

PREDATOR'S INVASION INTO AN ISOLATED PATCH WITH SPATIALLY HETEROGENEOUS PREY DISTRIBUTION

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The invasion success of a diffusing predator which changes its diffusion coefficient depending on whether the prey exists or not is investigated. The prey is assumed to be immobile and distributed in an isolated patch. The isolated patch consists of two kinds of region: prey-existing zone and prey-vacant zone. We discuss what relation a heterogeneity of prey distribution has with the predator's invasion success into the patch. Its spatial heterogeneity appears to affect significantly the predator's invasion. In an Appendix we briefly treat an analogous problem involving two competing species.

1. Introduction. In nature, population dispersion is influenced by the spatial environmental heterogeneity: the distribution of resources, geography, disturbance regime, etc. Patchy structure is an example of such heterogeneity that has been attracting many theoretical biologists (Wiens, 1976; Levin, 1986).

Skellam (1951) showed a starting point of mathematical study on population dispersion in a heterogeneous environment by his pioneer work, in which to explain a dispersion of muskrat population, he used a diffusion equation belonging to the following type:

$$\partial n/\partial t = \partial[D(n, x) \partial n/\partial x]/\partial x + F(n, x),$$

where n is population density at location x and time t . $D(n, x)$ is the diffusion coefficient at location x , generally depending also on population density n . $F(n, x)$ is a term related to population growth. He studied the simplest case when $D(n, x) = D$ and $F(n, x) = rn$, where D and r are constants independent of both population density n and location x .

Encouraged by his work, various mathematical studies on the effect of heterogeneous environmental structure on population dynamics have been developed (see Levin, 1976a,b, 1986; Okubo, 1980, for reviews). Kierstead and Slobodkin (1953) and Okubo (1982) studied plankton patchiness using diffusion equations of the above type. They studied population persistence in an isolated homogeneous patch with the absorbing condition, $n=0$, at the boundaries of isolated patch, and established a "critical patch size" below

which population becomes extinct. In Skellam's case, the critical size is given by $\pi\sqrt{D/r}$ (see also McMurtrie, 1978). Further, taking account of the spatial environmental heterogeneity within a patch, some other modified one-species models have also been studied (for example, Gurney and Nisbet, 1975; Namba, 1980; Shigesada, 1984). On the other hand, in nature, such patch size effects have been reported: for instance, for several montane Hispanolan anoles (Rand and Williams, 1969), for a small mammal fauna (Brown, 1971) and alpine plants (Harper *et al.*, 1978) in the Nevada mountains.

Diffusion systems of the above type have also been studied in the context of genetics, where, for example, Nagylaki (1975) studied the evolution of clines in allele frequency, considering such a heterogeneous environment that contains two environmental compartments which are adjacent to each other and their environmental parameters which are different from each other (also see Roughgarden, 1979).

Also, as for interacting populations in a heterogeneous environment, a number of mathematical approaches have been developed making use of diffusion systems of the above type (Levin, 1974, 1976a,b; Steele, 1974a,b, 1975; Dubois, 1975a,b; Platt and Denman, 1975; Wroblewski *et al.*, 1975; Segel and Levin, 1976; Shigesada *et al.*, 1979; Shigesada and Roughgarden, 1982; Teramoto and Seno, 1988). In this case, n , D and F are multi-dimensional vectors. Pacala and Roughgarden (1982) studied the coexistence condition of two competing species diffusing within two adjacent kinds of environments, that is, of Nagylaki's type mentioned above. They introduced the environmental heterogeneity as the difference of carrying capacity, which is assumed to be constant in each of two environmental compartments, and derived the existence of critical compartment size which determines the possibility of two species coexisting in the environment. Also, as for a prey-predator diffusion system of the same type, Guo Ben-Yu and Sleeman (1985) studied a critical size with respect to two-species coexistence by investigating the stationary solution. The biological context of their work is to determine the critical size of a patch in order to prevent an outbreak of predator, which is, for example, a spruce budworm whose host is a balsam fir. In the same context, there are some other mathematical works (Ludwig *et al.*, 1979; Guo Ben-Yu *et al.*, 1983).

On the other hand, making use of some spatially discrete systems, Allen (1983a,b, 1987) and Seno (1989) considered population dynamics in a multi-patchy environment, in which the number of patches is an important parameter. On a spatially discretized reaction-diffusion system of the above type, Allen (1987) discussed the "critical patch number" which corresponds to the critical patch size in the spatially continuous case. With a similar type of multi-patch system, Seno (1989) quantitatively discussed the effect of a "singular" (different kind of) patch on population persistence, and showed that

the location of such a singular patch has an important contribution to population persistence in the system.

In this paper a Lotka–Volterra type of prey–predator system will be analysed. We shall focus on the predator’s invasion success into a spatially heterogeneous distribution of prey. It is necessary for the coexistence of prey and predator. How a prey’s heterogeneous distribution contributes to the predator’s invasion success will be especially investigated. Two simple types of its heterogeneous distribution in an isolated patch will be considered: existence of a prey’s aggregation and existence of a gap without any prey. Since the prey is assumed immobile, the former case may correspond to a gregariousness of plant for instance. The latter may correspond to a spatial gap caused by an ecological disturbance regime. The predator is assumed to diffuse within the patch. At the edge of patch we shall consider both cases of the absorbing and the reflecting boundary conditions, and compare the results.

2. Statement of Model. We consider the following prey–predator system on a one-dimensional interval $\Omega = [-L/2, L/2]$:

$$\frac{\partial H}{\partial t} = \delta(P) \frac{\partial^2 H}{\partial x^2} + \gamma\beta PH - \rho H \quad \text{on } \Omega \tag{1}$$

$$\frac{\partial P}{\partial t} = \varepsilon \left(1 - \frac{P}{\kappa}\right) P - \beta HP \quad \text{on } I_p \tag{2a}$$

$$P \equiv 0 \quad \text{on } I_0 \tag{2b}$$

$$\delta(P) = \begin{cases} \delta_0 & \text{on } I_0 \\ \delta_p & \text{on } I_p, \end{cases} \tag{3}$$

where $\Omega = I_p \cup I_0$ and $I_p \cap I_0 = \emptyset$. In this system, prey is assumed to be able to exist only in a limited region I_p , the “prey-existing zone”, of an isolated patch Ω . I_0 is called the “prey-vacant zone”. The other symbols are defined as follows:

- $H(x, t)$: population density of predator at a position x , time t
- $P(x, t)$: population density of prey at a position x , time t
- $\delta(P)$: diffusion coefficient of predator, depending on the existence of prey as in equation (3)
- γ : contribution rate of predation to population growth of predator
- β : predation rate
- ρ : intrinsic death rate of predator
- ε : intrinsic growth rate of prey
- κ : carrying capacity of prey,

where all parameters are positive. We shall assume that the predator’s diffusion

coefficients, δ_0 and δ_p , are constants independent of space and time. This is a Lotka–Volterra type of prey–predator system. The prey is assumed immobile. Thus, this system may make us imagine a plant–herbivore relation. In a case when prey has a very small diffusion coefficient compared with that of predator, the following analysis may be applied as the first step in the singular perturbation analysis on a system (as for singular perturbation analysis; for example, see Nayfeh, 1973; Mimura *et al.*, 1979a,b). Here we shall focus on our system without mentioning any such advanced case.

