A COMPARISON OF DISPERAL STRATEGIES FOR SURVIVAL OF SPATIALLY HETEROGENEOUS POPULATIONS

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Abstract. This paper analyzes a discrete-time model of populations that grow and disperse in separate phases. The growth phase is a nonlinear process that allows for the effects of local crowding. The dispersion phase is a linear process that distributes the population throughout its spatial habitat. This study quantifies the issues of survival and extinction, the existence and stability of nontrivial steady states, and the comparison of various dispersal strategies. The results show that all of these issues are tied to the global nature of various model parameters. The extreme strategies of staying-in-place and going-everywhere-uniformly are compared numerically to diffusion strategies in various contexts. The mathematical analysis of our model is approached from a functional analysis and an operator theory point of view. Recent results from the theory of positive operators in Banach lattices are used.

Key words. integrodifference equation, spectral radius, dispersion

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1. Introduction. It is generally acknowledged that the spatial dispersion of individuals is important in determining the behavior of natural populations. It is intuitive that dispersion allows individuals to escape locations of adverse environmental change, crowding, or resource depletion. It is also intuitive that dispersion allows populations to average local effects in an environment that is changing in time and place.

Mathematical studies of biological populations have only recently incorporated dispersion into mathematical models. These investigations have for the most part treated dispersion as a within habitat phenomenon or a between habitat phenomenon. The within habitat studies have considered dispersion as a diffusion mechanism similar to those arising in thermodynamics. Between habitat studies, on the other hand, have viewed dispersion as a connecting mechanism for isolated discrete subpopulations.

Diffusion models of dispersion in ecological populations originated with Skellam [25], and Kierstead and Slobodkin [11]. Many authors have contributed to this study, including Levin [14], McMurtrie [19], Okubo [20], Cohen and Murray [3], and Levin and Segel [16]. These studies have focused upon the spatial effects produced by diffusion and in particular, upon critical habitat size for survival, homogenization of local spatial disturbances, and the development of spatial pattern and structure.

Between-habitat models of dispersion are known as patch models. These models have been investigated by many authors, including MacArthur and Wilson [17], Horn and MacArthur [10], Levin, Cohen, and Hastings [15], Gadgil [7], Hamilton and May [8], Vance [26], Elner [6], Allen [1], and DeAngelis, Post, and Travis [4]. These studies have focused upon the advantages gained by dispersion, the most advantageous amount of dispersal, the critical number of patches for survival, the increase of species diversity in patchy environments, the fraction of dispersing population yielding an evolutionary stable strategy, and the stabilizing influence of dispersion.

In this paper we consider another type of model for population dispersion. The model we treat was introduced by Kot and Schaeffer [12], who investigated it from a numerical point of view. This model describes a single species population in which individuals have a two-phase life cycle. The first phase is a growth phase, which is

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influenced by spatially dependent and crowding dependent growth conditions. The second phase is a dispersion phase, which distributes individuals throughout a heterogeneous habitat. The model has as its biological prototype plants which produce seeds in successive generations. The model is discrete in time and continuous in space, and thus consists of a nonlinear integrodifference equation. In [12] various examples of this model are examined numerically with emphasis upon the bifurcation to multiple steady states, cycles, period doubling, and chaotic behavior.

Our objectives are to analyze rigorously this model with regard to survival and extinction of the population and the existence and stability of equilibrium solutions. We will establish a necessary and sufficient condition for the existence of a nontrivial equilibrium (Theorems 3.1, 3.3, and 3.4). We will also compare different strategies of dispersion. The class of dispersion strategies we consider contains as extremes the strategy of staying-in-place and the strategy of going-everywhere-uniformly throughout the habitat. We will prove that, within the class of dispersion strategies we consider, the stay-in-place strategy is optimal in a time-invariant environment in the sense that it possesses the maximum likelihood for survival for various classes of spatially dependent growth conditions (Theorem 6.2). We will prove that the go-everywhere-uniformly strategy is optimal in a time-varying environment allowing these same growth conditions (Theorem 7.2).

