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INTEGRODIFFERENCE MODELS FOR PERSISTENCE IN FRAGMENTED HABITATS

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Integrodifference models of growth and dispersal are analyzed on finite domains to investigate the effects of emigration, local growth dynamics and habitat heterogeneity on population persistence. We derive the bifurcation structure for a range of population dynamics and present an approximation that allows straightforward calculation of the equilibrium populations in terms of local growth dynamics and dispersal success rates. We show how population persistence in a heterogeneous environment depends on the scale of the heterogeneity relative to the organism's characteristic dispersal distance. When organisms tend to disperse only a short distance, population persistence is dominated by local conditions in high quality patches, but when dispersal distance is relatively large, poor quality habitat exerts a greater influence. © 1997 Society for Mathematical Biology

1. Introduction. This study is motivated by the need to understand the role of dispersal and habitat quality on population dynamics and persistence in fragmented environments for organisms which reproduce and disperse during separate, discretely spaced time periods. Despite the tendency of most organisms to reproduce and disperse during separate time intervals, the most extensively developed and applied models of population growth and dispersal are reaction–diffusion equations, which assume that reproduction and dispersal occur simultaneously and continuously (see, e.g. Skellam, 1951; Ludwig *et al.*, 1979; Murray *et al.*, 1986; Lubina and Levin, 1988; Freedman *et al.*, 1989; Andow *et al.*, 1990; Holmes *et al.*, 1994). However, many plants and invertebrates have sessile adult stages and nonoverlapping generations; dispersal is undertaken by seeds or larvae during a specific time period when environmental conditions are favorable (see, e.g. Richter, 1970; Augspurger and Hogan, 1983; Berger, 1983; Hobbs *et al.*, 1992; Howe and Smallwood, 1982). The “year” of these organisms can be divided into a growth period during which the primary population processes are reproduction and growth and a dispersal period during which the primary population process is the permanent movement of individuals from one location to another.

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Integrodifference equations are discrete-time models capable of separating growth and dispersal phases. Slatkin (1973, 1975, 1978) formulated integrodifference equation models to study gene flow and selection and spatial patterning of polygenic characters. Lui (1982a, b, 1983, 1985, 1986, 1989a, b) and Weinberger (1978, 1982) studied the traveling wave properties of integrodifference and other types of discrete-time models of gene flow. The paper of Kot and Schaffer (1986) appears to be the first application of integrodifference equations specifically to problems in population ecology. Since then, integrodifference equations have been used to study dispersal-driven instability in predator-prey systems (Kot, 1989; Neubert *et al.*, 1995), traveling waves (Kot, 1992; Kot *et al.*, 1996), age-structured populations (Veit and Lewis, 1996), the effects of different dispersal strategies in both spatially and temporally variable environments (Hardin *et al.*, 1988a, b, 1990), plant growth and dispersal (Andersen, 1991) and long-term transient dynamics (Hastings and Higgins, 1994).

To use integrodifference equations in studying population persistence in fragmented habitats, we utilize finite and patchy spatial domains to reflect the observation that habitat fragmentation reduces expansive areas of suitable habitat into small remnant patches in which the boundary strongly influences population processes (Simberloff and Abele, 1982; Janzen, 1983, 1986; Harris, 1984, 1988; Wilcox and Murphy, 1985; Newmark, 1991; Saunders *et al.*, 1991). The following questions are addressed in this paper: (1) How does the qualitative behavior of local growth dynamics affect bifurcation and solution structure of integrodifference equations in the presence of dispersal loss from isolated habitat patches? (2) Is there a straightforward way to determine equilibrium population density and distribution if local growth conditions and dispersal success are known? (3) How does persistence in heterogeneous environments depend on spatial scales of dispersal and fragmentation? Section 2 presents analysis of scalar integrodifference equations on bounded domains using bifurcation theory and classical results on positive operators. Section 3 investigates in more detail how dispersal success and habitat quality affect population persistence in fragmented environments.

2. The Model.

2.1. *Formulation.* The general scalar integrodifference equation has the form

$$N_{t+1}(\mathbf{x}) = \int_{\Omega} k(\mathbf{x}, \mathbf{y}) f(N_t(\mathbf{y}); \mathbf{y}) d\mathbf{y}, \quad (1)$$

where $N_t(\mathbf{x})$ is the population density at a point $\mathbf{x} \in \Omega$ at the end of the dispersal period in year t , Ω is a subset of \mathfrak{R}^n and $k(\mathbf{x}, \mathbf{y})$ is a density

function governing the probability of successful dispersal from a point $y \in \Omega$ to x . Population growth is modeled by the nonnegative growth function $f(N) \equiv g(N)N$, where $g(N)$ is the per capita growth rate. Three commonly used growth maps are the Beverton–Holt (Beverton and Holt, 1957) model

$$f(N) = \frac{rN}{1 + [(r - 1)N/K]}, \quad (2)$$

the Ricker (1954) equation

$$f(N) = N \exp \left[\rho \left(1 - \frac{N}{K} \right) \right] \quad (3)$$

and the Allee growth model (Murray, 1989)

$$f(N) = \frac{(\rho^2 + 1)N^2}{1 + \rho^2 N^2 / K^2}. \quad (4)$$

Growth rate parameters in these models are given by r and ρ , and the carrying capacity of the environment is given by K .

The Beverton–Holt model is representative of compensatory growth; the nontrivial steady state K is globally stable for all $r > 1$. The Ricker model represents overcompensatory growth, which can occur in populations with discrete generations if recruitment is severely limited at very high population densities (see, e.g. Nicholson, 1954; Harcourt, 1971; Cushing, 1981). The equilibrium K loses stability via a period-doubling bifurcation as ρ exceeds 2. Further increases in ρ result in a series of period-doubling bifurcations leading to chaos (see May, 1974, 1975, 1976; Li and Yorke, 1975; Stefan, 1977; Li *et al.*, 1982). The third map exhibits an Allee effect or depensatory growth, which models the net population decline experienced by some organisms when population densities are very low (Dennis, 1989; Murray, 1989). The Allee model has a stable equilibrium $N_{*s} = K$ and an unstable equilibrium $N_{*u} = K/\rho^2$ for all $\rho > 1$. This unstable equilibrium represents a threshold population density above which the population persists and below which it goes extinct. The zero solution is stable for all positive parameter values. A comparison of these three models in the $N_t - N_{t+1}$ plane representing the discrete dynamical system is given in Fig. 1.

Dispersal is modeled by integration against the dispersal kernel $k(x, y)$, which is a nonnegative density function governing the probability that an individual at the point y at the beginning of the dispersal period has successfully dispersed and settled at the point x at the end of the dispersal

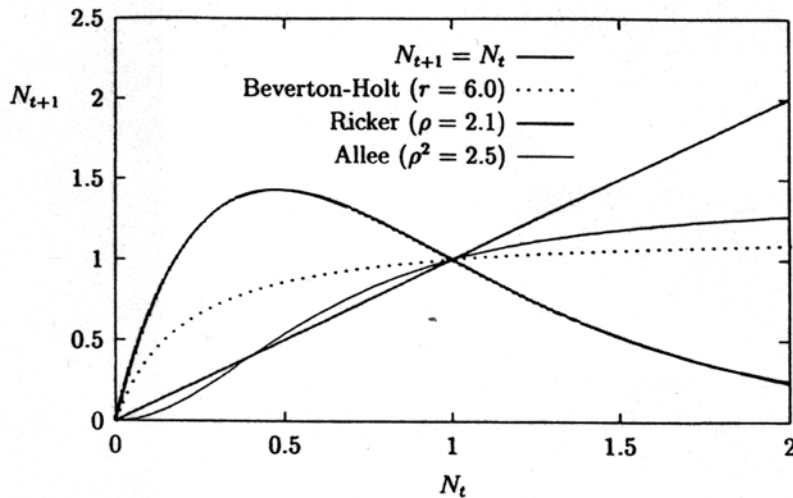


Figure 1. Comparison of normalized ($K = 1$) Beverton-Holt, Ricker and Allee growth functions.

period. It is assumed that no individuals can immigrate into Ω from outside, but dispersers may emigrate from Ω . Dispersal kernels may be constructed from either observational data or from a dispersal model describing movement, settlement, mortality and emigration of individuals during dispersal (Neubert *et al.*, 1995; Van Kirk, 1995). For example, the commonly used Laplace kernel

$$k(x, y) = \frac{a}{2} \exp(a|x - y|) \quad (5)$$

can be derived from assumptions that dispersers move randomly and settle at a constant rate during a sufficiently long dispersal period (Broadbent and Kendall, 1953; Williams, 1961). In one spatial dimension, the mean dispersal distance, given in terms of the diffusion coefficient D and the settling rate α , is simply $a = \sqrt{\alpha/D}$ (Neubert *et al.*, 1995). Alternative assumptions about movement, settlement, mortality and emigration lead to a variety of different kernels (Neubert *et al.*, 1995; Van Kirk, 1995). Emigration from an isolated patch and inability to encounter another suitable patch may cause loss of dispersers (Henderson *et al.*, 1985; Lefkovitch and Fahrig, 1985; Forrest *et al.*, 1988; Doak, 1987; Lamberson *et al.*, 1992; Bennett *et al.*, 1994). When dispersal is passive and dispersers do not interact strongly with habitat patch boundaries (for example, seeds blowing in the wind) a kernel initially derived over an infinite domain can simply be applied to those subsets suitable for settlement and subsequent reproduction. For example, the Laplace kernel (5) is truncated to a finite domain of length \hat{L} if all dispersers settling outside of the interval die because of unsuitable environmental conditions. The resulting dimensionless kernel

has the same form as equation (5) with the parameter a replaced by the effective domain length $L \equiv \hat{L}a$, which is a measure of the organism's characteristic dispersal distance relative to domain size.