Since this system includes a lot of parameters, it is convenient to non-dimensionalize it by the following change of variables:

$$X \equiv \frac{x}{L}; T \equiv \frac{\delta_0 t}{L^2}; P \equiv \frac{P}{\kappa}; H \equiv \frac{\beta H}{\varepsilon}$$

$$\Lambda \equiv \frac{\varepsilon L^2}{\delta_0}; \Gamma \equiv \frac{\gamma \beta \kappa L^2}{\delta_0}; B \equiv \frac{\rho}{\gamma \beta \kappa}; \Delta(P) \equiv \frac{\delta(P)}{\delta_0}; \Delta_p \equiv \frac{\delta_p}{\delta_0}.$$

Then, we obtain the following system with dimensionless variables:

$$\frac{\partial H}{\partial T} = \Delta(P) \frac{\partial^2 H}{\partial X^2} + \Gamma(P - B)H \quad \text{on } \Omega \tag{4}$$

$$\frac{\partial P}{\partial T} = \Lambda(1 - P - H)P \quad \text{on } \mathbf{I}_p \tag{5a}$$

$$P \equiv 0 \quad \text{on } \mathbf{I}_0 \tag{5b}$$

$$\Delta(P) = \begin{cases} 1 & \text{on } \mathbf{I}_0 \\ \Delta_p & \text{on } \mathbf{I}_p, \end{cases} \tag{6}$$

where Ω has the dimensionless length 1.

In this paper we assume that the region Ω consists of three compartments as shown in Fig. 1. \mathbf{S} has the length $k(0 \leq k \leq 1)$. \mathbf{J}_L and \mathbf{J}_R have the length $c(1 - k)$

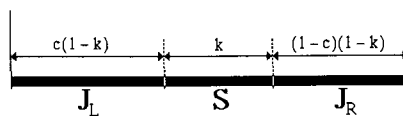


Figure 1. Considered interval Ω which consists of \mathbf{J}_L , \mathbf{S} and \mathbf{J}_R , where $0 \leq k \leq 1$ and $0 \leq c \leq 1$.

and $(1 - c)(1 - k)$, where, without loss of generality, $0 \leq c \leq \frac{1}{2}$. I_p and I_0 are alternatively assumed to be S or $J_L \cup J_R$. As for the case when $c = 0$, there have been some works carried out to consider two-species dynamics in such an environment (Ludwig *et al.*, 1979; Guo Ben-Yu and Sleeman, 1985; Pacala and Roughgarden, 1982).

We shall linearize equations (4) and (5) around an equilibrium $[H^*(X), P^*(X)]$, and investigate the condition of predator's invasion success into the equilibrium environment. Let us define functions $h(X, T)$ and $p(X, T)$ as small perturbations from an equilibrium (H^*, P^*) : $H(X, T) = H^*(X) + h(X, T)$; $P(X, T) = P^*(X) + p(X, T)$.

The equilibrium $(H^*, P^*) = (0, 0)$ is always globally unstable. Indeed, the linearized system around this equilibrium becomes:

$$\frac{\partial h}{\partial T} = \Delta(p) \frac{\partial^2 h}{\partial X^2} - \Gamma B h \quad \text{on } \Omega \tag{7}$$

$$\frac{\partial p}{\partial T} = \Lambda p \quad \text{on } I_p \tag{8a}$$

$$p \equiv 0 \quad \text{on } I_0, \tag{8b}$$

where p obviously increases as T does. Note that, in our system, prey is not able to exist on I_0 . Therefore, we can always assume the condition (8b). In other words, we shall not consider any perturbation of prey on I_0 , where prey density is assumed to be zero. Since the local instability of equilibrium means the global instability of it, this trivial equilibrium is globally unstable. If prey also diffuses, the linearized equation corresponding to equation (8) becomes a Skellam type of diffusion equation, and the equilibrium $(H^*, P^*) = (0, 0)$ can be locally stable under a condition (Skellam, 1951). In this paper, we do not consider this case further.

The equilibrium of type $(H^*, P^*) = (\Phi^*(X), 0)$, where $0 < \text{Sup}_X \{\Phi^*(X)\}$, does not exist because, in our system, the predator's population growth relies only on the predation, as seen in equation (4). Without prey, predator cannot persist. Thus, in this system, predators alternatively coexist with prey or become extinct.

We shall investigate the necessary and sufficient condition of a predator's invasion success into an environment where prey has a stationary distribution. To analyse it, we shall linearize equations (4) and (5) around the equilibrium $(H^*, P^*) = (0, C^*(X))$, where $C^*(X)$ is given by:

$$C^*(X) = \begin{cases} 1 & \text{on } I_p \\ 0 & \text{on } I_0. \end{cases} \tag{9}$$

This is the prey's stationary distribution with no predator. The linearized system is:

$$\frac{\partial h}{\partial T} = \Delta(p) \frac{\partial^2 h}{\partial X^2} + \Psi(X)h \quad \text{on } \Omega \tag{10}$$

$$\frac{\partial p}{\partial T} = -\Lambda(p+h) \quad \text{on } I_p \tag{11a}$$

$$p \equiv 0 \quad \text{on } I_0 \tag{11b}$$

$$\Psi(X) = \begin{cases} \Gamma(1-B) & \text{on } I_p \\ -\Gamma B & \text{on } I_0. \end{cases} \tag{12}$$

Note that $p \rightarrow 0$ as $T \rightarrow \infty$ if $h \rightarrow 0$ as $T \rightarrow \infty$, because, as easily seen from equation (11a), $|p|$ decreases with the order $\exp(-\Lambda T)$ when h becomes sufficiently small.

It is clear that predator fails to invade into the environment $(H^*, P^*) = (0, C^*(X))$ if $1 < B$, because, if so, the predator's dimensionless growth rate $\Psi(X)$ is negative everywhere in the patch. Indeed, since the parameter B corresponds to the ratio of death to birth of predator in the prey-existing zone at the moment of its invasion in it or when the predator is very rare in it, $1 < B$ means that the predator's death is beyond its birth in it. Hence, hereafter we shall assume that $B \leq 1$. Then, $\Psi(X)$ is non-negative in the region I_p and negative in I_0 .