We will illustrate these various results with some simple numerical examples which compare the stay-in-place strategy, the go-everywhere-uniformly strategy, and intermediate diffusion-type strategies. These examples will show the optimality of the different strategies in various environmental contexts, the spatial nature of various nontrivial equilibria, and the stabilizing influence of dispersion in uniformizing local disturbances and in suppressing the occurrence of cycles and chaos.

As for the organization of this article we introduce our problem in § 2 in terms of a dynamical system with discrete time. In § 3 we formulate necessary and sufficient conditions for the existence of a nontrivial solution to this dynamical system. We start with an abstract system in Theorem 3.1. From this result we deduce Theorems 3.3 (for local crowding) and 3.4 (for nonlocal crowding) which are directly applicable to the existence theory for our growth-dispersal model. Corresponding to these results, we formulate Corollaries 3.5 and 3.6, covering the special case when the growth of the population is modeled by either the logistic or the Ricker function. In § 4 we formulate sufficient conditions for the local stability of a nontrivial equilibrium solution to our dynamical system in the autonomous case with local crowding. We state this result as Theorem 4.1, with Corollary 4.2 covering the case when the growth is modeled by either the logistic or the Ricker function. In § 5 we formulate sufficient conditions for the global stability of a nontrivial equilibrium solution to our dynamical system under hypotheses similar to those in § 4. We state this result as Theorem 5.1, and Corollary 5.2 is used for the logistic or the Ricker function. Finally, Examples 3.7, 4.3, and 5.3 show restrictions on the growth rate required for the existence, local stability, and global stability, respectively, of a nontrivial solution to our dynamical system.

In § 6 we consider dispersion in a time-invariant environment. We introduce the concept of optimal dispersion, based on our existence theorems, Theorems 3.3 and 3.4, in Definition 6.1. We show the existence and uniqueness of optimal dispersion in Theorems 6.2 and 6.3, respectively. It turns out that the stay-in-place dispersal strategy is optimal. In § 7 we consider dispersion in a time-varying environment. Again, we introduce the concept of optimal dispersion in Definition 7.1. We show the existence and uniqueness of optimal dispersion in Theorems 7.2 and 7.3, respectively. It turns out that the go-everywhere-uniformly dispersal strategy is optimal. In § 8 we illustrate
our theoretical results with numerical examples. Finally, in § 9 we summarize our results and discuss their applicability to actual biological situations.

2. **Formulation of the problem.** We consider an organism with synchronous, non-overlapping generations. We assume that the life cycle of this organism consists of two stages: the sedentary stage and the dispersal stage. The growth of the population occurs exclusively during the sedentary stage and is described by a nonlinear operator. The relocation of the population occurs exclusively during the dispersal stage and is described by a linear operator.

We assume that our population lives in a spatially fixed habitat \( \Omega \), where \( \Omega \) is a compact subset of the \( n \)-dimensional Euclidean space \( \mathbb{R}^n \) with nonempty interior. The density of this population at time \( t (t = 0, 1, 2, \cdots) \) is described by a function \( N_t = N_t(x) \) of \( x \in \Omega \), where \( x \) denotes the position in the habitat \( \Omega \). As usual, we denote by \( C(\Omega) \) the Banach lattice of all complex-valued continuous functions on \( \Omega \), and by \( C_+(\Omega) \) its positive cone, i.e., \( C_+(\Omega) = \{ N \in C(\Omega) | N(x) \geq 0 \text{ for all } x \in \Omega \} \). All densities \( N_t \) considered in this work belong to \( C_+(\Omega) \).

The sedentary stage is described by a nonlinear operator \( F_t : C_+(\Omega) \to C_+(\Omega) \) which corresponds to the growth

\[
N_{t+1} = F_t(N_t), \quad t \geq 0.
\]

Note that we allow the growth to depend on time \( t \). For instance, \( F_t \) can be a logistic-type map of the following form.

