emigration from each patch is random and non-biased, half of the emigrants from an edge patch leak out of the system.

Population dynamics is assumed to be governed by the system of ordinary differential equations:

$$dn/dt = \mathbf{M} \cdot \mathbf{n}$$

where  $\mathbf{n} = (n_1, n_2, \dots, n_{N-1}, n_N)^T$  and  $n_i$  is the population density of the  $i$ th patch at time  $t$ ;  $\mathbf{M}$  is an  $N \times N$  matrix whose  $ij$ -element is  $m_{ij}$ , and:

$$m_{ii} = R - P \quad (i \neq k), \quad m_{kk} = R' - P'$$

$$m_{i+1,i} = m_{i-1,i} = PS/2 \quad (i \neq k)$$

$$m_{k+1,k} = m_{k-1,k} = P'S'/2$$

$$\text{otherwise, } m_{ij} = 0$$

$R$ ,  $P$ , and  $S$  are the rate of population growth within a patch, of emigration from a patch, and of immigration into the nearest-neighbor patch, respec-

tively;  $1 - S$  is the leakage rate of the migrants. Populations within all patches, except for the  $k$ th patch, have the same rates, whereas the population of the  $k$ th patch is assumed to have growth rate  $R'$ , emigration rate  $P'$ , and leakage rate  $1 - S'$ .

Obviously, the total population is less vulnerable in either of the following two cases: (a) the population in the singular patch has a higher growth rate or a smaller emigration rate than the populations of the other patches; and (b) it has a smaller leakage rate than other populations. To the contrary, the population becomes more vulnerable when the rates have the opposite tendency. The higher the growth rate within a patch, the lower the emigration rate from it. This will indeed be the best strategy with respect to our system for the persistence of the total population. If the emigrants from a patch of a higher growth rate have a smaller rate of leakage, the strategy will become more effective. We shall see these aspects quantitatively in the following analysis.

Population in our system either grows infinitely or becomes extinct as  $t \rightarrow \infty$ . This behavior is determined by the eigenvalues of matrix  $\mathbf{M}$  (Bellman, 1970). If and only if all the eigenvalues have negative real parts, then the extinction of population occurs independently of its initial distribution. Population instead increases infinitely when at least one eigenvalue has a positive real part. We shall estimate the maximum real part of the eigenvalues of  $\mathbf{M}$  and discuss quantitatively the dependence of population persistence on the parameters: location of the singular patch, different quality of a singular patch, and total number of patches in the system.

The above system of ordinary differential equations often appears as a linearized system about an equilibrium point (especially about the trivial solution) in the analysis of local stability of equilibria, or as a comparative system used to estimate a kind of global stability of solution (Allen, 1987). Thus our results, although obtained for a simple linear system, are also of interest for the analysis of nonlinear systems.

ANALYSIS OF THE MODEL

We shall solve the characteristic equation  $G(\lambda) = \det(\mathbf{M} - \lambda \mathbf{E}) = 0$  for the eigenvalue estimation, where  $\mathbf{E}$  is the unit matrix. May (1973) applied a useful technique in order to expand the following  $N \times N$  determinant:

$$\det \begin{pmatrix} \omega & 1 & 0 & \dots & 0 \\ 1 & \omega & 1 & & \\ 0 & & & \ddots & \\ \vdots & & & & 0 \\ 0 & & & 1 & \omega & 1 \\ & & \dots & 0 & 1 & \omega \end{pmatrix} = \frac{\sin\{(N+1)\theta\}}{\sin \theta} \tag{1}$$

where the parameter  $\omega$  is related to  $\theta$  through  $\omega = 2 \cos \theta$ ;  $\theta$  is a complex value in general. This determinant corresponds to  $G(\lambda)$  when  $R' = R$ ,  $P' = P$ , and  $S' = S$ , and the condition that all the eigenvalues have negative real parts is  $\cos\{\pi/(N+1)\} < (P-R)/SP$  (see May, 1973, appendix II). We can expand  $G(\lambda)$  for arbitrary  $R'$ ,  $P'$  and  $S'$ , applying the above technique to it:

$$G(\lambda) = (PS/2)^{N-1} (P'S'/2) g(\theta)/\sin^2\theta \quad (2)$$

$$g(\theta) = \omega' \sin(k\theta) \sin\{(N-k+1)\theta\} \\ - \sin\{(k-1)\theta\} \sin\{(N-k+1)\theta\} \\ - \sin(k\theta) \sin\{(N-k)\theta\} \quad (3)$$