3. Condition of Predator's Invasion Failure. For the two cases shown in Fig. 2,

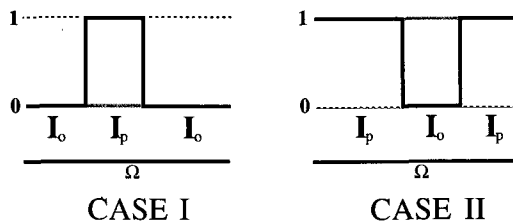


Figure 2. Schematical figures of equilibrium state $(H^*, P^*) = (0, C^*(X))$, where $C^*(X)$ is given by (9).

cases I and II, the following is the sufficient and necessary condition of predator's invasion *failure* for the equilibrium $(H^*, P^*) = (0, C^*(X))$:

Case I: when $I_p = S$ and $I_0 = J_L \cup J_R$

(i) with reflecting boundaries

$$\left\{ \begin{array}{l} E < \frac{1-k}{k} \\ f_{\coth}\left(\frac{1-k}{k} \pi M\right) + R\Delta_p f_{\tanh}\left(\frac{1-k}{k} \pi M\right) \geq -\sqrt{|R|\Delta_p} \cdot \cot\left\{\frac{1-k}{k} \pi E\right\} \end{array} \right.$$

(ii) with absorbing boundaries

$$\left\{ \begin{array}{l} E < \frac{1-k}{k} \\ f_{\tanh}\left(\frac{1-k}{k} \pi M\right) + R\Delta_p f_{\coth}\left(\frac{1-k}{k} \pi M\right) \geq -\sqrt{|R|\Delta_p} \cdot \cot\left\{\frac{1-k}{k} \pi E\right\}; \end{array} \right.$$

Case II: when $I_p = J_L \cup J_R$ and $I_0 = S$

(i) with reflecting boundaries

$$\left\{ \begin{array}{l} E < \frac{1}{2(1-c)} \\ M < \text{Sup}_z \left\{ z \mid \text{for } 0 < \forall x < z < \frac{1}{2(1-c)}, \right. \\ \left. \sqrt{\Delta_p \cdot g(x)} \cdot \coth[\pi M \sqrt{|R|g(x)}] \leq Q_{re}(x) \right\} \end{array} \right.$$

$$Q_{re}(x) = \left(\frac{R-1}{Rx} - x\right) \cdot E \cdot f_{\tan}(\pi x) + \frac{\Delta_p x}{E} f_{\cot}(\pi x)$$

(ii) with absorbing boundaries

$$\left\{ \begin{array}{l} E < \frac{1}{1-c} \\ M < \text{Sup}_z \left\{ z \mid \text{for } 0 < \forall x < z < \frac{1}{1-c}, \right. \\ \left. -\sqrt{\Delta_p \cdot g(x)} \cdot \coth[\pi M \sqrt{|R|g(x)}] \leq Q_{ab}(x) \right\} \end{array} \right.$$

$$Q_{ab}(x) = \left(\frac{R-1}{Rx} - x\right) \cdot E \cdot f_{\cot}(\pi x) + \frac{\Delta_p x}{E} f_{\tan}(\pi x)$$

$$g(x) = 1 - \frac{1}{R} - \frac{x^2}{E^2}.$$

Here we use the following notation:

$$E = \frac{1-k}{\pi} \sqrt{\frac{\Gamma(1-B)}{\Delta_p}}; M = \frac{k}{\pi} \sqrt{\Gamma B}; R = -\frac{1-B}{B}$$

$$f_\psi(z) \equiv \frac{1}{\psi(cz) + \psi\{(1-c)z\}}.$$

The above conditions can be obtained by the eigenvalue estimation on equation (10) (Appendix A).

4. Analysis. In this section, making use of the above conditions, we shall deduce some results about the predator’s invasion into $(H^*, P^*) = (0, C^*(X))$. Cases I and II will be discussed separately.

Case I. In this case, **S** in Fig. 1 is the prey-existing zone and $\mathbf{J}_L \cup \mathbf{J}_R$ is the prey-vacant one. It may be imaged that there is a gregariousness of plant in an isolated region. From the above condition for the predator’s invasion, we can obtain Fig. 3, in which regions for the invasion’s success and failure are shown

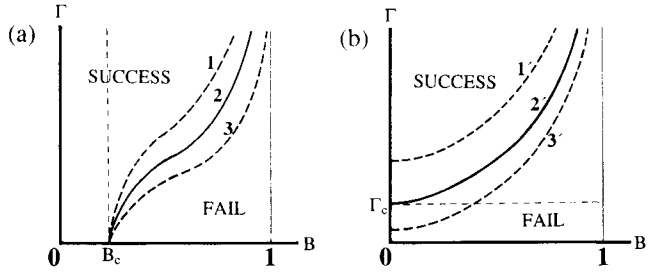


Figure 3. Boundary curves in the Γ - B space, with respect to the predator’s invasion. (a) The reflecting boundary case. (b) The absorbing boundary case. The curves 2 and 2' show critical boundaries for a value c ($0 < c < 1$). In (a), curve 1 is for $c = \frac{1}{2}$, 3 is for $c = 0$. In (b), curve 1' is for $c = 0$ in case I, and for $c = \frac{1}{2}$ in case II; 2' is for $c = \frac{1}{2}$ in case I and for $c = 0$ in case II. $B_c = k$ in case I and $B_c = 1 - k$ in case II. Γ_c is respectively given by equations (14) and (17) in cases I and II.

in the Γ - B space. Figure 3a is for the case of the reflecting boundary, and Fig. 3b for the case of the absorbing boundary. Between the two boundary cases, the contribution of the location of the prey-existing zone **S** in the patch is characteristically different as follows:

CHARACTERISTIC II. *The predator’s invasion is more likely to fail as the location of prey-existing zone gets:*
more central in the patch when the patch boundary is reflecting;

nearer to the edge of patch when the patch boundary is absorbing.

This can be proved by the c -dependency of the condition for the invasion success. The contrasting results between the two boundary conditions above indicate a significant effect of population dissipation at the boundary on the predator's invasion. However, when the prey-existing zone is sufficiently rich (or poor), it is likely that the predator's invasion success (or failure) is independent of its location.

There is a stronger condition of the predator's invasion success in the reflecting boundary case, as seen in Fig. 3a.

CHARACTERISTIC I2. *In the reflecting boundary case, if*

$$B \leq k, \tag{13}$$

then the predator's invasion succeeds independently of any other conditions.

Therefore, if the prey-existing zone is wide enough to satisfy condition (13), the invasion of predator succeeds independently of the other parameters. This condition (13) can be translated as follows: in the moment of invasion, the predator's population growth in the prey-existing zone overcompensates its population death in the whole patch. Indeed, in such a moment, condition (13) can be approximately rewritten to:

$$\int_{\Omega} \rho H \, dx \leq \int_{\Omega} \gamma \beta P H \, dx,$$

where P is approximately a constant κ in the prey-existing zone and 0 in the other. However, it should be noted that, in fact, the distribution of predator gradually changes by the specific interaction and the diffusion process as well as the distribution of prey changing in the prey-existing zone. Thus, the above rewriting is approximately valid only at the moment of invasion of the predator or only when the predator's density is very low throughout and its distribution is almost uniform.