**Example 2.1.** Given \( t \geq 0 \), \( N \in C_+(\Omega) \) and \( x \in \Omega \), we set

\[
F_t(N)(x) = \lambda_t(x) N(x) (1 - \kappa_t(x)^{-1} N(x))^+, \tag{2}
\]

where \( a^+ = \max \{ a, 0 \} \) for any real number \( a \). Here \( \lambda_t \) is the intrinsic growth rate, and \( \kappa_t \) is the carrying capacity of the environment. The map \( F_t \) is called the *logistic function*. Another example is the so-called *Ricker-function* defined by

\[
F_t(N)(x) = \lambda_t(x) N(x) \exp(-\kappa_t(x)^{-1} N(x)). \tag{3}
\]

More generally, we may take the Nemyskii operator

\[
F_t(N)(x) = N(x) g_t(x, N(x)), \quad x \in \Omega, \quad N \in C_+(\Omega), \tag{4}
\]

where \( g_t : \Omega \times [0, \infty) \to [0, \infty) \) is a continuous function of the variable \((x, N)\) which is called the *growth rate*.

In this example we modeled crowding of population as a local phenomenon through the expressions

\[
(1 - \kappa_t(x)^{-1} N(x))^+ \text{ in (2)}, \quad \exp(-\kappa_t(x)^{-1} N(x)) \text{ in (3)}. \]

However, the crowding phenomenon is not necessarily local. A more realistic and general example of the operator \( F_t \) is the following one.

**Example 2.2.** Given \( t \geq 0 \), \( N \in C_+(\Omega) \) and \( x \in \Omega \), we set either

\[
F_t(N)(x) = \lambda_t(x) N(x) (1 - \kappa_t(x)^{-1} L_t N(x))^+ \tag{5}
\]

or

\[
F_t(N)(x) = \lambda_t(x) N(x) \exp(-\kappa_t(x)^{-1} L_t N(x)), \tag{6}
\]

where \( L_t \) is a bounded linear operator on \( C(\Omega) \) which maps \( C_+(\Omega) \) into itself. For instance, we may take

\[
L_t N(x) = \int_{\Omega} l_t(x, y) N(y) \, dy, \quad x \in \Omega, \quad N \in C(\Omega), \tag{7}
\]
where \( I_i(x, y) \) is a nonnegative continuous function on \( \Omega \times \Omega \). More generally, we may consider the following generalization of (4):

\[
F_i(N)(x) = N(x)g_i(x, N(x), L_i N(x)), \quad x \in \Omega, \quad N \in C_+(\Omega),
\]

where \( g_i: \Omega \times [0, \infty) \times [0, \infty) \to [0, \infty) \) is a continuous function of the variable \((x, N, L)\) which is called the growth rate again.

Note that the maps \( F_i \) from these two examples are Fréchet differentiable at the point \( 0 \in C_+(\Omega) \) with the Fréchet derivative

\[
[F_i'(0)N](x) = g_i(x, 0, 0)N(x), \quad x \in \Omega, \quad N \in C(\Omega),
\]

in the most general case (8).

The dispersal stage is described by a linear operator \( K_i: C(\Omega) \to C(\Omega) \) which maps \( C_+(\Omega) \) into itself. This operator corresponds to dispersion of population after the sedentary stage:

\[
N_{i+1} = K_i F_i(N_i), \quad t \geq 0.
\]

Since in nature organisms tend to develop time-independent dispersal strategies, we will be concerned mostly with \( K = K \) independent of \( t \). For instance, \( K \) can be a pointwise multiplication operator or an integral operator of the following form.