$$2(R-P-\lambda)/SP = 2 \cos \theta \quad (4)$$

$$2(R'-P'-\lambda)/S'P' = \omega' \quad (5)$$

The eigenvalue estimation using this general result, too long and mathematically cumbersome to be reported here, is given in Seno (1988). Here we shall limit ourselves to mentioning its main implications for the considered model. First we shall consider two special cases: (a) the central patch is singular; and (b) the edge patch is singular. Then we shall analyze the general case. We shall always assume that  $R \leq P$  and  $R' \leq P'$ . Indeed, if  $R > P$  or  $R' > P'$  in at least one patch, then the population of any patch will eventually increase and no extinction occurs. This is because the population of a patch overcompensates for the loss due to emigration.

### *Singular central patch case*

Let  $N = 2m + 1$  and  $k = m + 1$  in (3):

$$g(\theta) = \sin\{(m+1)\theta\} [\omega' \sin\{(m+1)\theta\} - 2 \sin(m\theta)] \quad (6)$$

We can solve  $g(\theta) = 0$ , and can show the existence of  $2m + 1$  distinct roots  $\theta_j$  ( $j = 1, 2, \dots, 2m + 1$ ) such that:

$$\theta_{2j} = j\pi/(m+1) \quad (j = 1, 2, \dots, m)$$

$$\theta_{2j} < \theta_{2j+1} < \theta_{2j+2} \quad (j = 1, 2, \dots, m-1) \quad (7)$$

$$0 < \theta_1 < \theta_2 \quad \text{when} \quad 2m/(m+1) - 2SP/S'P' < \alpha \quad (8a)$$

$$\theta_{2m} < \theta_{2m+1} \leq \pi \quad \text{when} \quad \alpha \leq -2m/(m+1) + 2SP/S'P' \quad (8b)$$

$$\theta_1 = i\phi_1 \quad \text{when} \quad \alpha \leq 2m/(m+1) - 2SP/S'P' \quad (8c)$$

$$\theta_{2m+1} = \pi + i\phi_{2m+1} \quad \text{when} \quad -2m/(m+1) + 2SP/S'P' < \alpha \quad (8d)$$

where  $i$  is the imaginary unit, and  $\phi_1, \phi_{2m+1}$  are positively real. The constant  $\alpha$  is given by:

$$\alpha = 2\{R' - P' - (R - P)\}/S'P' \quad (9)$$

Using the above roots and equation (4), it is easily proved that the eigenvalues of  $\mathbf{M}$  are all real and that the maximum eigenvalue  $\lambda_{\max}$  is given by:

$$\lambda_{\max} = \begin{cases} R - P + SP \cosh \phi_{2m+1} & \text{when } 2SP/S'P' - 2m/(m+1) < \alpha \quad (10a) \\ R - P - SP \cos \theta_{2m+1} & \text{when } \alpha \leq 2SP/S'P' - 2m/(m+1) \quad (10b) \end{cases}$$

The condition for all the eigenvalues to be negative,  $\lambda_{\max} < 0$  is instead (Seno, 1988):

$$h_c(\theta^*) < \beta' \quad (0 \leq \beta \leq 1) \quad (11a)$$

$$h_c(\pi + i\phi^*) < \beta' \quad (1 < \beta) \quad (11b)$$

where we have set

$$h_c(\theta) = -\sin(m\theta)/\sin\{(m+1)\theta\} \quad (12)$$

and where  $\beta = (P - R)/SP$ ,  $\beta' = (P' - R')/S'P'$ . Note that both  $\beta$  and  $\beta'$  are not negative, since  $R \leq P$ ,  $R' \leq P'$ . Finally  $\theta^*$  and  $\phi^*$  satisfy  $-\cos \theta^* = \beta$  ( $0 \leq \beta \leq 1$ ) and  $\cosh \phi^* = \beta$  ( $1 < \beta$ ), respectively.

*Singular edge patch case*

By virtue of the symmetric nature of our system, we can assume that the 1st patch is singular. Setting  $k = 1$  in (3), we have:

$$g(\theta) = \sin \theta [\omega' \sin(N\theta) - \sin\{(N-1)\theta\}] \quad (13)$$

We shall solve  $g(\theta) = 0$ .