We define the dispersal success function by

$$s(y) = \int_{\Omega} k(x, y) dx, \quad (6)$$

which gives the probability that an individual starting dispersal at y is settled in Ω at the end of the dispersal period. Average dispersal success is defined by

$$S \equiv \frac{1}{V_{\Omega}} \int_{\Omega} s(y) dy, \quad (7)$$

where V_{Ω} is the volume of Ω . In the absence of dispersal-specific mortality, loss of dispersers from a finite habitat patch surrounded by unsuitable habitat is due to emigration outside of the patch. Dispersal success then becomes a function of effective domain size. For example, dispersal success for the truncated Laplace kernel is given by

$$s(y; L) = 1 - \exp\left(-\frac{L}{2}\right) \cosh L\left(y - \frac{1}{2}\right) \quad (8)$$

and average dispersal success by

$$S(L) = 1 - \frac{1 - \exp(-L)}{L}. \quad (9)$$

Graphs of these functions are shown in Figs. 2 and 3. In general, as average dispersal distance increases relative to domain size, dispersal success de-

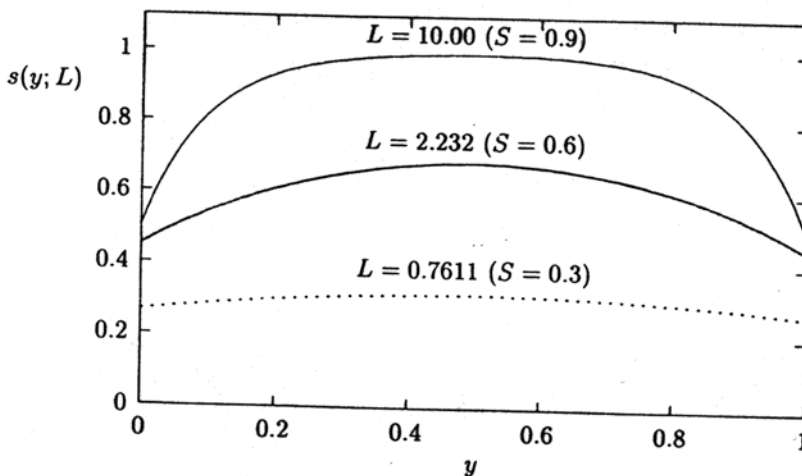


Figure 2. Dispersal success functions for the truncated Laplace kernel for various values of effective domain length.

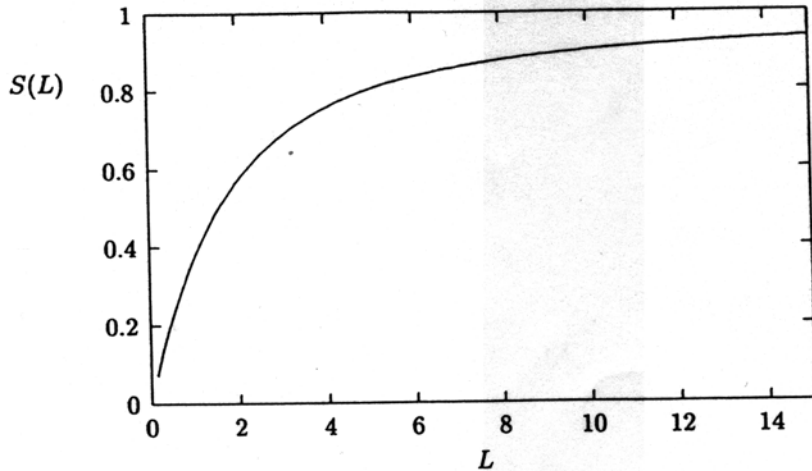


Figure 3. Average dispersal success rate versus effective domain length for the truncated Laplace kernel.

creases, since dispersers are more likely to emigrate from the domain. It is also possible to construct kernels on bounded domains from active dispersal models that incorporate physical or psychological factors affecting a disperser's ability or willingness to cross habitat patch boundaries (see Van Kirk, 1995, for this approach). Dispersal success for these kernels depends on dispersers' behavior at the boundary in addition to effective domain size.

To focus on the relationships between habitat quality and quantity, dispersal success and population persistence and size, a number of biological assumptions will be made unless otherwise stated. These are that (i) the habitat is finite (Ω is a closed, bounded subset of \mathfrak{R}^n); (ii) it is possible for an individual to move from any point (except possibly one on the boundary) in the habitat to any other point in the habitat during the dispersal period (for almost every $\mathbf{x}, \mathbf{y} \in \Omega$, $k(\mathbf{x}, \mathbf{y}) > 0$); (iii) loss of individuals during the dispersal process is due only to emigration; (iv) population growth is finite even at arbitrarily large population densities ($f(N; \mathbf{y}) = Ng(N; \mathbf{y})$ is bounded above for all $N \geq 0$ and $\mathbf{y} \in \Omega$, implying that $\lim_{N \rightarrow \infty} g(N) = 0$); (v) the per capita growth rate attains its maximum at arbitrarily low densities and decreases with increasing population density ($g'(N; \mathbf{y}) < 0$ for all $N \geq 0$ and for all $\mathbf{y} \in \Omega$); and (vi) the maximum per capita growth rate may be a function of location in the habitat but is always strictly positive at any given location ($g(0; \mathbf{y})$ is bounded away from zero). The Beverton-Holt and Ricker growth functions satisfy these conditions; the Allee growth function does not satisfy condition (v).

It is convenient to work in the real Hilbert space $L_2(\Omega)$ so that both the linear dispersal operator

$$\mathcal{K}\phi \equiv \int_{\Omega} k(\mathbf{x}, \mathbf{y}) \phi(\mathbf{y}) \, d\mathbf{y} \quad (10)$$

and the nonlinear Hammerstein operator

$$\mathcal{A}\phi \equiv \int_{\Omega} k(\mathbf{x}, \mathbf{y}) f(\phi(\mathbf{y}); \mathbf{y}) \, d\mathbf{y} \quad (11)$$

map $L_2(\Omega)$ into $L_2(\Omega)$. Because biologically meaningful solutions will be nonnegative, it is useful to consider such solutions as elements of the cone K_+ of nonnegative $L_2(\Omega)$ functions (see Krein and Rutman, 1950, or Krasnoselskii, 1964). The foregoing assumptions imply the following properties, which follow from theorems of Krasnoselskii (1964) and Krasnoselskii and Zabreiko (1984).

Property 1. The nonlinear operator $\mathcal{A}: L_2(\Omega) \mapsto L_2(\Omega)$ as defined by (11) is completely continuous.

Property 2. The nonlinear operator \mathcal{A} is strongly Fréchet differentiable with respect to the cone K_+ at $N=0$, and its Fréchet derivative is the completely continuous linear operator

$$\mathcal{B}\phi \equiv \mathcal{A}'(0)\phi = \int_{\Omega} k(\mathbf{x}, \mathbf{y}) \frac{\partial f}{\partial N}(0; \mathbf{y}) \phi(\mathbf{y}) \, d\mathbf{y}. \quad (12)$$

Property 3. The nonlinear operator \mathcal{A} has a strong asymptotic derivative with respect to the cone K_+ , which is the completely continuous linear operator given by

$$\mathcal{A}'(\infty)\phi = \int_{\Omega} \lim_{N \rightarrow \infty} k(\mathbf{x}, \mathbf{y}) \frac{1}{N} f(N(\mathbf{y}); \mathbf{y}) \phi(\mathbf{y}) \, d\mathbf{y} \equiv 0. \quad (13)$$

See Van Kirk (1995) for details.