**Example 2.3.** Given \( N \in C(\Omega) \) and \( x \in \Omega \), we set either

\[
KN(x) = \phi(x) \cdot N(x)
\]

where \( \phi \in C_+(\Omega) \), or

\[
KN(x) = \int_{\Omega} k(x, y) N(y) \, dy
\]

where \( k(x, y) \) is a nonnegative continuous function on \( \Omega \times \Omega \) satisfying

\[
\int_{\Omega} k(x, y) \, dx \leq \psi(y) \quad \text{for all } y \in \Omega,
\]

where \( \psi \in C_+(\Omega) \) is a given function with the following meaning. The number \( 1 - \psi(y) \) is the probability that the population from a small neighborhood of the point \( y \in \Omega \) is lost during the dispersal stage. In fact, if

\[
\mathcal{P}N = \int_{\Omega} N(x) \, dx, \quad N \in C_+(\Omega),
\]

denotes the total number of individuals, then (12) holds if and only if the inequality

\[
\mathcal{P}KN \equiv \mathcal{P}(\psi N) \quad \text{holds for all } N \in C_+(\Omega).
\]

It will turn out later that the following two types of kernels \( k(x, y) \) are of special interest:

\[
k(x, y) = \phi(|x - y|)\psi(y)
\]

where \( \phi: [0, \infty) \to [0, \infty) \) is a continuous function and \( \psi \in C_+(\Omega) \), and

\[
k(x, y) = \phi(x)\psi(y)
\]

where \( \phi, \psi \in C_+(\Omega) \) satisfy \( \int_{\Omega} \phi(x) \, dx \leq 1 \) and \( \psi(y) \leq 1 \) for each \( y \in \Omega \).

The operator \( K \) given by (10) occurs with a population that does not disperse (e.g., plants which tend to drop their seeds straight down). On the other hand, \( K \) given by (11) occurs with a population that actually disperses. The kernel \( k \) from (14) models
the case when the population is carried a certain fixed distance $|x - y|$ by wind or animals, while $k$ from (15) models the case when the population is carried to any place within or out of the habitat. In particular, diffusion is a special case of (14).

Hence, the evolution of our population is governed by the dynamical system

$$N_{t+1} = \Phi_t(N_t), \quad t = 0, 1, 2, \cdots ,$$

where the operator $\Phi_t : C_+(\Omega) \to C_+(\Omega)$ is the composition of $K_t$ and $F_t$, i.e., $\Phi_t = K_t \circ F_t$.

In the rest of this paper we investigate some interesting properties of this dynamical system: existence as well as local and global stability of periodic solutions, asymptotic behavior of $N_t$ as $t \to \infty$, and the influence of dispersal on these properties. We find optimal dispersion $K$ which guarantees the existence of nontrivial periodic solutions to (16) in the case when $K_t = K$ is a time-independent unknown operator and $F_t (t \geq 0)$ ranges over a set $\mathcal{F}$ of nonlinear operators. This turns out to be an optimization problem for $K$ over all possible choices of $F_t \in \mathcal{F} (t \geq 0)$.

Our methods of investigation are based on operator theory. For the theory of linear operators on Banach lattices we refer to the monographs by Schaefer [23] and [24], and for the theory of nonlinear operators to Deimling [5]; and Krasnoselskii and Zabreiko [13]. For an earlier treatment of a similar equation in the case of a monotone nonlinearity we refer to Amann [2].

3. Existence of nontrivial $p$-periodic solutions. In this section we formulate necessary and sufficient conditions on the operators $\Phi_t$, under which the dynamical system (16) has a nontrivial $p$-periodic solution $N^* \in C_+(\Omega) \setminus \{0\}$, where $p \geq 1$ is a fixed integer. More precisely, we want to solve the fixed-point equation

$$N^* = \Psi_p(N^*) \quad \text{for} \quad N^* \in C_+(\Omega) \setminus \{0\},$$

where $\Psi_p = \Phi_{p-1} \circ \cdots \circ \Phi_1 \circ \Phi_0$. We will see later that this problem is closely connected with the spectral radius $r$ of the Fréchet derivative $\Psi'_p(0)$ of the map $\Psi_p$ at the point $0 \in C_+(\Omega)$. Note that

$$\Psi'_p(0) = \Phi'_{p-1}(0) \cdots \Phi'_1(0) \Phi'_0(0)$$

whenever $\Phi_t(0) = 0$ and the Fréchet derivative $\Phi'_t(0)$ exists for all $t = 0, 1, \cdots , p-1$.