In a way similar to that for the former case,  $N$  distinct real eigenvalues are obtained, and the condition for  $\lambda_{\max} < 0$  is:

$$h_e(\theta^*) < \beta' \quad (0 \leq \beta \leq 1)$$

$$h_e(\pi + i\phi^*) < \beta' \quad (1 < \beta)$$

with  $h_e(\theta)$  defined by

$$h_e(\theta) = -\sin\{(N-1)\theta\}/\sin(N\theta)$$

and  $\theta^*$  and  $\phi^*$  are the same as before.

*General case*

Because of the symmetric nature of the system, we shall consider the case when  $1 \leq k \leq (N+1)/2$ . The roots of  $g(\theta) = 0$  can be investigated by a

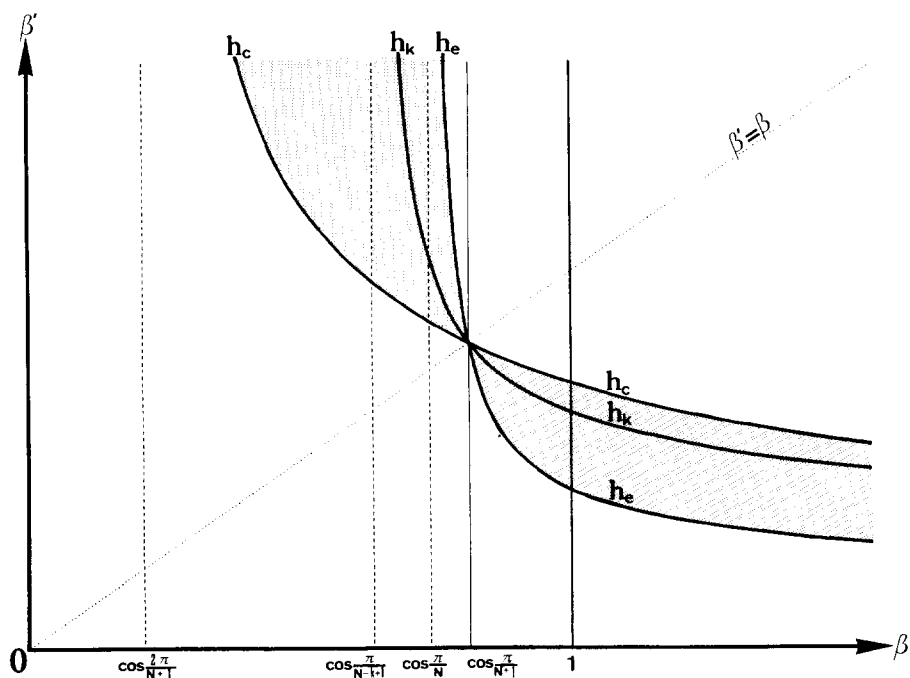


Fig. 2. Critical curves in the  $\beta$ - $\beta'$  plane for the population persistence. The curve  $h_c$  is of the singular central patch case,  $h_e$  of the singular edge patch case, and  $h_k$  of a general case. In each case, the region above the critical curve is that of the extinction of population and the region below it is that of the persistence. Population can necessarily persist in the region where  $\beta < 0$  or  $\beta' < 0$ .

procedure similar to those used in the two special cases. The resulting condition which assures that all the eigenvalues are negative is:

$$h_k(\theta^*) < \beta' \quad (0 \leq \beta \leq 1) \quad (14a)$$

$$h_k(\pi + i\phi^*) < \beta' \quad (1 < \beta) \quad (14b)$$

where

$$h_k(\theta) = -\sin\{(k-1)\theta\}/\sin(k\theta) - \sin\{(N-k)\theta\}/\sin\{(N-k+1)\theta\}$$

Note that, for a fixed  $\beta$ ,  $h_k(\theta)$  is a monotonic function of  $k$ , increasing when  $\beta < \cos\{\pi/(N+1)\}$  and decreasing when  $\cos\{\pi/(N+1)\} < \beta$  (Fig. 2). Due to this monotonicity, the parameter region can be divided into the following four sets:

- (A) the region where at least one positive eigenvalue exists independently of  $k$ ;
- (B) the region where all eigenvalues are negative, independently of  $k$ ;
- (C) the region where all eigenvalues are negative when  $\exists k^* < k$ , and at least one positive eigenvalue exists when  $k < k^*$ ;

(D) the region where at least one positive eigenvalue exists when  $\exists k^{**} < k$ , and all eigenvalues are negative when  $k < k^{**}$ .