In the absorbing boundary case, there is also a stronger condition.

CHARACTERISTIC I3. *In the absorbing boundary case, if*

$$\begin{cases} k\sqrt{\frac{\Gamma}{\Delta_p}} < \pi \\ c(1-c)(1-k)\sqrt{\Delta_p\Gamma} - \frac{1}{(1-k)\sqrt{\Delta_p\Gamma}} \leq \cot\left\{k\sqrt{\frac{\Gamma}{\Delta_p}}\right\}, \end{cases} \tag{14}$$

then the invasion fails independently of B (see Fig. 3b).

This result can be obtained when $B \rightarrow 0$ for the condition of invasion failure.

The condition (14) is principally on the environmental heterogeneous structure in the patch. We can say that the effect of population dissipation at the patch boundary brings it. Moreover, the population dissipation at the boundary brings another particular aspect.

CHARACTERISTIC I4. *In the absorbing boundary case, if*

$$1 < \Delta_p, \tag{15}$$

then there is a unique optimal size k ($0 < k < 1$) of prey-existing zone for the predator's invasion success. Otherwise, the predator's invasion is the most likely to succeed when $k = 1$, this is, when prey is distributed everywhere in the patch (see Fig. 4).

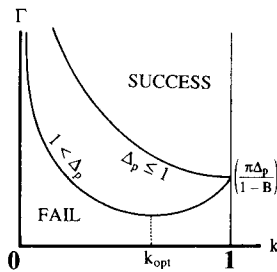


Figure 4. Boundary curves in the Γ - k space, with respect to the predator's invasion in case I. Two boundaries are schematically shown for $1 < \Delta_p$ and for $\Delta_p \leq 1$. When $1 < \Delta_p$, the boundary curve has a minimum at $k = k_{opt}$.

Here the word “optimal” means that the parameter region expanded by the parameters except for the size of the prey-existing zone is the widest for the predator's invasion success. The optimal size is less than the size of the whole patch. Unless condition (15) is satisfied, the invasion is most likely to succeed when the prey-existing zone expands throughout the patch. Condition (15) means that the diffusion coefficient in the prey-existing zone is greater than that in the other zone. If the predator behaves as in condition (15), it is better for the prey, in order to prevent or at least modify the predator's invasion, that it distributes more in the patch even if the total population may reduce, or that it distributes more widely. The latter strategy of prey can be regarded as relying on the effect of predator population dissipation at the boundary. However, if the predator changes its strategy so that it does not satisfy (15), then the prey's wider distribution becomes rather better for the predator's invasion success. In this case, prey may evolutionarily have to become distributed in a more concentrated fashion. As a whole, the prey's concentrated, that is, patchy distribution is evolutionarily rather adaptable. Rigorously speaking, in such a co-evolutionary process, since the available strategy may be restricted for prey and predator, depending on their evolutionary capability, there may be an

evolutionarily stable strategic stage between them (that is an “ESS”: as for this concept, for example, see Maynard Smith, 1982).

Case II. In this case, S in Fig. 1 is the prey-vacant zone and $J_L \cup J_R$ is the prey-existing one. There is a gap without any prey in an isolated patch. The gap may be imaged as that by an ecological disturbance. From the obtained condition for the predator’s invasion, we can investigate the parameter dependency of the invasion and arrive at qualitatively similar results with those for case I.

As for the contribution of the location of the prey-vacant zone to the predator’s invasion, we can obtain the following.

CHARACTERISTIC II1. *The predator’s invasion is more likely to fail as the location of prey-vacant zone gets more central in the patch, independently of whether the patch boundary is reflecting or absorbing.*

We remark that, in the absorbing boundary case, the tendency is contrary between cases I and II. However, depending on the environmental richness in the patch, the location of prey-vacant zone loses its contribution to the predator’s invasion. As in case I, there is a stronger condition for each boundary case.

CHARACTERISTIC II2. *In the reflecting boundary case, if*

$$B \leq 1 - k, \tag{16}$$

then the predator’s invasion succeeds independently of any other conditions.

CHARACTERISTIC II3. *In the absorbing boundary case, if*

$$\left\{ \begin{array}{l} (1-k)\sqrt{\frac{\Gamma}{\Delta_p}} < \pi \\ -\frac{1}{k\sqrt{\Delta_p\Gamma}} \leq f_{tan}\left((1-k)\sqrt{\frac{\Gamma}{\Delta_p}}\right), \end{array} \right. \tag{17}$$

then the invasion fails independently of B.

This is obtained when $B \rightarrow 0$ for the condition of invasion failure.

In case II, the absorbing boundary does not bring any particular characteristics corresponding to Characteristic I4. Instead, the narrower the prey-vacant zone, the more likely the predator’s invasion success.

5. A Generalization. Results obtained in this paper are applicable to a general family of prey–predator systems. Let us consider the following type of such a system:

$$\frac{\partial H}{\partial t} = \delta(P) \frac{\partial^2 H}{\partial x^2} + F(P, H)H \quad \text{on } \Omega \quad (18)$$

$$\frac{\partial P}{\partial t} = G(P, H)P \quad \text{on } \mathbf{I}_p \quad (19)$$

$$P \equiv 0 \quad \text{on } \mathbf{I}_0,$$

where $\delta(P)$ is given by (3). The diffusion term in equation (18) is the same as in equation (1). F and G are functions of P and H such that:

- (A) F and G are C^1 on $[0, +\infty) \times [0, +\infty)$;
- (B) $G(K, 0) = 0$; K has a unique finite positive value;
- (C) $0 < G(0, 0)$;
- (D) $\partial G / \partial H < 0$;
- (E) $[\partial G / \partial P]_{H=0} \leq 0$;
- (F) $F(0, H) < 0$;
- (G) $F(K, 0) \geq 0$;
- (H) $0 \leq \partial F / \partial P$.