By Fréchet derivative at the point $0 \in C_+(\Omega)$ we mean the Fréchet derivative from the right with respect to the cone $C_+(\Omega)$ (cf. Deimling [5, §§ 7.7 and 19.4]).

To formulate our existence theorem we need the following well-known concepts: Let $\| \cdot \|_{C_+}$ denote the maximum norm on $C_+(\Omega)$, and let $\leq$ denote the pointwise ordering on $C(\Omega)$ (i.e., $f \leq g$ in $C(\Omega)$ if and only if $f(x) \leq g(x)$ for all $x \in \Omega$). We write $f < g$ if $f \leq g$ and $f \neq g$ in $C(\Omega)$, and $f \ll g$ if $f(x) < g(x)$ for all $x \in \Omega$. We denote by $1$ the constant function on $\Omega$ which is equal to one. We say that a linear operator $A$ on $C(\Omega)$ is positive (shortly $A \geq 0$) if $A f \geq 0$ whenever $f \geq 0$, and strictly positive (shortly $A > 0$) if $A f > 0$ whenever $f > 0$.

By the Riesz representation theorem (cf. Rudin [21]) we identify the dual space of $C(\Omega)$ with the Banach lattice $M(\Omega)$ of all complex-valued regular bounded Borel measures on $\Omega$, with respect to the duality

$$\langle f, \mu \rangle = \int f(x) \, d\mu(x) \quad \text{for all} \quad f \in C(\Omega) \quad \text{and} \quad \mu \in M(\Omega).$$

We denote by $M_+(\Omega)$ the positive cone of all nonnegative measures from $M(\Omega)$. Finally, we say that a positive operator $A$ on $C(\Omega)$ is irreducible if, given $0 \neq f \in C_+(\Omega)$ and $0 \neq \mu \in M_+(\Omega)$, there exists an integer $n \geq 1$ such that $\langle A^n f, \mu \rangle > 0$. For instance,
if $K$ is an integral operator with a nonnegative continuous kernel $k(x, y)$ on $\Omega \times \Omega$, then $K \geq 0$ on $C(\Omega)$. If, in addition, the interior of $\Omega$ is a connected subset of $\mathbb{R}^n$, and

$$k(x, x) > 0 \quad \text{for all } x \in \Omega,$$

then $K$ is also irreducible. (Proof. By (20), there exists $\delta > 0$ such that $k(x, y) > 0$ for $|x - y| \leq \delta$. Given $\tilde{x}, \tilde{y} \in \Omega$, we can find a finite set of points $x_0 = \tilde{x}, x_1, \ldots, x_{n-1}, x_n = \tilde{y}$ in $\Omega$ such that $|x_i - x_{i-1}| \leq \delta$ for $1 \leq i \leq n$. Hence, the kernel

$$k_n(x, y) = \int_\Omega \int_\Omega \cdots \int_\Omega k(x, x_1) k(x_1, x_2) \cdots k(x_{n-1}, y) \, dx_1 \, dx_2 \cdots \, dx_{n-1}$$

of the operator $K^n$ satisfies $k_n(\tilde{x}, \tilde{y}) > 0$. Furthermore, given $0 \neq f \in C_c(\Omega)$ and $0 \neq \mu \in M_c(\Omega)$, we can find $\tilde{x}, \tilde{y} \in \Omega$ such that $f(\tilde{y}) > 0$ and $\mu(\tilde{y}) > 0$ for every open neighborhood $U$ of $\tilde{x}$. Thus, $k_n(\tilde{x}, \tilde{y}) > 0$ implies $\langle K^n f, \mu \rangle > 0$.)

We have already mentioned that the sets $C_c(\Omega)$ and $M_c(\Omega)$ are cones. In general, a subset $C$ of a Banach space $X$ is said to be a cone (with vertex at zero) if it is closed, convex, and satisfies $Af \in C$ whenever $\lambda \geq 0$ and $f \in C$, and $f, -f \in C$ implies $f = 0$. We will always assume that $C \neq \{0\}$.