These four sets are bounded by the curves  $\beta' = h_c(\cdot)$  and  $\beta' = h_e(\cdot)$  in the  $\beta$ - $\beta'$  plane (see Fig. 2).

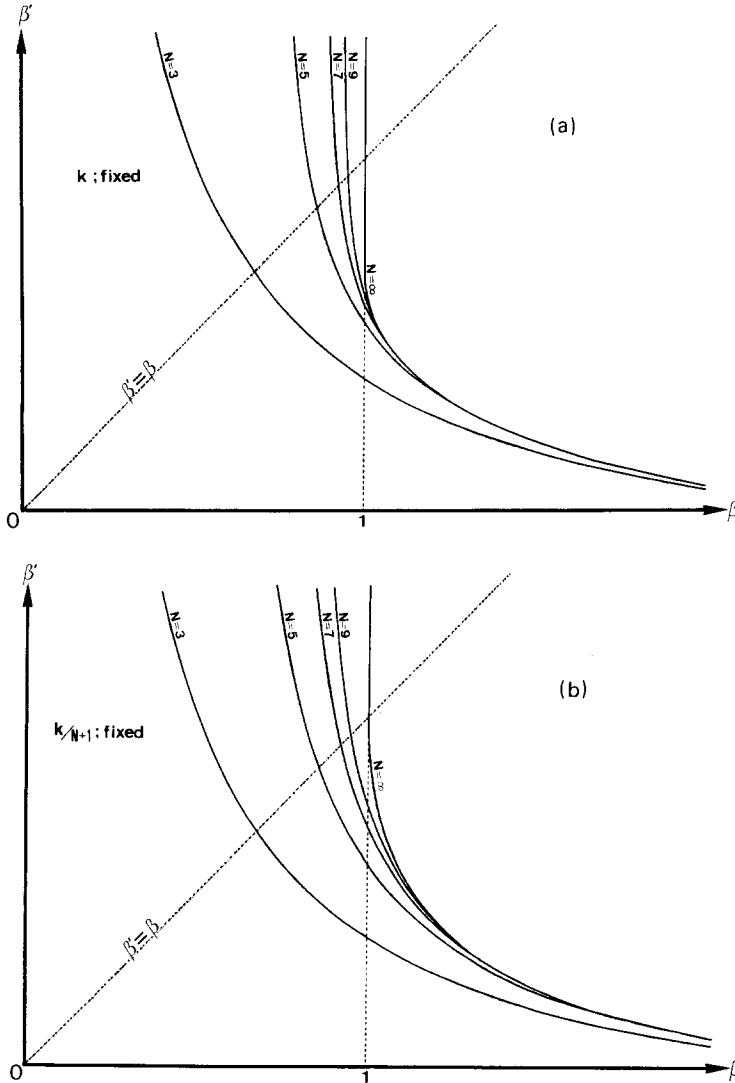


Fig. 3. Critical curves for different total numbers of patches in case of: (a) the location of a singular patch  $k = 2$  fixed, and (b) the ratio  $k/(N + 1) = 1/2$  fixed. In both cases, the critical curve will converge to a curve as  $N \rightarrow \infty$ . For a fixed  $k$ , the limit curve approaches  $(2k - 1)/2k$  at  $\beta = 1$ . For a fixed  $k/N$ , it approaches 1 at  $\beta = 1$ . In each case, the limit critical boundary for the population persistence consists of the limit curve and the semi-infinite line  $\beta = 1$ , whose connecting point is the limit point mentioned above.



Next we shall turn our attention to the dependence of condition (14a,b) on the total number of patches. The asymptotic line  $\beta = \cos\{\pi/(N - k + 1)\}$  approaches  $\beta = 1$  as the  $N$  increases (see Fig. 2). If we let  $N \rightarrow \infty$  with fixed  $k$ , the asymptotic line monotonically approaches  $\beta = 1$  and the critical curve  $\beta' = h_k(\pi + i\phi^*)$  monotonically converges to (see Fig. 3a):

$$\beta' = \sinh\{(k - 1)\phi^*\} / \sinh(k\phi^*) + \exp(-\phi^*)$$

On the other hand, if we keep the ratio  $k/N$  constant, then  $\beta' = h_k(\pi + i\phi^*)$  monotonically converges to  $\beta' = \exp(-\phi^*)$  as  $N \rightarrow \infty$  (Fig. 3b). In each case, the critical curve monotonically converges to a limit curve. This indicates that when the parameters  $\beta$  and  $\beta'$  lie between two critical curves of the total patch numbers  $N_c - 1$  and  $N_c$ , then either all the eigenvalues will be negative if the total patch number  $N$  satisfies  $N < N_c$ , or at least one positive eigenvalue appears if  $N_c \leq N$  (see Fig. 3).