2.2. Linear analysis. We first briefly review the linear analysis of equilibrium solutions to equation (1) as detailed in Kot and Schaffer (1986) and Hardin *et al.* (1990). Adopting the definition of \mathcal{A} given above, the integrodifference equation (1) may be expressed as the operator equation

$$N_{t+1}(\mathbf{x}) = \mathcal{A}N_t. \quad (14)$$

An equilibrium solution to (14) is a fixed point of the nonlinear operator \mathcal{A} , that is, a solution $N_*(\mathbf{x})$ of the equation

$$\mathcal{A}N_*(\mathbf{x}) \equiv \int_{\Omega} k(\mathbf{x}, \mathbf{y}) f(N_*(\mathbf{y}); \mathbf{y}) \, d\mathbf{y} = N_*(\mathbf{x}). \quad (15)$$

An equilibrium solution is locally stable if the spectral radius $\rho_\sigma(\mathcal{A}'(N_*))$ of the Fréchet derivative $\mathcal{A}'(N_*)$ is less than 1 and unstable if $\rho_\sigma(\mathcal{A}'(N_*)) > 1$. Because of the assumption that $f(0; \cdot) = 0$, the identically zero function is an equilibrium solution of equation (1). The zero solution is locally stable when the spectral radius of the linear operator \mathcal{B} (equation (12)) is less than 1 and locally unstable when $\rho_\sigma(\mathcal{B}) > 1$.

Under assumptions nearly identical to those given above, Hardin *et al.* (1988a, b, 1990) showed that not only is the zero solution unstable when $\rho_\sigma(\mathcal{B}) > 1$, but also that equation (1) has a nonnegative, nonzero equilibrium solution if and only if $\rho_\sigma(\mathcal{B}) > 1$. They also showed that when $f(N; \cdot)$ is monotonically increasing and bounded above, as with Beverton–Holt dynamics, the nontrivial equilibrium is globally stable when $\rho_\sigma(\mathcal{B}) > 1$, and the zero solution is globally stable otherwise. Under other assumptions, the nontrivial equilibrium is shown to be locally stable for some range of values of $\rho_\sigma(\mathcal{B})$ (Hardin *et al.*, 1988a, b, 1990).

The main bifurcation result of this paper draws on the general theory of bifurcation from the largest eigenvalue of the linear operator

$$\mathcal{B}\phi \equiv \int_{\Omega} k(\mathbf{x}, \mathbf{y}) \frac{\partial f}{\partial N}(0; \mathbf{y}) \phi(\mathbf{y}) \, d\mathbf{y}. \quad (16)$$

To apply this theory, it must first be shown that this operator possesses a simple eigenvalue of maximum modulus. Because of the positivity of $f'(0; \mathbf{y})$ and the dispersal kernel, the operator \mathcal{B} leaves invariant the cone K_+ of nonnegative L_2 functions. Thus by the classical theorem of Krein and Rutman (1950), \mathcal{B} has a positive eigenvalue corresponding to a nonnegative eigenvector. Furthermore, this eigenvalue is simple, is strictly larger in magnitude than all other eigenvalues and its eigenfunction is the only nonnegative eigenfunction of \mathcal{B} . The results follow from theorems of Krasnoselskii (1964), which require demonstration that for a fixed nonzero $u_0 \in K_+$ and any nonnegative $u \in K_+$, there exist j , $\alpha > 0$ and $\beta > 0$ such that $\alpha u_0 \leq \mathcal{B}^j u \leq \beta u_0$. This condition is satisfied because of the positivity and continuity of \mathcal{B} .

Property 4. Under the assumptions of this paper, the linear operator

$$\mathcal{B}\phi \equiv \int_{\Omega} k(\mathbf{x}, \mathbf{y}) \frac{\partial f}{\partial N}(0; \mathbf{y}) \phi(\mathbf{y}) \, d\mathbf{y}. \quad (17)$$

has a positive, simple eigenvalue λ_1 corresponding to a nonnegative eigenfunction $\phi_1(\mathbf{x})$. This eigenvalue is strictly larger in modulus than any other eigenvalue of \mathcal{B} , and its eigenfunction is the only (up to a constant multiple) nonnegative eigenfunction of \mathcal{B} .

It is now useful to investigate the relationship of this eigenvalue to biological parameters. For notational convenience, $(\partial f / \partial N)(0; \mathbf{y}) = g(0; \mathbf{y})$ will be denoted by the function $g_0(\mathbf{y})$. By definition, λ_1 satisfies

$$\lambda_1 \phi_1(\mathbf{x}) = \int_{\Omega} k(\mathbf{x}, \mathbf{y}) g_0(\mathbf{y}) \phi_1(\mathbf{y}) d\mathbf{y}. \quad (18)$$

For this analysis, it is useful to utilize the L_1 normalization $\int_{\Omega} \phi_1(\mathbf{x}) d\mathbf{x} = 1$ and integrate equation (18) to obtain

$$\lambda_1 = \int_{\Omega} \int_{\Omega} k(\mathbf{x}, \mathbf{y}) g_0(\mathbf{y}) \phi_1(\mathbf{y}) d\mathbf{y} d\mathbf{x}. \quad (19)$$

By the bounds on $g_0(\mathbf{y})$ and the integrability properties of $k(\mathbf{x}, \mathbf{y})$, the order of integration on the right may be interchanged to obtain

$$\lambda_1 = \int_{\Omega} s(\mathbf{y}) g_0(\mathbf{y}) \phi_1(\mathbf{y}) d\mathbf{y}. \quad (20)$$

Because dispersal success is a function of dispersal ability and domain size, shape and boundary conditions, and because the intrinsic growth rate function g depends on habitat quality, λ_1 is a measure of the biological parameters of interest in this problem.

As a simple example, consider the situation in which emigration occurs by loss through the boundary of Ω and where dispersal success is an increasing function of the effective length scale parameter L , as discussed above. In general, for each \mathbf{y} , $s(\mathbf{y}; L)$ is an increasing function of L ; as domain length relative to dispersal ability increases, fewer organisms reach the boundary before settling. Suppose further that $g_0(\mathbf{y}; P)$ is a strictly increasing function of the general growth parameter P (e.g. $P = r$ in the Beverton-Holt growth function). Then

$$\lambda_1(L, P) = \int_{\Omega} s(\mathbf{y}; L) g_0(\mathbf{y}; P) \phi_1(\mathbf{y}) d\mathbf{y}. \quad (21)$$

Thus $\lambda_1(L, P)$ is an increasing function of both L and P . Assuming that for each \mathbf{y} , $g_0(\mathbf{y}; P)$ has a bounded, strictly positive derivative with respect to P , the derivative $\partial \lambda_1 / \partial P$ may be computed by differentiation inside the integral, and this derivative is strictly positive. Thus by the implicit function theorem, the relationship

$$\lambda_1(L, P) = 1 \quad (22)$$

may be solved for P in terms of L , and at $\lambda_1 = 1$,

$$\frac{dP}{dL} = - \left(\frac{\partial \lambda_1}{\partial P} \right)^{-1} \frac{\partial \lambda_1}{\partial L}. \quad (23)$$

Since both of the derivatives on the right are positive, $P(L)$ is a decreasing function at the stability exchange point. A similar analysis can be performed for λ_1 as a function of any relevant biological parameters, where those measuring dispersal ability and habitat quantity appear in the dispersal success function and those measuring habitat quality appear in the intrinsic growth rate function g_0 .

2.3. Nonlinear analysis. The linear analysis suggests that instability of the zero solution when $\lambda_1 > 1$ should be accompanied by existence of a stable nonzero solution; Hardin *et al.* (1990) verified this in the space of continuous functions on Ω . It is not necessary to reproduce their work here, but two similar results in $L_2(\Omega)$ follow directly from Krasnoselskii's theorems, and these will be listed before presenting the bifurcation result.

The ideas behind the existence and uniqueness results which we now give for integrodifference equations are nicely illustrated with a simple, nonspatial model: consider a discrete map $N_{t+1} = f(N_t) \equiv N_t g(N_t)$ for which $f(0) = 0$ and $f'(0) \equiv g(0) > 1$. If f is continuous and $\lim_{N \rightarrow \infty} f'(N) = 0$, then the function $f(N)$ must intersect the identity function $I(N) = N$ at some positive point N_* , that is, $f(N_*) = N_*$. Thus the discrete map has a positive equilibrium. Note that at this equilibrium, $g(N) = 1$. Suppose further that $f(N)$ is monotonically increasing and that $g(N) \equiv f(N)/N$ is a strictly decreasing function of N . Since $g(0) > 1$, the restriction that $g(N)$ is strictly decreasing implies that $g(N) = 1$ at one and only one point, that is, the positive equilibrium is unique. Because $f(N)$ is monotonically increasing, this positive equilibrium must be globally stable in the sense that for any $N > 0$, the sequence $N_{t+1} = f(N_t)$ converges to the fixed point $N_* = f(N_*)$.

The existence and uniqueness theorems for equation (1) which are listed here are based on these ideas. The uniqueness theorem requires that the nonlinear operator \mathcal{A} be continuous, that its Fréchet derivative $\mathcal{A}(0)$ exist and have dominant eigenvalue greater than 1, and that its asymptotic derivative $\mathcal{A}(\infty)$ be the zero operator. These requirements are exactly analogous to those in the preceding simple example.