Now we are ready to state our existence theorem in which the key role is played by the spectral radius $r = \text{spr} \left( \Psi'_p(0) \right)$ of the operator $\Psi'_p(0)$ on $C(\Omega)$.

**Theorem 3.1.** Let $C \subset C_c(\Omega)$ be a cone, and let $\Phi_t : C_c(\Omega) \to C_c(\Omega)$ be a continuous map such that $\Phi_t(C)$ is a relatively compact subset of $C$, for $t = 0, 1, \ldots, p - 1$. Assume that $\Phi_t$ is Fréchet differentiable at zero, and there exists a function $\eta : [0, \infty) \to [0, 1]$, with $\eta(s) \to 1$ as $s \to 0$, such that

$$\eta(\|N\|_\infty) \cdot \Phi'_t(0) N \leq \Phi_t(N) \leq \Phi'_t(0) N \quad \text{for all } 0 \neq N \in C.$$

Finally, assume that the operator $\Psi'_p(0)$ (cf. (18)) is completely continuous and irreducible on $C(\Omega)$. Then the map $\Psi_p$ (cf. (17)) has a fixed point $N^* \in C \setminus \{0\}$ if and only if

$$r = \text{spr} \left( \Psi'_p(0) \right) > 1.$$

**Proof.** First let us assume that (17) holds with $N^* \in C \setminus \{0\}$. To show that $r > 1$ we observe that, by induction on $p$, (21) implies

$$N^* = \Psi_p(N^*) < \Psi'_p(0) N^*.$$

Since $\Psi'_p(0)$ is completely continuous and irreducible on $C(\Omega)$, we have $r > 0$ (cf. Schaefer [24, Thm. V.6.3]). Moreover, $r$ is an eigenvalue of $\Psi'_p(0)$ with a strictly positive spectral projection $P$ of rank one (cf. Schaefer [24, Cor. III.8.5]). Applying this projection to (22) we obtain

$$PN^* < P \Psi'_p(0) N^* = rPN^*.$$

Finally, $N^* > 0$ entails $PN^* > 0$, and consequently, $r > 1$.

Let now $r > 1$. To prove the solvability of equation (17) in $C \setminus \{0\}$ we need the following result (cf. Deimling [5, Thm. 20.1]).

**Lemma 3.2.** Let $\Psi$ be a compact map from a cone $C \subset C_c(\Omega)$ into itself. Suppose that there exist two numbers $R$ and $\rho$ with $0 < \rho < R < \infty$ such that

(a) $\Psi(N) \neq \lambda N$ for all $N \in C$ with $\|N\|_\infty = R$ and all $\lambda > 1$.

(b) There exists $e \in C \setminus \{0\}$ such that $N - \Psi(N) \neq \lambda e$ for all $N \in C$ with $\|N\|_\infty = \rho$ and all $\lambda > 0$. Then $\Psi$ has a fixed point in $\{ N \in C \mid \rho \leq \|N\|_\infty \leq R \}$.

Thus, it remains to show that the map $\Psi_p$ restricted to the cone $C$ is compact and satisfies hypotheses (a) and (b) of this lemma.
First of all, the relative compactness of each \( \Phi_i(C) \) in \( C \) shows that \( \Psi_p(C) \) is relatively compact in \( C \). The continuity of \( \Psi_p \) follows from that of each \( \Phi_i \).

(a) Since the set \( \Psi_p(C) \) is relatively compact in \( C(\Omega) \), we have

\[
\tilde{R} = \sup \{ \| \Psi_p(N) \|_{\infty} \mid N \in C \} < \infty.
\]

Hence, we may choose any \( R \geq \tilde{R} \) to satisfy hypothesis (a).