## DISCUSSION

We shall discuss the influence of a singular patch on the persistence of population migrating over  $N$  patches under the extinction condition of a subpopulation:  $R \leq P$ ,  $R' \leq P'$ . Note that a larger  $\beta$  (or  $\beta'$ ) indicates a worse environment. We have arrived at the following results:

(1) The more centrally located a singular patch is, the greater is its effect on the population persistence. In some cases, there exists a critical location of a singular patch. Population can or cannot persist depending on whether the location of a singular patch is more central than the critical location or not. It seems reasonable to assume that the persistence seriously depends on the location of a singular patch.

The location of a local qualitative change of environment may be critical for the persistence of a population. Under identical kinds of change, a population becomes extinct in some cases and persists in others. More generally speaking, this is a case when the effect of a local environmental change on the population persistence has a close relation to the spatial environmental structure.

*Explanation.* The following cases occur: On one hand, the population cannot persist if the location of a singular patch is more central than the critical location and, for the population of a singular patch,  $\beta'$  is larger than  $\beta$ . Hence, the environment of a singular patch is worse than that of others. On the other hand, the population can persist if it is more centrally located than the critical one and  $\beta'$  is smaller than  $\beta$ . The environment of a singular patch is thus better than that of others. These are cases (C) and (D) considered in the previous section (see also Fig. 2).

(2) When the edge patch is not singular, two subsystems containing only identical patches can be defined, and a singular patch is located between them. Population will persist independently of a singular patch under the condition that the population of the larger subsystem can persist if the subsystem is isolated.

Even if a part of an environment qualitatively changes to the worse, the change might have no effect on the population persistence if the remaining part of the system has a sufficient environment for its persistence. This indicates a kind of population tolerance to local environmental changes.

*Explanation.* The line  $\beta = \cos\{\pi/(N - k + 1)\}$  in Fig. 2 is the asymptote of the critical curve  $\beta' = h_k(\theta^*)$ . If  $\beta < \cos\{\pi/(N - k + 1)\}$ , then the population will persist independently of  $\beta'$ , i.e. independently of the singular patch. The condition for the persistence in the isolated system containing identical  $N - k + 1$  patches, which corresponds to the larger subsystem mentioned above, is  $\beta < \cos\{\pi/(N - k + 1)\}$ .

(3) In some cases, there exists a critical total number of patches. If the total number of patches is below the critical number, a population cannot persist. Even though the environment of a singular patch is the worst, it is possible that population persists if the number of available patches is sufficiently large, that is, larger than the critical number.

In an environment with a critical total number of patches, a population can be regarded as relatively less tolerant to a spatial environmental change, since the population may become extinct if an environmental disturbance reduces the number of available habitats.

*Explanation.* This result has already been mentioned in the previous section. A critical total number of patches  $N_c$  will exist when  $\beta$  and  $\beta'$  satisfy the following conditions:

$$h_k(\theta^*) |_{N=N_c-1} \leq \beta' < h_k(\theta^*) |_{N=N_c} \quad (0 \leq \beta \leq 1)$$

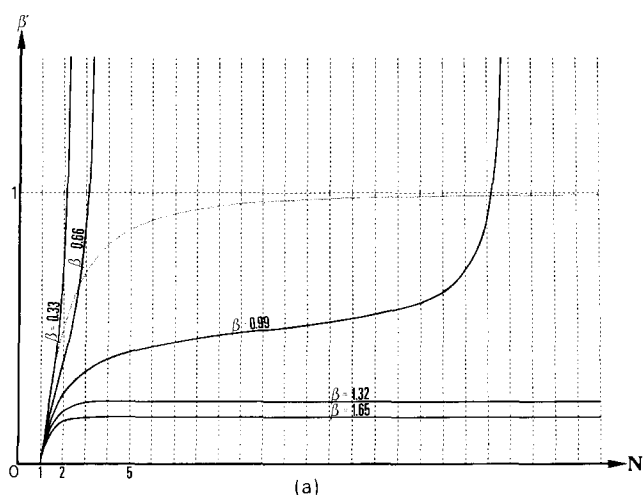
$$h_k(\pi + i\phi^*) |_{N=N_c-1} \leq \beta' < h_k(\pi + i\phi^*) |_{N=N_c} \quad (1 < \beta).$$

Note that  $N_c$  is defined differently in cases (a) and (b) in Fig. 3 (see also Fig. 4).