Result 1 (Existence). Under the assumptions of this paper, the integrodifference equation (1) has at least one nonzero, nonnegative equilibrium solution for all $\lambda_1 > 1$.

For the uniqueness result, a monotonicity property analogous to that imposed on $f(N)$ in the foregoing example is required. Because the dispersal kernel $k(\mathbf{x}, \mathbf{y})$ is strictly positive, the nonlinear operator \mathcal{A} inherits its monotonicity from the growth function $f(N)$. Under the assumption that $f(N)$ is monotonic and that the function $k(\mathbf{x}, \mathbf{y})g(N; \mathbf{y})$ decreases uniformly with N , \mathcal{A} is a concave, monotonic operator which has exactly one positive solution which is globally stable.

Result 2 (Uniqueness). Under the further assumption that $f(N; \cdot)$ is nondecreasing, there exists a unique nonnegative equilibrium solution for $\lambda_1 > 1$, and this solution is globally stable.

The existence theorem applies to growth functions such as the Ricker or Beverton–Holt models, in which the per capita growth rate decreases strictly with population density and approaches zero at arbitrarily large densities. For Allee growth dynamics, $g(N; \cdot)$ increases with N at low densities, and the existence of solutions cannot be determined from knowledge of the growth rate at zero. The uniqueness theorem applies to monotonic growth functions such as the Beverton–Holt model, which is analogous to the continuous-time logistic model. In this case, existence, uniqueness and global stability of a nonnegative, nonzero population equilibrium are dependent only on the single sufficient condition $\lambda_1 > 1$.

It can now be shown that a continuous branch of positive solutions bifurcates from the zero solution at $\lambda_1 = 1$. Bifurcation will be considered with respect to a general growth parameter P , which appears explicitly in the per capita growth function $g(N; \mathbf{y}; P)$. It is assumed that g has a strictly positive derivative with respect to P . As a secondary parameter, consider the effective length scale L , which appears in the kernel. Let b denote the value of P at which the bifurcation occurs. From equations (22) and (23),

$$\frac{db}{dL} = - \left(\frac{\partial \lambda_1}{\partial b} \right)^{-1} \frac{\partial \lambda_1}{\partial L} < 0. \quad (24)$$

The bifurcation result follows from the standard Lyapunov–Schmidt reduction technique described in Krasnoselskii and Zabreiko (1984). Near the bifurcation point, the nonlinear operator $\mathcal{A}N$ can be expanded in a Taylor series in N around the zero solution and in the bifurcation parameter P around the bifurcation point b . Because bifurcation is considered from the zero solution, the constant term in the expansion is absent and thus the leading order term in N is the Fréchet derivative $\mathcal{B}N$. From Property 4, it is known that \mathcal{B} possesses a simple, positive dominant eigenvalue λ_1 with nonnegative eigenfunction $\phi_1(\mathbf{x})$. Furthermore, the transpose operator \mathcal{B}^T has an eigenfunction $\psi_1(\mathbf{x})$ corresponding to λ_1 . The linear term in $(P - b)$ is given by the linear operator $\mathcal{B}_1 N$. Because λ_1

is simple, bifurcation occurs at $P = b$ if the nondegeneracy condition $\langle \mathcal{B}_1 \phi, \psi \rangle \neq 0$ is satisfied. The direction of the bifurcation is determined by the higher-order terms in the Taylor expansion.

Result 3 (Bifurcation result). The point $P = b(L)$ is a bifurcation point for the equation $\mathcal{A}N = N$, and a continuous branch of nonzero solutions intersects the zero solution at $P = b(L)$. Furthermore, the nonzero solution is positive in some neighborhood of b when $P > b$ and negative in some neighborhood of b when $P < b$.

Thus the positive equilibrium exists when population growth, measured by P , exceeds a critical value b . Because $b(L)$ is a decreasing function, this critical value increases with decreasing effective domain size. As dispersal loss from the domain increases, population growth must also increase to ensure persistence.

2.4. *An example.* To illustrate the results of the preceding analysis, consider an example on the homogeneous domain $[0, \hat{L}]$ in which dispersal is modeled with the truncated Laplace kernel and growth is modeled with the Beverton–Holt function (2). An appropriate dimensionless integrodifference equation obtained by scaling the spatial variable by the domain length \hat{L} is given by

$$N_{t+1}(x) = \int_0^1 \frac{L}{2} \exp(-L|x-y|) \frac{rN_t(y)}{1+(r-1)N_t(y)} dy, \quad (25)$$

where $L = a\hat{L}$ is the effective domain length and $N_t(x)$ is dimensionless population density expressed as a fraction of the scaled carrying capacity $K\hat{L}$. The dispersal success function $s(y; L)$ and the average dispersal success rate $S(L)$ are given by equations (8) and (9), respectively.

The eigenvalue equation for the operator \mathcal{B} is given by

$$\lambda \phi(x) = \int_0^1 \frac{L}{2} \exp(-L|x-y|) r \phi(y) dy. \quad (26)$$

It can be shown by differentiation that this eigenvalue problem is equivalent to the boundary value problem

$$\begin{aligned} \phi''(x) &= -L^2(\mu r - 1)\phi(x), \\ L\phi(0) - \phi'(0) &= 0, \\ L\phi(1) + \phi'(1) &= 0, \end{aligned} \quad (27)$$

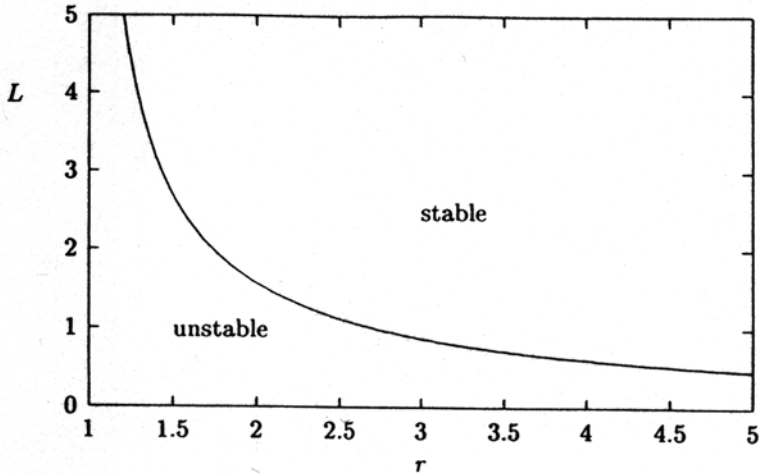


Figure 4. Global stability regions for the positive equilibrium solution of equation (25).

where $\mu = 1/\lambda$. Upon setting $\lambda_1 = 1$, the boundary value problem yields the function

$$L(r) = \frac{2 \tan^{-1} [1/\sqrt{r-1}]}{\sqrt{r-1}}, \tag{28}$$

which describes the relationship between effective domain length and intrinsic growth rate at the bifurcation point. Because the Beverton–Holt function is strictly increasing, the positive solution is unique and globally stable when $\lambda_1 > 1$. Thus the linear analysis yields the global stability diagram shown in Fig. 4. Bifurcation diagrams generated with the AUTO software package (Doedel *et al.*, 1994) showing the positive solution versus the parameter r appear in Fig. 5, and equilibrium solutions are shown in Fig. 6.

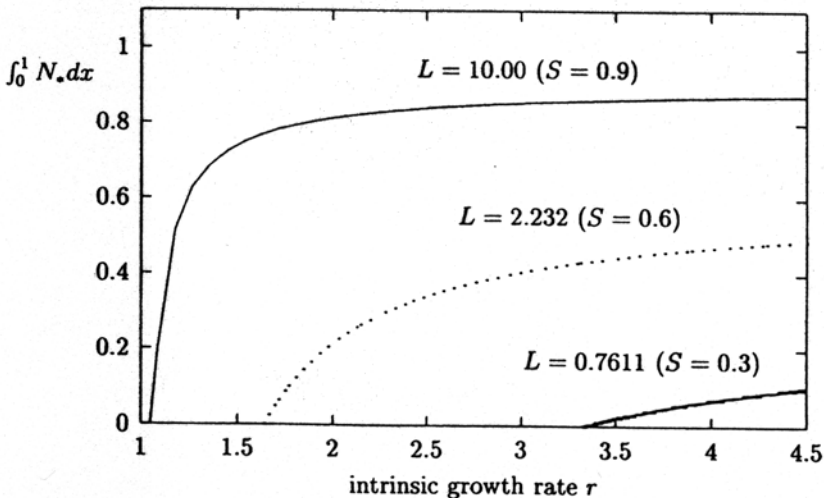


Figure 5. Bifurcation diagram for equation (25) showing the population size of the stable solution versus the intrinsic growth rate r for various domain lengths.