(b) Making use of induction on \( p \), we deduce from (21) that

\[
\Theta_p(N) \cdot \Psi_p'(0) N \leq \Psi_p(N) \quad \text{for all } n \in C,
\]

where \( \Theta_p(N) = \eta(\| \Psi_p(-1) \|_{\infty}) \cdots \eta(\| \Psi_1(N) \|_{\infty}) \eta(\| N \|_{\infty}) \) is a map with \( \Theta_p(N) \to 1 \) as \( \| N \|_{\infty} \to 0 \). Thus,

\[
N - \Psi_p(N) = N - \Theta_p(N) \cdot \Psi_p'(0) N \quad \text{for all } N \in C.
\]

Now we apply the projection \( P \) from the first half of this proof to the last inequality, thus obtaining

\[
P(N - \Psi_p(N)) \leq PN - \Theta_p(N) r \cdot PN = (1 - \Theta_p(N) r) PN \quad \text{for all } N \in C.
\]

Next we choose \( \rho \in (0, R) \) so small that \( 1 - \Theta_p(N) r \equiv 0 \) for \( \| N \|_{\infty} \equiv \rho \). Then we have \( P(N - \Psi_p(N)) \equiv 0 \) whenever \( \| N \|_{\infty} \equiv \rho \). In particular, the strict positivity of \( P \) implies

\[
P(N - \Psi_p(N)) < \lambda P \text{e} \quad \text{for all } N \in C \text{ with } \| N \|_{\infty} \equiv \rho \text{ for all } \lambda > 0,
\]

and for any \( e \in C \setminus \{0\} \). Hence, (b) also is valid.

In the following two results we apply Theorem 3.1 to the situations arising in Examples 2.1 and 2.2, respectively. These two cases differ in the choice of the cone \( C \) which, in turn, depends on the choice of the operator \( K \) in Example 2.3.

**Theorem 3.3.** Let \( g_i : \Omega \times [0, \infty) \to [0, \infty) \) \( (i = 0, 1, \cdots, p - 1) \) be a continuous function with the following properties:

- **(G1)** The function \( f_i(x, N) = Ng_i(x, N) \) is uniformly bounded on \( \Omega \times [0, \infty) \).
- **(G2)** For all \( x \in \Omega \) and \( N > 0 \) we have

\[
g_i(x, N) < g_i(x, 0).
\]

Let \( K \) be a completely continuous and irreducible positive operator on \( C(\Omega) \). Finally, let \( F_i \) be defined by (4), and \( \Phi_i = K \circ F_i \). Then the map \( \Psi_p \) has a fixed point \( N^* \in C_+(\Omega) \setminus \{0\} \) if and only if \( r = \text{spr} (\Psi_p'(0)) > 1 \).

**Proof.** Since the function \( g_i \) is continuous, the Nemyskii operator \( F_i \) is a continuous map from \( C_+(\Omega) \) into itself which is Fréchet differentiable at zero with the Fréchet derivative \( F'_i(0) \) given by the formula

\[
[F'_i(0) N](x) = g_i(x, 0) N(x), \quad x \in \Omega, \quad N \in C(\Omega).
\]

The same is true of \( \Phi_i \), with \( \Phi_i'(0) = KF'_i(0) \). Property (G1) shows that \( F_i(C_+(\Omega)) \) is a bounded subset of \( C_+(\Omega) \). Hence, the complete continuity of \( K \) implies that \( \Phi_i(C_+(\Omega)) \) is a relatively compact subset of \( C_+(\Omega) \). So we may take \( C = C_+(\Omega) \) in Theorem 3.1.

To verify (21) we observe that, by (23), the function \( \Theta_i(x, N) = g_i(x, N)/g_i(x, 0) \) maps the set \( \Omega \times [0, \infty) \) into \( [0, 1] \). Moreover, the continuity of \( g_i \) shows that \( \Theta_i \) is continuous. Consequently, the function \( \eta : [0, \infty) \to [0, 1] \) defined by

\[
\eta(s) = \inf \{ \Theta_i(x, N) \mid 0 \leq t \leq p - 1, x \in \Omega, 0 \leq N \leq s \}
\]