These assumptions define a family of F and G . Focusing on the predator's invasion, we can obtain a formal linearized system for equations (18) and (19) as we did in the previous section. Then it appears that the equilibrium $(H^*, P^*) = (0, 0)$ is globally unstable due to assumption (C). Besides, assumption (F) assures that an equilibrium such as $(H^*, P^*) = (\phi^*(x), 0)$ does not exist, where $0 < \text{Sup}_x \{\phi^*(x)\}$. With linearization around the equilibrium $(H^*, P^*) = (0, C^*(x))$, we obtain:

$$\frac{\partial h}{\partial t} = \delta(p) \frac{\partial^2 h}{\partial x^2} + F(C^*(x), 0)h \quad \text{on } \Omega \quad (20)$$

$$\frac{\partial p}{\partial t} = K \left\{ h \left(\frac{\partial G}{\partial H} \right)^* + p \left(\frac{\partial G}{\partial P} \right)^* \right\} \quad \text{on } \mathbf{I}_p \quad (21)$$

$$P \equiv 0 \quad \text{on } \mathbf{I}_0,$$

where

$$C^*(x) = \begin{cases} K & \text{on } \mathbf{I}_p \\ 0 & \text{on } \mathbf{I}_0. \end{cases}$$

In equation (21), $(\cdot)^*$ means the value for (H^*, P^*) . Equation (20) is practically independent of p and corresponds to (10). From assumptions (D) and (E), $p \rightarrow 0$

as $t \rightarrow \infty$ if $h \rightarrow 0$ as $t \rightarrow \infty$. Through the comparison between equations (10) and (20), we can find the following correspondences:

$$B \leftrightarrow \frac{F(0, 0)}{F(0, 0) - F(K, 0)} \quad (22)$$

$$\Gamma \leftrightarrow F(K, 0) - F(0, 0). \quad (23)$$

Assumptions (F) and (G) assure that the right-hand sides of the above correspondences are positive. Moreover, assumption (G) corresponds to $B < 1$. These correspondences can afford us to apply those results obtained for equations (1) and (2) to the system (18) and (19).

As for those results with respect to the position of \mathbf{I}_p and \mathbf{I}_0^* for equations (1) and (2) they are also the same for equations (18) and (19), because they have been obtained for any fixed set of parameters except for c and k . Further, for equations (18) and (19), it is likely that there may be a unique optimal size k of prey-existing zone for the predator's invasion success when $\delta_0 < \delta_p$ as mentioned in Characteristic I4.

As a whole, our results for equations (1) and (2) can be reliably extended for a more general system than (18) and (19). Since our main interest is in equations (1) and (2), we shall not consider further the system of (18) and (19) in this paper.

6. Discussion. We have analysed the relation between a prey's heterogeneous distribution and its predator's invasion success. It was shown that the spatial structure of prey distribution seriously affects the predator's invasion.

In case I when prey has a unique gregariousness, if the predator does not leak from the considered isolated region (i.e. the boundary is reflecting), the predator's invasion is more difficult as the gregariousness becomes more centrally located in the region. If the dissipation of the predator's population is hard at the boundary of the region (i.e. the boundary is absorbing), the invasion is more difficult as the prey gets distributed closer to the boundary. This result shows that the predator's invasion is influenced by the spatial position of the prey's gregariousness. However, when the quality of gregariousness is sufficiently rich or poor, the invasion succeeds or fails independently of the location. In such a case, in order to prevent the predator's outbreak, a reduction of its size may be effective, which makes its quality poorer. In the reflecting boundary case, it may also make the reduction more effective that it was for the part near to the boundary of the considered isolated region. This is because, after such a reduction, the position of gregariousness corresponds to having moved more centrally in the region. In the absorbing boundary case, involving the effect of population dissipation at the boundary,

an interesting feature is revealed: if the predator behaves such that it disperses faster in the prey-existing zone than in the prey-vacant one, there may be a unique size of prey-existing zone that makes the predator's invasion more likely to succeed. In such a case, to prevent the predator's outbreak, the gregariousness must be reduced or expanded in size. In the latter case, however, the wider distribution of prey can improve the predator's invasion success if the predator switches its behavioural strategy to disperse faster in the prey-vacant zone than in the prey-existing one. Therefore, as for the prey's distribution, the centrally concentrated patchy one is rather adaptable as a whole. Also in this case, the reduction of the part nearer to the boundary of the considered region is effective in preventing the predator's outbreak. In detail, however, such a reduction of gregariousness may affect the prey's reproductivity to make it become extinct. Thus, in reality, the degree of reducing the gregariousness should not be imprudently selected.

On the other hand, case II considers when the prey distribution had a spatial gap, for example, created by an ecological disturbance regime. Making use of our results, we can argue the effect of position and quality of such a gap on the predator's invasion. Analysis of the position concludes that the invasion is more likely to fail as the gap becomes located more centrally in the considered isolated region, independent of the boundary condition. According to this result, if defoliation is projected to prevent the outbreak of an insect in an isolated region, the effective defoliation has to take place in a middle part of the region. Of course, also in this case, the position of the gap makes no contribution to the predator's invasion if the prey-existing zone is sufficiently rich or poor. Besides, the predator's invasion becomes more difficult as the gap gets wider. Therefore, since a wider gap makes the quality of the prey-existing zone poorer, a sufficiently large gap prevents the predator's invasion, independently of its location. A gap sufficient to prevent the outbreak of predator has the smallest size when it is created in the centre of the considered isolated region.

The spatially heterogeneous distribution treated in this paper is one of the simplest types of mathematical models. However, the results show some interesting features to consider the effect of such heterogeneity on population dynamics. A spatial environmental structure was shown to significantly affect the predator's invasion of a prey-predator system.

By the way, this type of analysis can be applied to a competing two-species system, which corresponds to that investigated by Pacala and Roughgarden (1982). It is likely that some new features may be obtained by it (see Appendix B).

The spatial environmental structure is one of the environmental factors which can be easily changed by some artificial regimes. Whether the purpose of such an artificial change is to stabilize an ecosystem to conserve species or to

eliminate the immigration of a species to protect a present ecosystem, our results would give an implicit warning to make such a change with sufficient care to the spatially environmental structure around where it is done. Without such care, a spatially artificial change of environment might do serious damage to the present ecosystem. Any environmental project should be carried out with as much research as possible on the relation between the present ecosystem and the spatial environmental structure around it, such as those in Geographical Ecology (for instance, see MacArthur, 1972). It is expected that this paper will give some stimuli to such research.

Special thanks are due to Ms Hidemi Koito for her heartfelt encouragement. This work was supported in part by a cooperative agreement on Applied Mathematics and Mathematical Biology between Kyoto University and The University of Naples, and by the Ishizaka Foundation.

APPENDIX A

Instead of equation (10) itself, for convenience, we consider the following general kind of one-dimensional diffusion system (see Fig. 1):

$$\partial n / \partial t = \partial [d(x) \partial n / \partial x] / \partial x + r(x)n \quad \text{on } \Omega \quad (\text{A1})$$

$$\alpha n + \beta d(x) \partial n / \partial x = 0 \quad \text{on } \partial \Omega \quad (\text{A2})$$

$$d(x) = \begin{cases} d_e & \text{for } x \in \mathbf{J}_L, \mathbf{J}_R \\ d_s & \text{for } x \in \mathbf{S} \end{cases}$$

$$r(x) = \begin{cases} r_e & \text{for } x \in \mathbf{J}_L, \mathbf{J}_R \\ r_s & \text{for } x \in \mathbf{S} \end{cases},$$

where "n" is population density at point x , time t . $d(x)$ is the diffusion coefficient which is constant in each of \mathbf{J}_L , \mathbf{S} , and \mathbf{J}_R : d_e, d_s, d_e . $r(x)$ is the intrinsic growth rate which is also constant in each region: r_e, r_s, r_e . At the boundary $\partial \Omega$, condition (A2) is assumed, and we shall investigate only two special cases: (i) the reflecting boundary case (i.e. $\alpha = 0$), (ii) absorbing boundary case (i.e. $\beta = 0$). With the following results, we can easily derive the corresponding result for equation (10).