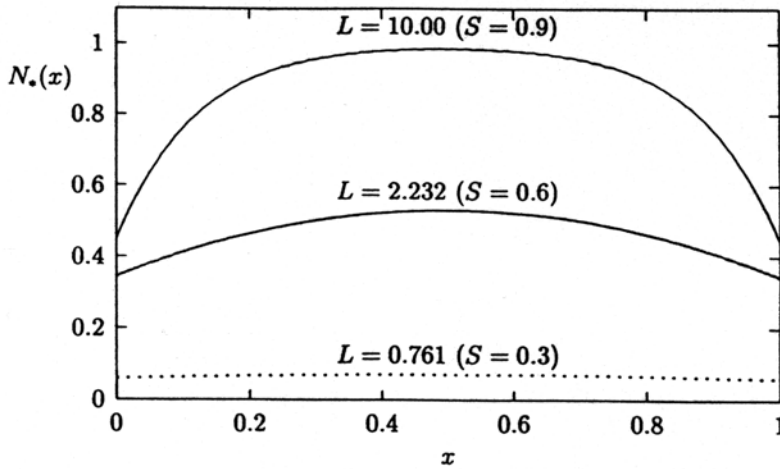


Figure 6. Stable equilibrium solutions of equation (25) for $r = 4$.

A more complete bifurcation diagram illustrating secondary bifurcations is given in Fig. 7. This diagram plots the solution value $N_*(0)$ at the left domain boundary instead of the integral, since some branches are indistinguishable from others in size and differ only in reflection around the x axis. All unstable solutions are negative over at least some subset of the domain. The first and third bifurcations are transcritical, and the second is a pitchfork.

Comparison of Figs. 2 and 6 shows that the equilibrium solutions are very similar in shape to the dispersal success functions, suggesting that at least in this simple case of a homogeneous habitat and truncated dispersal kernel, dispersal success is a key biological parameter which is directly related to the size and shape of the population equilibrium. To pursue this relationship a step further, consider the nonspatial difference equation

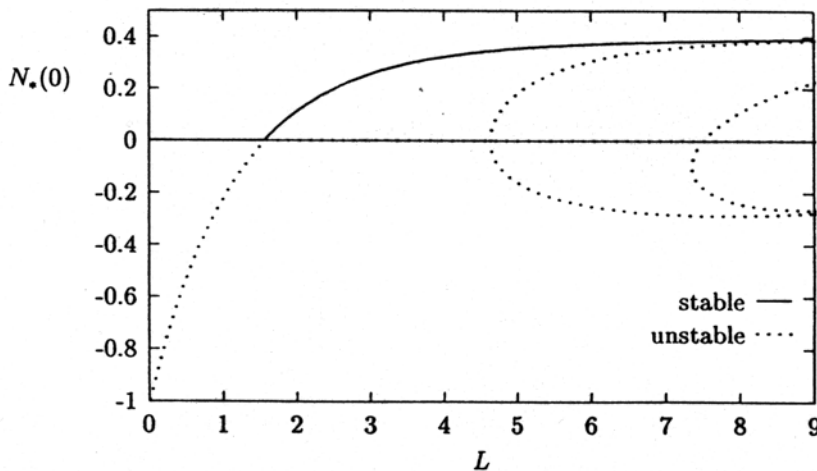


Figure 7. Bifurcation diagram for the integrodifference equation with Laplace kernel and Beverton-Holt growth ($r = 2.0$) showing the first three bifurcations.

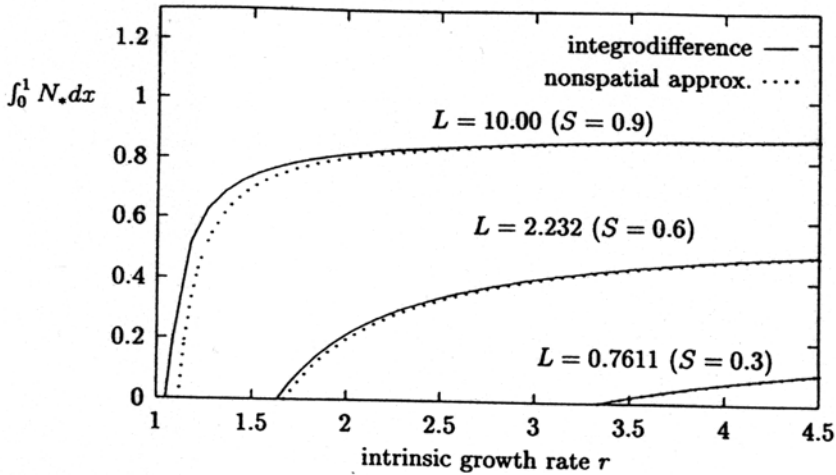


Figure 8. Bifurcation diagram showing population size versus r for the integrodifference equation (25) and the nonspatial model (29).

model

$$N_{t+1} = \frac{SrN_t}{1 + (r-1)N_t}, \quad (29)$$

where S is the average dispersal success rate for a given kernel. The nonzero equilibrium solution to this equation is

$$N_* = \frac{Sr - 1}{r - 1}, \quad (30)$$

which is stable and positive for all $S > 1/r$. Figure 8 shows that the bifurcation diagrams for the integrodifference equation model (25) and the (1) nonspatial model considered for the same average dispersal success rate have bifurcation structures which are very similar, suggesting that the nonlinear analysis of the integrodifference equation can be reduced to analysis of a simple difference equation if the average dispersal success rate is known. Since this reduction is potentially a very useful tool for analyzing biological problems it is pursued in more mathematical detail in the following section.

3. Dispersal Success and Habitat Quality.

3.1. *The dispersal success approximation.* To further investigate the relationship between the dispersal success function and the equilibrium solution to the integrodifference equation, consider the general equation (1) in

which the kernel is symmetric. Let

$$\bar{N} \equiv \frac{1}{V_\Omega} \int_\Omega N_*(\mathbf{x}) \, d\mathbf{x} \quad (31)$$

denote the spatial average of the equilibrium solution, which is given by

$$N_*(\mathbf{x}) = \int_\Omega k(\mathbf{x}, \mathbf{y}) f(N_*(\mathbf{y})) \, d\mathbf{y}. \quad (32)$$

If $f(N)$ and $N(\mathbf{y})$ are sufficiently smooth, then for each $\mathbf{y} \in \Omega$, $f(N_*(\mathbf{y}))$ has a Taylor polynomial

$$f(N_*(\mathbf{y})) = f(\bar{N}) + f'(\hat{N}(\mathbf{y}))(N_*(\mathbf{y}) - \bar{N}) \quad (33)$$

for some $\hat{N}(\mathbf{y})$ between \bar{N} and $N_*(\mathbf{y})$. Substituting this into equation (32) and using $\int k(\mathbf{x}, \mathbf{y}) \, d\mathbf{y} = s(\mathbf{x})$,

$$N_*(\mathbf{x}) = f(\bar{N})s(\mathbf{x}) + \int_\Omega k(\mathbf{x}, \mathbf{y}) f'(\hat{N}(\mathbf{y}))(N_*(\mathbf{y}) - \bar{N}) \, d\mathbf{y} \quad (34)$$

and thus

$$\bar{N} = Sf(\bar{N}) + \frac{1}{V_\Omega} \int_\Omega s(\mathbf{y}) f'(\hat{N}(\mathbf{y}))(N_*(\mathbf{y}) - \bar{N}) \, d\mathbf{y} \quad (35)$$

Thus a first-order approximation to the equilibrium population size is the solution to the algebraic equation

$$\bar{N}_{\text{appr}} = Sf(\bar{N}_{\text{appr}}), \quad (36)$$

as suggested by the previous example. The accompanying approximate solution is

$$N_{\text{appr}}(\mathbf{x}) = \frac{\bar{N}_{\text{appr}}}{S} s(\mathbf{x}), \quad (37)$$

Approximate solutions computed by this method are compared with true solutions for equation (25) in Fig. 9.