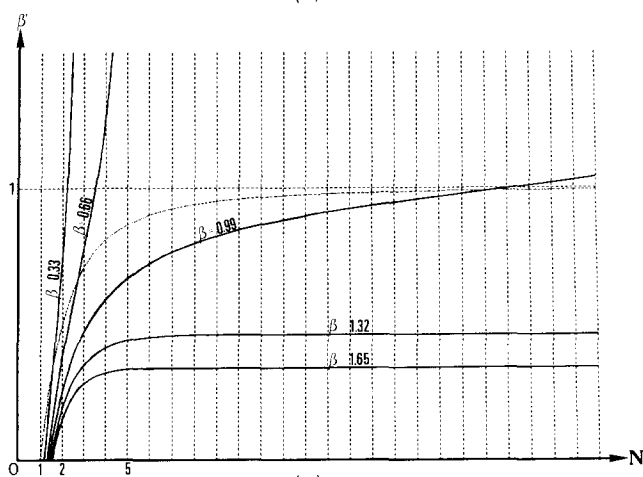
*Remark.* The critical patch number  $N_c^\wedge$  derived by Allen (1987) can be restated in our case as:

$$N_c^\wedge = \text{Arccos}\{-\min(\beta, \beta')\} / [\pi - \text{Arccos}\{-\min(\beta, \beta')\}]$$

The correspondence between the two models is valid only when  $SP = S'P'$  in our model. This is because the population in her model obeys the



(a)



(b)

Fig. 4. Graphs of critical total patch number depending on  $\beta$  and  $\beta'$  in case of: (a) the location of a singular patch  $k=1$  fixed, and (b) the ratio  $k/N=1/2$  fixed. The region above the each curve is of the population extinction, and the region below is of the persistence. When  $\beta < 1$ , each curve has an asymptote  $N = k - 1 + \pi/\text{Arccos}(\beta)$ . The dotted curve is the critical total patch number in the case when all the patches are identical.

diffusion process in proportion to the gradient of population density between two adjacent patches, whereas in our model the population emigrates in proportion only to the density of the source patch itself. As for our model, the condition  $N < N_c^\Delta$  is a sufficient (but not necessary) condition for the population extinction, as we can see in Fig. 4. In our model, there exists a critical patch number also in the case when a population can persist independently of the total number of patches if every patch is identical. This

is essentially due to the existence of a singular patch which has a relatively worse environment.

(4) There are other cases for which there is no critical total number of patches so that population can persist independently of the number of patches ( $\geq 3$ ) even though it could not persist if all patches were identical or isolated. This is because a singular patch has a relatively and sufficiently better environment. In this case, the effect of a singular patch essentially stabilizes the population persistence for the spatial environmental change, that is, the change of available habitat number.

On the other hand, although a singular patch effects the whole system independently of the total number of patches, the singularity of a patch contributes less to the population persistence as the total number of patches increases. In a large system, a local environmental change might not matter for the persistence of a population in it.

*Explanation.* This result follows from the dependence of the critical curve on the total number of patches (Fig. 3). On the one hand, the region of population extinction in  $\beta < 1$  decreases as the total number of patches becomes larger, to vanish as  $N \rightarrow \infty$ . The condition  $\beta < 1$  is sufficient for the persistence in the case of an infinite number of patches. Note that this condition is also necessary for the persistence when all patches are identical. On the other hand, in the region  $1 < \beta$ , where a population becomes extinct if all patches were identical, a singular patch influences the system independently of the total number of patches (Fig. 3). Indeed, if the growth in a singular patch can overcompensate for the leakage of the emigrant, which means  $\beta' < 1$ , the singular patch will make the system persistent even in case of an infinite number of patches with  $1 < \beta$ .