Since this system is linear, the population becomes extinct or increases infinitely at the limit $t \rightarrow \infty$. There is no stationary distribution except for the zero-solution.

Obviously, the population becomes extinct if the intrinsic growth rate is negative throughout Ω . Let us assume that $0 < \max(r_e, r_s)$. Moreover, in the reflecting boundary case, the population never becomes extinct if the growth rate is non-negative throughout Ω . Thus, we shall assume $\min(r_e, r_s) < 0$ in the reflecting boundary case. However, in the absorbing boundary case, even though the growth rate is positive throughout, population extinction is likely to occur. This is due to the population leakage from the boundary of patch. Equation (A1) can be solved by means of the variable separation method. That is, the solution can be written in the following form:

$$n(x, t) = \sum_{j=0}^{+\infty} \varphi_j(x) \cdot \exp(\lambda_j t), \quad (\text{A3})$$

where $\varphi_j(x)$ is the j th eigenfunction depending on the j th eigenvalue λ_j of our system. Eigenvalues of our system are distinct and all real because the system is regular and self-adjoint (Berg and McGregor, 1966). If all eigenvalues are negative, as easily seen from equation (A3), the population becomes extinct at $t \rightarrow \infty$ independently of its initial distribution. Estimating the eigenvalue λ_j , we shall derive the necessary and sufficient condition that all eigenvalues are negative. If at least one eigenvalue is positive, the population increases infinitely.

In order to derive the condition that all eigenvalues are negative, at first, we shall obtain the characteristic equation which determines eigenvalues, making use of boundary conditions of Ω and continuity conditions at discontinuous boundaries between \mathbf{J}_L and \mathbf{S} , and between \mathbf{S} and \mathbf{J}_R . Next, by investigating the characteristic equation, we shall derive the search condition. The method of analysis is basically the same as that of Nagylaki (1975).

Reflecting boundary case. In this case, λ_j is given as a root λ of the following characteristic equation:

$$\mu^s d_s \cdot \cot\{kL\mu^s\} = \{(r_e - r_s) d_s / \mu^e d_e - \mu^e d_s\} \cdot f_{\tan}\{(1-k)L\mu^e\} + \mu^e d_e \cdot f_{\cot}\{(1-k)L\mu^e\}, \quad (\text{A4})$$

where

$$\begin{aligned} \mu^e &= \sqrt{(r_e - \lambda) / d_e} \\ \mu^s &= \sqrt{\{r_s - r_e + d_e \cdot (\mu^e)^2\} / d_s} \\ f_{\tan}(z) &= [\tan\{c \cdot z\} + \tan\{(1-c) \cdot z\}]^{-1} \\ f_{\cot}(z) &= [\cot\{c \cdot z\} + \cot\{(1-c) \cdot z\}]^{-1}. \end{aligned}$$

For convenience, we shall also define the following:

$$\begin{aligned} f_{\tanh}(z) &= [\tanh\{c \cdot z\} + \tanh\{(1-c) \cdot z\}]^{-1} \\ f_{\coth}(z) &= [\coth\{c \cdot z\} + \coth\{(1-c) \cdot z\}]^{-1}. \end{aligned}$$

The characteristic equation (A4) has an infinite number of discrete roots with respect to μ^e . Hereafter we shall use the following dimensionless variables:

$$\begin{aligned} D &= d_e / d_s; \quad R = r_e / r_s \\ M &= (kL / \pi) \sqrt{|r_s| / d_s}; \quad E = \{(1-k)L / \pi\} \sqrt{|r_e| / d_e}. \end{aligned}$$

The existence of positive root λ of equation (A4) can be estimated, and consequently the necessary and sufficient condition of non-existence of positive root λ can be derived:

(i) $r_s < 0 < r_e$

$$\begin{cases} E < \frac{1}{2}(1-c) \\ M < \sup_z \{z\} \end{cases} \text{ for } 0 < \forall x < z < \frac{1}{2}(1-c), \sqrt{D \cdot g(x)} \cdot \coth\{\pi M \sqrt{|R| \cdot g(x)}\} \leq Q_{r_e}(x)$$

$$\begin{aligned} Q_{r_e}(x) &= E\{(R-1)/Rx - x\} \cdot f_{\tan}(\pi x) + (Dx/E) \cdot f_{\cot}(\pi x) \\ g(x) &= 1 - 1/R - x^2/E^2 \end{aligned}$$

(ii) $r_e < 0 < r_s$

$$\begin{cases} M < 1 \\ f_{\tanh}(\pi E) + RD \cdot f_{\coth}(\pi E) \leq \sqrt{|R|D} \cdot \cot\{\pi M\}. \end{cases}$$

Absorbing boundary case. The characteristic equation is

$$-\mu^s d_s \cdot \cot\{kL\mu^s\} = \{(r_e - r_s) d_s / \mu^e d_e - \mu^e d_s\} \cdot f_{\cot}\{(1-k)L\mu^e\} + \mu^e d_e \cdot f_{\tan}\{(1-k)L\mu^e\}. \tag{A5}$$

We use the same notation as before. From equation (A5), the condition for non-existence of positive root λ can be obtained:

(i) $r_s < 0 < r_e$

$$\begin{cases} E < 1/(1-c) \\ M < \sup_z \{z\} \text{ for } 0 < \forall x < z < 1/(1-c), -\sqrt{D \cdot g(x)} \cdot \coth\{\pi M \sqrt{|R| \cdot g(x)}\} \leq Q_{ab}(x) \end{cases}$$

$$Q_{ab}(x) = E\{(R-1)/Rx - x\} \cdot f_{\cot}(\pi x) + (Dx/E) \cdot f_{\tan}(\pi x)$$

$$g(x) = 1 - 1/R - x^2/E^2$$

(ii) $0 \leq r_e, r_s$

$$\begin{cases} E < 1 \\ M < 1 \\ f_{\cot}(\pi E) - RD \cdot f_{\tan}(\pi E) \leq \sqrt{RD} \cdot \cot\{\pi M\} \end{cases}$$

(iii) $r_e < 0 < r_s$

$$\begin{cases} M < 1 \\ f_{\coth}(\pi E) + RD \cdot f_{\tanh}(\pi E) < \sqrt{|R|D} \cdot \cot\{\pi M\}. \end{cases}$$

The results obtained in the main text are easily derived from the above results, considered the correspondence between equations (A1) and (10).