The dispersal success approximation is valid when the equilibrium solution $N_*(\mathbf{x})$ is close to the spatially averaged solution \bar{N} for all \mathbf{x} , so that the integral terms in equations (34) and (35) are very small. However, numerical results suggest that the approximation may be good even when the equilibrium solution is not approximately constant. An explanation is that

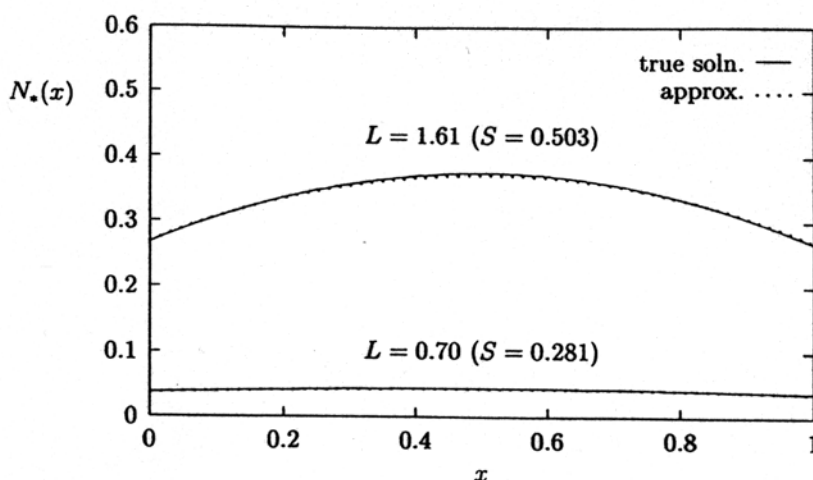


Figure 9. True and approximate solutions for equation (25) with $r = 4.0$.

locations near the boundary that lose more dispersers to emigration have a higher per capita growth rate due to lower population density. This can be seen graphically from Fig. 1; lower population densities occur further to the left of the nonspatial equilibrium, where $f'(N)$ is greater. Conversely, in higher density areas, dispersal success is greater, but local growth rate is lower. Thus the products $k(x, y)f'(N_*(y))$ and $s(y)f'(N_*(y))$ are expected to be approximately constant over the domain, and the integral term will be small even when $|\bar{N} - N_*(x)|$ is not.

The assumption that the kernel be symmetric is not critical to formulating the preceding approximation. In the case that the kernel is not symmetric, the integral $\int k(x, y) dy$ is not the dispersal success function $s(x)$, but rather a closely related function representing the probability of a disperser successfully settling at x . A generalized dispersal success approximation that can account for nonsymmetric kernels and heterogeneous habitat quality is developed at the end of this section.

3.2. Overcompensatory and dependant growth dynamics. The effects of dispersal success on population persistence and stability in the presence of overcompensatory and dependant growth are illustrated with numerical examples. The nonspatial Ricker growth model (3) displays a sequence of period-doubling bifurcations as ρ increases beyond 2. Integro-difference models with the Ricker growth function also display this behavior. Many numerical solutions to such models are found in Kot and Schaffer (1986), Kot (1989), Andersen (1991) and Hastings and Higgins (1994), but here we focus on bifurcation structure. While bifurcation diagrams of the nonspatial Ricker equation have appeared in a variety of publications, (e.g. Peitgen and Richter, 1986; Murray, 1989; Andersen, 1991), they have not been analyzed for the spatial models (but see Andersen, 1991). A bifurcation diagram generated by AUTO (Doedel *et al.*, 1994) for a dimensionless

integrodifference equation with Ricker dynamics, a Laplace kernel truncated to $[0, 1]$ and average dispersal success $S = 0.5$ is given in Fig. 10.

This diagram is qualitatively very similar to that of the nonspatial Ricker model. The primary effect of dispersal loss on the Ricker dynamics is to increase the growth rate at which bifurcations occur. For example, in the nonspatial model with no dispersal loss, the equilibrium $N_* = 1$ is stable for $0 < \rho < 2$, and the period-2 solution is stable for $2 < \rho < 2.526$. Chaos and solutions of arbitrary period exist for $\rho > 2.692$ (May, 1974). With dispersal success rate $S = 0.5$, the positive equilibrium solution is stable for $0.682 < \rho < 2.694$, and the period-2 solution is stable for $2.694 < \rho < 3.232$. Thus in a population which exhibits overcompensatory growth, net loss of individuals due to emigration can maintain a stable equilibrium at high intrinsic growth rates which would otherwise imply periodic or chaotic behavior. This mathematical observation agrees with the experiments of Krebs *et al.* (1969), who observed cyclic behavior in vole populations which were enclosed by a dispersal barrier but not in a control population from which emigration was possible.

To illustrate the effects of depensatory growth, consider an integrodifference equation with truncated Laplace kernel ($S = 0.5$) and the Allee growth function (4), which does not satisfy the conditions of section 2 because $g(0) = 0$. The bifurcation diagram for this integrodifference equation is shown in Fig. 11.

In the nonspatial model (4), the unstable solution branch defines a critical population size below which extinction is certain. A similar phenomenon occurs in the spatial model, but it is not as easily determined how the spatial distribution of the population relates to this threshold: if the initial density is above the threshold in some parts of the domain and below in others, does the population tend to the stable positive equilibrium or the

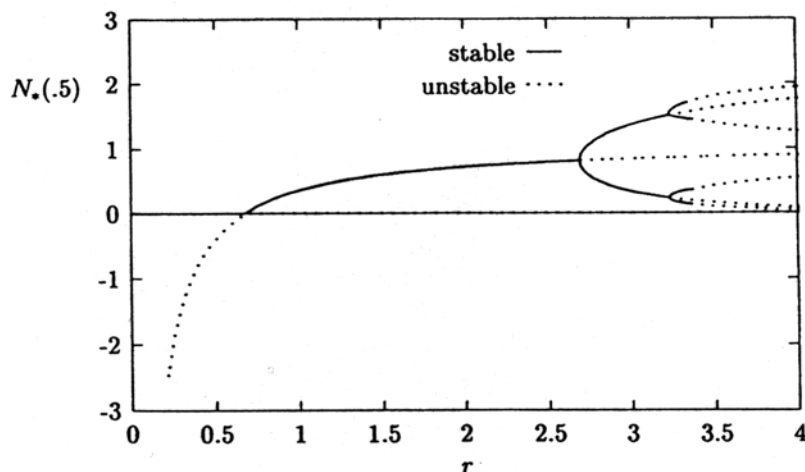


Figure 10. Bifurcation diagram for the Laplace kernel with Ricker dynamics ($S = 0.5$).

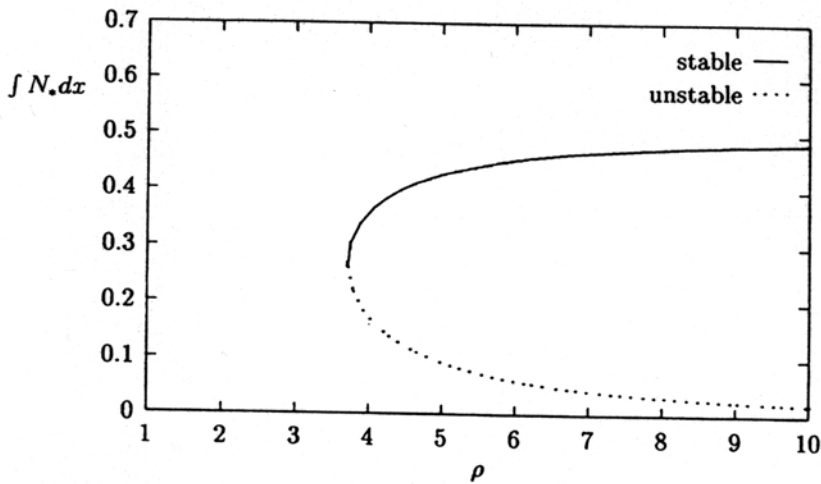


Figure 11. Bifurcation diagram for the integrodifference equation with Laplace kernel and Allee dynamics ($S = 0.5$).

stable zero equilibrium? This problem can be analyzed on infinite domains using traveling wave methods, and, at least in some cases, conditions sufficient for persistence have been shown (Kot *et al.*, 1996). Preliminary numerical investigations on finite domains indicate that persistence is dependent not only on initial population size, but also on distribution. A population with total size greater than that of the unstable branch will persist when its density is concentrated in the center of the domain, but will go extinct if most of the density is near the edges. This observation illustrates another mechanism by which habitat fragmentation can affect population persistence through dispersal loss.

3.3. *Heterogeneous habitats.* To investigate population persistence in heterogeneous habitats, we first consider the problem without dispersal loss in order to isolate the effects of the heterogeneity per se. We then incorporate the effects of dispersal loss through a generalization of the dispersal success approximation to an environment consisting of an arbitrary number of habitat patches of different quality.

Suppose that heterogeneity of the habitat is modeled by variation in the growth function $f(N; x)$; in particular, suppose that f has the form $g(N; x)N$, where $g(\cdot; x)$ is periodic in x with period \hat{L} . Though periodicity in habitat quality is idealized, patterns of habitat fragmentation can resemble those modeled by periodic functions (see, e.g. Forsman *et al.*, 1984). Assume further that $g(N; x)$ is a strictly decreasing function of N and that it is strictly positive for all x so that it satisfies the assumptions of section 2.