These results are sensitive to the boundary condition of the system: the 'edge effect' mentioned by many authors (for example, Othmer and Scriven, 1971; Renshaw, 1972; May, 1973; Allen, 1987). The boundary condition in our model has already been mentioned in the third assumption on modeling: the 'absorbing' boundary. This boundary condition is not absolutely unrealistic, because some organisms, especially those that move only by an external random force, can be regarded to disperse randomly (Okubo, 1980): for example, some subjects dispersing through membranes, seed dispersal, plankton dispersal, an epidemic. The 'absorbing' boundary condition has a negative effect on the persistence of population in the system considered, because, under this boundary condition, half of the migrants from each 'edge' patch leave the system and never return, which is the 'largest' leakage from the system. But, as the total number of patches increases, the effect of

this boundary condition, that is, of the leakage of half emigrant from the 'edge' patch, becomes relatively less significant, compared with that of the total net leakage of a portion of migrants between every two adjacent patches. In other words, in a large number of patches the leakage during the migration between every two adjacent patches becomes relatively more significant for the population persistence.

In contrast, another typical boundary condition is the 'reflecting' condition such that half of the migrants from each 'edge' patch return to the patch. In this case, an analysis similar to that of this paper is possible. However, it turns out to be much more complicated because this case ultimately implies the existence of three types of patches. Although this is still an open problem, it should be emphasized that it is an interesting one because some organisms may be regarded as identifying their habitat space and not exiting from it. For example, territory recognition, the geographical or temperature limitation of habitat, and a potential barrier for the organisms subjected to an environmental potential. Incidentally, if the boundary condition is 'cyclic', that is, if the first patch is one of the two neighboring patches of the  $N$ th patch, the location of a singular patch makes no contribution to the population persistence because the topological relation among the patches is identical whatever patch is singular. But it is unlikely that patches may be spatially arranged in a cycle, though the migrating relation among patches might become cyclic like some cyclic chemical reactions. This boundary condition may sometimes make the mathematical analysis so easy that it has been used in the following sense (Turing, 1951; Othmer and Scriven, 1971; May, 1974). In case of a sufficiently large number of patches, the eigenvalues of those three boundary cases become close to each other (May, 1973, 1974, appendix II). Hence, the result of the absorbing boundary case is approximately applicable to the other boundary case when the total number of patches is sufficiently large, though the result may essentially depend on the boundary condition when it is small. In some cases, the system with a large size may be analyzed in this sense: for example, a multi-membrane system, a large cellular network, a widespread epidemic, and generally, a spatially discretized compartmental system.

In other cases, the 'edge' effect may be important to discuss theoretically population dynamics, because, of course, not a few systems in nature seem to have such a small size that this effect is not negligible: for example, an infectious endemic, and an archipelago.

In the case of epidemics in a group of some relatively isolated susceptible units such as towns or animal herds, our results can be interpreted as follows: For the purpose of stopping the outbreak through the group, immunization is more effective when it is done for the more centrally located unit. But, if this susceptible group is very large, a local immunization

cannot be effective, while some treatment for the infectors between units is more effective. In contrast, even if an epidemic breaks out in a unit, its outbreak may not matter for the whole group if the source unit is located in the edge or if the group size is sufficiently large, while it may become serious if it is located in the central part of the group.

Further, we can interpret our results in another practical case: the artificial local change of environment for a population such as some plankton inhabiting a multi-patch system, or some birds inhabiting in an archipelago. Suppose that a patch or an island is polluted for some reason. The more centrally located the patch or the island is, the more serious the pollution is for the population persistence. And even if the pollution does not seem serious when it is pointed out, it may become serious after some disturbance reduces the number of available patches or islands. In another case, suppose that its population is decreasing and an artificial environmental change is projected in order to preserve the organism. The more effective way is to make an artificial enrichment of environment of the patch or the island which is more centrally located in the system, or to increase the number of available patches or islands.

A similar interpretation is possible in various contexts such as a cancerous cell in a multi-membrane system through which some organic or inorganic matters diffuse, and an agitational or antisocial community of many communities among which some information propagates.

The discussion in this paper, as well as that in Allen (1987), sheds some light on population persistence. This has been seen to depend on the total number of patches available for the habitat. Moreover, it has been shown that population persistence is seriously influenced by a qualitatively different patch in a system. An experimental study by Fahrig and Merriam (1985) clearly indicates the importance of such aspects for the population dynamics, too. The study of island biogeography and that of a cellular-like system in which a subject disperses should pay attention to the number of islands (cellular components) and the qualitative relationships among them. It is of course clear that our model is too simple to allow for some direct comparisons with specific data. But even some simple models may make some debating points clear. The one-dimensional model has been the starting point of mathematical study of biological phenomena; we expect the same to happen for the model considered in this paper.

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