APPENDIX B

In this Appendix, applying our method of analysis, we treat a competing two-species system which corresponds to that investigated by Pacala and Roughgarden (1982):

$$\partial N_1 / \partial t = D_1 \partial^2 N_1 / \partial x^2 + r_1(1 - N_1/K_1 - \alpha_{12}N_2/K_1)N_1 \tag{B1}$$

$$\partial N_2 / \partial t = \partial [D_2(x) \partial N_2 / \partial x] / \partial x + r_2\{1 - N_2/K_2(x) - \alpha_{21}N_1/K_2(x)\}N_2 \tag{B2}$$

$$D_2(x) = \begin{cases} D_{2e} & \text{on } \mathbf{J}_L \text{ and } \mathbf{J}_R \\ D_{2s} & \text{on } \mathbf{S} \end{cases} \tag{B3a}$$

$$\tag{B3b}$$

$$K_2(x) = \begin{cases} K_{2e} & \text{on } \mathbf{J}_L \text{ and } \mathbf{J}_R \\ K_{2s} & \text{on } \mathbf{S}, \end{cases} \tag{B4a}$$

$$\tag{B4b}$$

where Ω , \mathbf{S} , \mathbf{J}_L , and \mathbf{J}_R are defined as before. Other symbols are defined as follows:

- $N_i(x, t)$: population density of species i at a position x , time t
- D_1 : diffusion coefficient of species 1, a positive constant independent of position
- $D_2(x)$: diffusion coefficient of species 2, depending on position as (B3)
- r_i : intrinsic growth rate of species i , a positive constant independent of position

- K_1 : carrying capacity of species 1, a positive constant independent of position
- $K_2(x)$: carrying capacity of species 2, depending on position as (B4)
- α_{ij} : coefficient representing inter-specific competition effect.

Species 1 is assumed to be totally insensitive to the environmental heterogeneity in the patch. Our following analysis corresponds to the analysis on finding (I) in Pacala and Roughgarden (1982). They obtained the following result: "The invasion of species 2 succeeds if the suitable region is larger than a threshold minimum."

The condition of invasion success of species 2 into such an environment is considered where only species 1 exists, taking its stationary distribution in the patch. The reflecting boundary is assumed, when the stationary distribution of species 1 is uniform in the patch: $N_1^* = K_1$. Pacala and Roughgarden (1982) analysed only the reflecting boundary case. The linearized system around the equilibrium point $(N_1^*, N_2^*) = (K_1, 0)$ is given by:

$$\partial n_1 / \partial t = D_1 \partial^2 n_1 / \partial x^2 - r_1 n_1 - r_1 \alpha_{12} n_2 \tag{B5}$$

$$\partial n_2 / \partial t = \partial [D_2(x) \partial n_2 / \partial x] / \partial x + S(x) n_2 \tag{B6}$$

$$S(x) = \begin{cases} S_e \equiv r_2(1 - \alpha_{21} K_1 / K_{2e}) & \text{on } J_L \text{ and } J_R \\ S_s \equiv r_2(1 - \alpha_{21} K_1 / K_{2s}) & \text{on } S. \end{cases}$$

As in Pacala and Roughgarden (1982), it is assumed that $K_{2e}/K_1 < \alpha_{21} < K_{2s}/K_1$. This assumption means that the region S is "suitable" for the invasion of species 2 but the other is "unsuitable" for it, in terms of the possibility of its invasion success in the absence of diffusion. Note that $n_1 \rightarrow 0$ as $t \rightarrow \infty$, because equation (B5) has only negative growth terms. Therefore, the perturbation of species 1 always damps down and the distribution of species 1 returns to N_1^* .

Our analysis can show that the invasion of species 2 is more likely to fail as the suitable region gets more centrally located in the patch. Therefore, we find that Pacala and Roughgarden (1982) investigated the case when the invasion of species 2 is the most likely to succeed with respect to the location of the suitable region. Thus, even if the size of the suitable region is larger than the threshold minimum given by their analysis, it is possible that the invasion fails in our system, depending on the location of the suitable region.

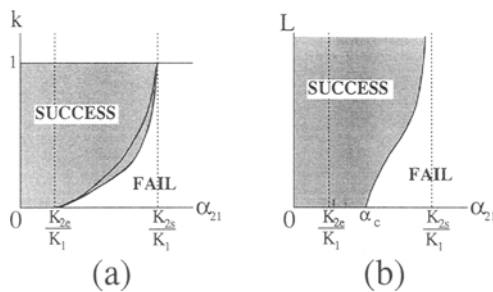


Figure 5. The parameter region of invasion success of species 2 for a fixed set of other parameters: (a) in the $\alpha_{21}-k$ space; (b) in the $\alpha_{21}-L$ space. The arrow indicates how the curve moves as c increases from 0 to $\frac{1}{2}$. The critical curve by Pacala and Roughgarden (1982) is always below the lowest critical curve for any size of suitable region. In (a), the top curve in the region of invasion success is given by equation (B7) in the text, and the bottom curve is a critical curve for a fixed set of other parameters. In (b), the critical curve has the asymptote $\alpha_{21} = K_{2s}/K_1$. The critical value α_c given by equation (B8) increases from K_{2e}/K_1 to K_{2s}/K_1 as k increases from 0 to 1.

Further we can find a critical relation:

$$K_{2s}(\alpha_{21} - K_{2e}/K_1) / \{\alpha_{21}(1 - K_{2e}/K_{2s})\} \leq k. \quad (\text{B7})$$

As α_{21} changes from K_{2e}/K_1 to K_{2s}/K_1 , the left-hand side of condition (B7) monotonically changes from 0 to 1. If the size k of the suitable region satisfies relation (B7), then the invasion succeeds independently of the other parameters. As α_{21} changes from K_{2e}/K_1 to K_{2s}/K_1 , the invasion of species 2 is less likely to succeed. And it succeeds for any α_{21} less than the following critical value, say α_c :

$$\alpha_c \equiv \{k(K_1/K_{2s}) + (1-k)(K_1/K_{2e})\}^{-1}, \quad (\text{B8})$$

α_c increases from K_{2e}/K_1 to K_{2s}/K_1 as k increases from 0 to 1. On the other hand, it can be shown that, with α_{21} beyond α_c , there is a critical size of the whole patch. Only when the patch size is greater than the critical size, does the invasion of species 2 succeed. Consequently, we get Fig. 5. Figure 5a shows that the size effect of the suitable region is significant when α_{21} is small; that is, when the competition is mild between two species. Moreover, the effect of competition is more sensitive when the suitable region is large than when it is small. Figure 5b shows that the invasion of species 2 succeeds independently of the patch size if the competition is milder for species 2 than a critical degree.