A specific example that can be analyzed utilizes the Laplace kernel. The integrodifference model can be nondimensionalized by dividing the spatial

variable by the period \hat{L} to obtain the formulation

$$N_{t+1}(x) = \int_{-\infty}^{\infty} \frac{L}{2} \exp(-L|x-y|) f(N_t(y); y) dy, \quad (38)$$

where $L \equiv a\hat{L}$. The dimensionless parameter L is the period length divided by the mean dispersal distance and is a measure of the effective spatial scale of the habitat fragmentation. The scaling of the spatial variable by the period results in the function $g(\cdot; x)$ having period 1. Differentiation of (38) shows that the equilibrium equation is equivalent to the differential equation

$$-\frac{1}{L^2} N_*''(x) + N_*(x) = f(N_*(x); x) \quad (39)$$

Because $f(\cdot; x)$ has period 1 the desired solution and its first derivative also have period 1 so that the boundary conditions which accompany equation (39) are given by $N_*(0) = N_*(1)$ and $N_*'(0) = N_*'(1)$. The eigenvalue problem is thus given by

$$-\frac{1}{L^2} \phi_{xx} + \phi(x) = \mu g(0; x) \phi(x), \quad (40)$$

where $\mu = 1/\lambda$, with boundary conditions

$$\begin{aligned} \phi(0) &= \phi(1), \\ \phi'(0) &= \phi'(1). \end{aligned} \quad (41)$$

The periodic differential equation (40) is a form of Hill's equation and thus possesses a countable set of real eigenvalues μ (Eastham, 1973; Magnus and Winkler, 1979). The equivalent integral formulation of this eigenvalue problem can be shown to satisfy the conditions of Property 4, and thus the largest eigenvalue λ_1 is positive and corresponds to a positive eigenfunction $\phi_1(x)$. A sufficient condition for this eigenvalue may be obtained directly from equation (40) without any further assumptions on the periodic function $g(0; x)$. For notational convenience, let $r(x) \equiv g(0; x)$. Equation (40) for the dominant eigenvalue may be written in the form

$$\lambda_1 \left[1 - \frac{1}{L^2} \frac{\phi_1''}{\phi_1} \right] = r(x), \quad (42)$$

which can now be integrated from $x = 0$ to $x = 1$. Upon letting

$$h \equiv \frac{\phi_1'}{\phi_1} = \frac{d}{dx} \log \phi_1, \quad (43)$$

the integral of the second term on the right becomes

$$\int_0^1 \frac{\phi_1''}{\phi_1} dx = \int_0^1 h' + h^2 dx. \tag{44}$$

Because $\phi_1(x)$ is periodic in x , $h(x)$ is also periodic in x and thus the first integral term on the right side of (44) vanishes. Denote the second term by $I \equiv \int_0^1 h^2 dx$, which is strictly positive. Thus the dominant eigenvalue can be expressed as

$$\lambda_1 = \frac{\int_0^1 r(x) dx}{1 - (I/L^2)} > \int_0^1 r(x) dx. \tag{45}$$

Thus for I sufficiently large, the population can persist even when the spatial average of the intrinsic growth rate is less than 1.

In order to solve the eigenvalue problem explicitly, a specific form for the periodic function $g(0; x)$ must be specified. Thus suppose that the environment consists of alternating patches of "bad" and "good" habitat with intrinsic growth rates $r_1 < 1$ and $r_2 > 1$, respectively. Because $g(0; x)$ has period 1, suppose that $g(0; x) = r_1$ for $0 < x < 1 - R$ and $g(0; x) = r_2$ for $1 - R < x < 1$ (see Shigesada and Kawasaki, 1986). The parameter R represents the total fraction of the environment that consists of "good" habitat. The function $g(0; x)$ is thus given by the periodic extension of the piecewise-constant function

$$g(0; x) \equiv r(x) = \begin{cases} r_1, & 0 < x < 1 - R, \\ r_2, & 1 - R < x < 1. \end{cases} \tag{46}$$

The eigenvalue problem (40) is now given by

$$\phi_{xx} = \begin{cases} -L^2(\mu r_1 - 1)\phi, & \text{bad patches,} \\ -L^2(\mu r_2 - 1)\phi, & \text{good patches,} \end{cases} \tag{47}$$

with boundary conditions (41). Because the kernel of the original integrodifference model is continuous, the eigenfunction $\phi(x)$ and its first derivative must be continuous at the discontinuity $x = 1 - R$ of $r(x)$. As usual, the desired result from the linear analysis is a relationship between dispersal ability and habitat quality at the bifurcation point $\mu = 1$. Upon letting $\mu = 1$, setting $b^4 = (r_2 - 1)/(1 - r_1) > 0$ and making the substitution $H^2 = L^2\sqrt{(r_2 - 1)(1 - r_1)}$, the eigenvalue equations (47) become

$$\phi_{xx} = \begin{cases} \frac{H^2}{b^2}, & x \in [0, 1 - R), \\ -H^2 b^2 \phi, & x \in (1 - R, 1]. \end{cases} \tag{48}$$

The parameter H is the heterogeneity of the habitat relative to dispersal ability. When the organisms are highly mobile and/or the difference in quality between the good and the poor patches is small, H is close to zero. On the other hand, when organisms are relatively sedentary and/or the difference between the growth rates is large, H becomes large.

Finding the general solution to (48), applying the boundary conditions (41) and enforcing the continuity conditions of $\phi(x)$ and its derivative at $x = 1 - R$ yields the relationship between H and b at the bifurcation point as the first-branch solution to

$$\left(\frac{1}{b^2} - b^2\right) \sinh \frac{H(1-R)}{b} \sin Hrb + 2 \left(\cosh \frac{H(1-R)}{b} \cos Hrb - 1 \right) = 0. \quad (49)$$

The two extreme cases $H \rightarrow 0$ and $H \rightarrow \infty$ can be treated analytically. As $H \rightarrow 0$, equation (49) reduces to

$$R = \frac{1}{1 + b^4} \quad (50)$$

or, equivalently,

$$Rr_2 + (1 - R)r_1 = 1. \quad (51)$$

Thus when the effective heterogeneity approaches zero, that is, when the organisms are highly mobile relative to the patchiness and/or the difference between good and bad habitat patches is very small, the positive equilibrium solution exists and is stable when the spatially averaged growth rate exceeds 1. In this case the high mobility of the organisms effectively averages habitat conditions over the entire domain.

At the other extreme, when the organisms disperse very little relative to the scale of habitat periodicity ($H \rightarrow \infty$), equation (49) has solution $b = 0$. In this case, the condition for existence of the nonzero solution is $b > 0$ or, equivalently, $r_2 > 1$. When dispersal does not tend to shuffle organisms among the patches, the condition for population persistence is simply that the good patches have growth rate greater than 1. Solutions to equation (49) and the resulting stability regions for values of H between these two extremes are shown in Fig. 12.

To conclude this section, it is instructive to generalize the dispersal success approximation to an environment which consists of an arbitrary number of discrete habitat patches D_i , each with a constant internal habitat quality. In this case, a spatially constant growth function $f_i(N)$

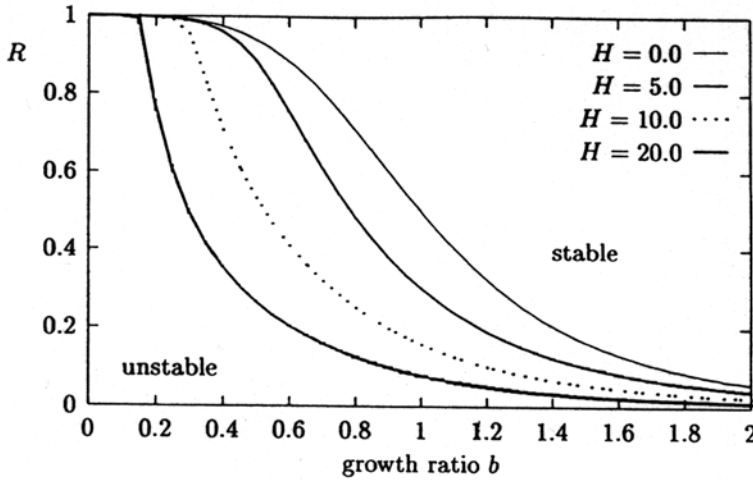


Figure 12. Stability of the positive equilibrium for the periodic problem. The graph for the extreme case $H = \infty$ is the vertical line $b = 0$.

models growth within patch i . Performing a derivation analogous to that used previously to derive the dispersal success approximation yields the generalized approximations

$$\bar{N}_{\text{appr}} = \sum_i S_i f_i(\bar{N}_{\text{appr}}) \tag{52}$$

and

$$N_{\text{appr}}(\mathbf{x}) = \sum_i f_i(\bar{N}_{\text{appr}}) s_i(\mathbf{x}), \tag{53}$$

where

$$s_i(\mathbf{x}) = \int_{D_i} k(\mathbf{x}, \mathbf{y}) \, d\mathbf{y} \tag{54}$$

and

$$S_i = \frac{1}{V_\Omega} \int_\Omega s_i(\mathbf{x}) \, d\mathbf{x}. \tag{55}$$

The quantity $s_i(\mathbf{x})/V_\Omega$ defines a density function governing the probability that an organism beginning dispersal in patch i settles at \mathbf{x} , and S_i is the probability that an organism beginning dispersal in patch i successfully settles somewhere in Ω .

4. Discussion. Conservation biologists realize the importance of connecting population persistence with the scale of habitat fragmentation relative to dispersal distances (Doak *et al.*, 1992; Dunning *et al.*, 1992). Making this

connection requires a simple way to relate parameters measuring dispersal success and local growth conditions to population persistence. Using dispersal success rate as a precise measure of the effect of fragmentation on successful dispersal, we have shown how dispersal success and population growth interact to determine persistence. Not surprisingly, when local growth dynamics are compensatory, a positive, stable equilibrium solution relies upon intrinsic population growth being large enough to outweigh dispersal loss due to emigration. However, when fragmentation of habitat results in isolated patches that are much smaller than the average dispersal distance of the organism, extinction results even when per capita growth rates remain high.

The dispersal success approximation describes how both the size and shape of equilibrium solutions are largely determined by the dispersal success function. Our results are consistent with the observation of Sievert and Keith (1985) that equilibrium density of snowshoe hares near the southern limit of their range was lower than it was farther north due to decreased dispersal survivorship near the boundary, suggesting that dispersal loss may be a reason why population density generally decreases near the boundary of a specie's geographic range (Hengeveld and Haeck, 1982; Brown, 1984, 1995; Hengeveld, 1990; Maurer, 1994). When the environment consists of multiple patches of variable quality, equations (52)–(55) provide a recipe for calculating the approximate population density $N_{\text{appr}}(\mathbf{x})$ and size $\bar{N}_{\text{appr}}V_{\Omega}$ if the dispersal kernel and the growth functions are known. Once $s_i(\mathbf{x})$ and S_i are computed from the kernel, the algebraic equation (52) can be solved for N_{appr} . Substituting this value into each of the functions $f_i(N)$ provides the coefficients for the linear combination of the dispersal success functions $s_i(\mathbf{x})$ in equation (53), which yields the approximate equilibrium population distribution.

The accuracy with which the dispersal success approximation predicts population densities even when equilibrium solutions are not constant suggests a close relationship between the bifurcation structures of the integrodifference model (1) and the nonspatial model (36) utilizing the average dispersal success rate (7). Our numerical bifurcation analyses showed this to be true not only for compensatory (Beverton–Holt) dynamics, but also for overcompensatory (Ricker) and depensatory (Allee) dynamics. For sufficiently high dispersal success, integrodifference equations with Allee dynamics possess two positive solution branches; the larger of these two is stable, and the other is unstable. In the nonspatial Allee model, the unstable solution provides a threshold population value below which the population goes extinct. However, in the spatial model, a total population size exceeding that of the unstable branch can go extinct if too much of the population density is located in areas with poor dispersal success. Overcompensatory growth, modeled with the Ricker dynamics, was shown to be stabilized by dispersal loss, which increased the intrinsic growth rates at

which the various bifurcations occur (but see Hastings and Higgins, 1994, for evidence that these models can exhibit long-term transient dynamics not reflected by the bifurcation structure).

Construction of an integrodifference model on an infinite domain of periodically varying quality allowed investigation of the effects of habitat heterogeneity on population persistence. The minimum fraction R of the habitat consisting of good patches that is necessary for persistence is a decreasing function of habitat quality. The rate at which R decreases with habitat quality depends on the effective heterogeneity H , which measures the organism's dispersal ability relative to the scale of the fragmentation and the difference in quality between good and poor patches. Figure 12 shows that for a population of highly mobile organisms (H small) to persist, either the good patches must be relatively close together ($R \sim 1$) or must support very high fecundities (b large) in order to mediate losses incurred by settlement of dispersers in the poor habitat. On the other hand, if the organisms are fairly sedentary or patch size is large (H large), the good patches may be separated by larger distances. The effect of increased dispersal ability in this case is to average environmental conditions, allowing the poor quality patches to affect overall persistence of the population to a greater degree than they would if the organisms tended to disperse less. Doak *et al.* (1992) have theorized that spatial scale of habitat fragmentation relative to dispersal distance is an important determinant of population persistence, but their extensive review of published field data discovered such vague reporting of the relative spatial scales of dispersal and fragmentation that they were unable to determine any empirical relationships between spatial scale and population persistence.

In both the cases of heterogeneous habitats and single isolated patches, increased dispersal ability is detrimental to the population. Increased mobility leads to increased settlement in poor quality habitat ("sinks") and to larger dispersal loss from isolated patches of good quality habitat ("sources"). Although dispersal from source areas can maintain local populations in sink areas and thus increase the probability of overall population persistence (Roughgarden and Iwasa, 1986; Pulliam, 1988; Kadmon and Shmida, 1990; Pulliam and Danielson, 1991; Amarasekare, 1994), if the sink habitats are too large or the intrinsic growth rate in the source habitats is too small, dispersal from the source areas can result in extinction (Howe *et al.*, 1991; Davis and Howe, 1992). These results are consistent with those of Hardin *et al.* (1990) for similar types of integrodifference equations on finite domains. They proved that in a time-invariant environment, the optimal dispersal strategy is to not disperse at all. As long as at least some of the habitat is of high enough quality to ensure existence of a positive equilibrium solution to the appropriate nonspatial growth map, the population is certain to persist if no individuals leave the high quality patches.

However, most organisms have evolved dispersal strategies over a long period of time in environmental conditions that do not change rapidly. A significant body of literature devoted to the evolutionary aspects of dispersal generally supports theories that dispersal is advantageous to population persistence in the long term because it serves to promote genetic fitness (Lidicker, 1962; Dobson, 1979; Greenwood, 1980; Greenwood and Harvey, 1982; Hoogland, 1982; Moore and Ali, 1984; Cockburn *et al.*, 1985; Flowerdew, 1987; Wolff *et al.*, 1988; Johnson and Gaines, 1990), colonize depopulated areas (Howard, 1960; Smith, 1974, 1980; Wiens, 1976; Gaines and McClenaghan, 1980; Howe and Smallwood, 1982; Hansson, 1991), regulate population density (Krebs *et al.*, 1969; Gurney and Nisbet, 1975; Bownan and Robel, 1977; Namba, 1980; Flowerdew, 1987; Krebs, 1992), reduce competition for mates and other resources (Dobson, 1979; Waser, 1985; Shields, 1987; Anderson, 1989; Ribble, 1992) and connect spatially separated subpopulations (Forrest *et al.*, 1988; Pulliam, 1988; Howe *et al.*, 1991; Pulliam and Danielson, 1991; Davis and Howe, 1992). These advantages generally outweigh the costs of dispersal, which include increased mortality during dispersal due to predation and unfamiliarity with the terrain (Jenkins *et al.*, 1964; Metzgar, 1967; Bownan and Robel, 1977; Keppie, 1979; Sievert and Keith, 1985; Barash, 1989; Small *et al.*, 1993), establishment of dispersers in habitat of poorer quality than that which they emigrated from (Carl, 1971; Fleming, 1979), reduction in the fecundity of dispersing individuals (Shields, 1987) and net population losses in areas which receive few immigrants (Hanski and Zhang, 1993). It is the rapid fragmentation of habitat that has occurred because of human activity that has greatly increased the risk of dispersal to populations occupying artificially created heterogeneous environments (Howe *et al.*, 1991; Davis and Howe, 1992). These observations suggest that organisms such as the northern spotted owl *Strix occidentalis caurina* (Foreman *et al.*, 1984; Doak, 1987; Lamberson *et al.*, 1992) and the black-footed ferret *Mustela nigripes* (Forrest *et al.*, 1988) that possess inherently low intrinsic growth rates, tend to undertake long dispersal movements and evolved in large areas of contiguous habitat that are particularly susceptible to the effects of habitat fragmentation. Organisms with high fecundities and smaller characteristic dispersal distances may be better able to withstand habitat fragmentation.

In some cases there may be a correlation between dispersal success and growth conditions: dispersers originating in high quality habitat may have greater dispersal success than those originating in poor quality habitat if the organism's characteristic dispersal distance is small enough relative to the size of the patch that most dispersers settle in their patch of origin. This is the case in which little spatial averaging of habitat quality occurs, and population persistence is generally determined by conditions in the good quality patches. On the other hand, if characteristic dispersal distance is large relative to patch size, dispersal success is more likely to be deter-

mined by the proximity of the patch to poor quality habitat or the edge of the domain. In this case, not only are habitat conditions averaged over the domain, but dispersers originating in good patches surrounded by poor or unsuitable habitat may experience high mortality. The risks associated with settlement of dispersers in low quality patches become even greater in organisms susceptible to Allee effects. These results show quantitatively how habitat fragmentation decreases population persistence when the organism's characteristic dispersal distance is large compared to the scale of the fragmentation, when the poor quality patches are of much lower quality than the good patches and when the good patches are surrounded by poor quality or unsuitable habitat.

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