LITERATURE

- Allen, L. J. S. 1983a. Persistence and extinction in Lotka–Volterra reaction–diffusion equations. *Math. Biosci.* **65**, 1–12.
- Allen, L. J. S. 1983b. Persistence and extinction in single-species reaction–diffusion models. *Bull. math. Biol.* **45**, 209–227.
- Allen, L. J. S. 1987. Persistence, extinction, and critical patch number for island populations. *J. math. Biol.* **24**, 617–625.
- Berg, P. W. and J. L. McGregor. 1966. *Elementary Partial Differential Equations*. San Francisco: Holden-Day.
- Brown, J. H. 1971. Mammals on mountain tops: nonequilibrium insular biogeography. *Am. Nat.* **104**, 547–559.
- Dubois, D. M. 1975a. Simulation of the spatial structuration of a patch of prey–predator plankton populations in the Southern Bight of the North Sea. *Proc. Liege Colloq. Ocean Hydrodyn. 6th Mem. Soc. Roy. Sci. Liege VII*, 75–82.
- Dubois, D. M. 1975b. A model of patchiness for prey–predator plankton populations. *Ecol. Modelling* **1**, 67–80.
- Guo Ben-Yu and B. D. Sleeman. 1985. Spatial patterning of the spruce budworm in the presence of defoliation. In: *Lecture Notes in Mathematics*, Vol. 1151, B. D. Sleeman and R. J. Jarvis (Eds), pp. 192–203. Berlin: Springer-Verlag.
- Guo Ben-Yu, A. R. Mitchell and B. D. Sleeman. 1983. Spatial patterning of the spruce budworm in a circular region. *UDDM Report DE 83-5*.
- Gurney, W. S. C. and R. M. Nisbet. 1975. The regulation of inhomogeneous populations. *J. theor. Biol.* **52**, 441–457.
- Harper, K. T., D. C. Freeman, Ostler and L. G. Kikoft. 1978. The flora of Great Basin mountain ranges: diversity, sources and dispersal ecology. *Great Basin Nat. Mem.* **2**, 81–103.
- Kierstead, H. and L. B. Slobodkin. 1953. The size of water masses containing plankton blooms. *J. mar. Res.* **12**, 141–147.
- Levin, S. A. 1974. Dispersion and population interactions. *Am. Nat.* **108**, 207–228.
- Levin, S. A. 1976a. Population dynamic models in heterogeneous environments. *Ann. Rev. Ecol. Syst.* **7**, 287–310.

- Levin, S. A. 1976b. Spatial patterning and the structure of ecological communities. In: *Some Mathematical Questions in Biology, Lectures on Mathematics in the Life Sciences*, Vol. 7, S. A. Levin (Ed.), pp. 1–36. Providence, RI: Ann. Math. Soc.
- Levin, S. A. 1986. Population models and community structure in heterogeneous environments. In: *Mathematical Ecology: An Introduction, Biomathematics*, Vol. 17, T. G. Hallam and S. A. Levin (Eds), pp. 295–320. Berlin: Springer-Verlag.
- Ludwig, D., D. G. Aronson and H. F. Weinberger. 1979. Spatial patterning of the spruce budworm. *J. math. Biol.* **8**, 259–263.
- MacArthur, R. H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. New York: Harper & Row.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- McMurtrie, R. 1978. Persistence and stability of single-species and prey–predator systems in spatially heterogeneous environments. *Math. Biol.* **39**, 11–51.
- Mimura, M., M. Tabata and Y. Hosono. 1979a. Multiple solutions of two-point boundary value problems of Neumann type with a small parameter. Researching Report 1, Konan Univ.
- Mimura, M., Y. Nishiura and M. Yamaguti. 1979b. Some diffusive prey and predator systems and their bifurcation problems. In: *Bifurcation Theory and Applications in Scientific Disciplines*, O. Gurel and O. E. Röessler (Eds), pp. 490–510. New York: Ann. N.Y. Acad. Sci.
- Nagylaki, T. 1975. Conditions for the existence of clines. *Genetics* **80**, 595–615.
- Namba, T. 1980. Density-dependent dispersal and spatial distribution of a population. *J. theor. Biol.* **86**, 351–363.
- Nayfeh, A. H. 1973. *Perturbation Methods*. New York: John Wiley.
- Okubo, A. 1980. *Diffusion and Ecological Problems: Mathematical Models*. New York: Springer-Verlag.
- Okubo, A. 1982. Critical patch size for plankton and patchiness. In: *Lecture Notes in Biomathematics*, Vol. 54, S. A. Levin (Ed.), pp. 456–477. Berlin: Springer-Verlag.
- Pacala, S. W. and J. Roughgarden. 1982. Spatial heterogeneity and interspecific competition. *Theor. Pop. Biol.* **21**, 92–113.
- Platt, T. and K. L. Denman. 1975. A general equation for the mesoscale distribution of phytoplankton in the sea. *Mem. Soc. Roy. Sci. Liege* **7**, 31–42.
- Powell, T. and P. J. Richerson. 1985. Temporal variation, spatial heterogeneity, and competition for resources in plankton system: a theoretical model. *Am. Nat.* **125**, 431–464.
- Rand, A. S. and E. E. Williams. 1969. The anoles of La Palma: aspects of their ecological relationships. *Breviora* **327**, 1–18.
- Roughgarden, J. 1979. *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. New York: Macmillan.
- Segel, L. A. and S. A. Levin. 1976. Application of nonlinear stability theory to the study of the effects of diffusion on predator–prey interactions. In: *Topics in Statistical Mechanics and Biophysics: A Memorial to Julius L. Jackson*, R. A. Piccirelli (Ed.), pp. 123–152. Proc. AIP Conf.
- Seno, H. 1989. The effect of a singular patch on population persistence in a multi-patch system. *Ecol. Modelling* **43**, 271–286.
- Shigesada, N. 1984. Spatial distribution of rapidly dispersing animals in heterogeneous environments. In: *Lecture Notes in Biomathematics*, S. A. Levin and T. G. Hallam (Eds), pp. 478–491. Berlin: Springer-Verlag.
- Shigesada, N. and J. Roughgarden. 1982. The role of rapid dispersal in the population dynamics of competition. *Theor. Pop. Biol.* **21**, 353–373.
- Shigesada, N., K. Kawasaki and E. Teramoto. 1979. Spatial segregation of interacting species. *J. theor. Biol.* **79**, 83–99.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**, 196–218.
- Steele, J. H. 1974a. Spatial heterogeneity and population stability. *Nature* **83**, 248.
- Steele, J. H. 1974b. Stability of plankton ecosystems. In: *Ecological Stability*, M. B. Usher and M. H. Williamson (Eds), pp. 179–191. London: Chapman & Hall.

- Steele, J. H. 1975. *The Structure of Marine Ecosystems*. Cambridge, MA: Harvard University Press.
- Teramoto, E. and H. Seno. 1988. Modeling of biological aggregation patterns. In: *Biomathematics and Related Computational Problems*, R. M. Ricciardi (Ed.), pp. 409–419. Dordrecht: Kluwer Academic Publishers.
- Wiens, J. A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7, 81–120.
- Wroblewski, J. S., J. J. O'Brien and T. Platt. 1975. On the physical and biological scales of phytoplankton patchiness in the ocean. *Mem. Soc. Roy. Sci. Liege* 7, 43–57.

Received 19 April 1990

Revised 19 June 1990