(for \( s \geq 0 \)) satisfies \( \eta(s) \to 1 \) as \( s \to 0 \), and

\[
\eta(s) \cdot g_i(x, 0) \leq g_i(x, N) < g_i(x, 0) \quad \text{whenever } x \in \Omega \text{ and } 0 < N \leq s.
\]

It follows that

\[
\eta(\| N \|_{\infty}) \cdot F'_i(0) N \leq F_i(N) < F'_i(0) N \quad \text{for all } 0 \neq N \in C_+(\Omega).
\]

Since \( K \) is irreducible it is also strictly positive on \( C(\Omega) \), and so (24) implies (21).
Finally, the complete continuity of $K$ implies that also $\Phi'_r(0)$ is completely continuous. Hence, (18) shows that the same is true of $\Psi'_r(0)$. To prove that $\Psi'_r(0)$ is also irreducible we first note that (23) implies $\gamma = \inf \{g_r(x,0) \mid 0 \leq t \leq p - 1, x \in \Omega\} > 0$. Hence, $F'_r(0)N \equiv \gamma N$ and also $\Phi'_r(0)N \equiv \gamma KN$ for all $N \in C_+(\Omega)$. Again, (18) shows that $\Psi'_r(0)N \equiv \gamma^p KN^p$ for $N \in C_+(\Omega)$, and therefore $\Psi'_r(0)$ is irreducible since $K$ is irreducible by hypothesis.

We conclude that all hypotheses of Theorem 3.1 are satisfied, and so the conclusion of this theorem applies to our situation. □

**Theorem 3.4.** Let $g_r : \Omega \times [0, \infty) \times [0, \infty) \rightarrow [0, \infty)$ $(t = 0, 1, \ldots, p - 1)$ be a continuous function with the following properties:

\[ (G'1) \text{ Given } 0 < c_1 \leq c_2 < \infty, \text{ the function} \]

\[ \phi_r(x, N) = \sup \{f_r(x, N, L) \mid c_1 \leq L/N \leq c_2 \} \]

is uniformly bounded on $\Omega \times [0, \infty)$, where $f_r(x, N, L) = N g_r(x, N, L)$.

\[ (G'2) \text{ For all } x \in \Omega, \ N > 0 \text{ and } L > 0 \text{ we have} \]

\[ g_r(x, N, L) < g_r(x, 0, 0). \]

Let $L_r$ be a positive operator on $C(\Omega)$ such that $L_r 1 > 0$, and let $K$ be a completely continuous and irreducible positive operator on $C(\Omega)$ with the following property:

\[ (K') \text{ There exists a constant } \alpha > 0 \text{ such that } K(C_+(\Omega)) \subset C_\alpha \text{ where} \]

\[ C_\alpha = \{N \in C_+(\Omega) \mid N \equiv \alpha \|N\|_\infty 1 \}. \]

Finally, let $F_r$ be defined by (8) and $\Phi_r = K \circ F_r$. Then the map $\Psi'_r$ has a fixed point $N^* \in C_\alpha \setminus \{0\}$ if and only if $r = \text{spr}(\Psi'_r(0)) > 1$.

**Proof.** The continuity and Fréchet differentiability of the map $F_r$ follows from the continuity of $g_r$ in the same way as in the proof of Theorem 3.3. Note that the positivity of $L_r$ implies its boundedness (cf. Schaefer [24, Thm. II.5.3]). We claim that $(G'1)$ and $L_r 1 > 0$ imply that $F_r(C_\alpha)$ is a bounded subset of $C_+(\Omega)$. In fact, we have $L_r 1 \equiv \beta 1$ for $0 \leq t \leq p - 1$, with some constant $\beta > 0$. Thus, for every $N \in C_\alpha$, we have

\[ \alpha \beta \|L_r\|_\infty 1 \leq L_r N \leq \|L_r\| \|N\|_\infty 1 \]

where $\|L_r\| = \|L_r 1\|_\infty$ is the operator norm of $L_r$. Consequently, taking $c_1 = \alpha \beta$ and $c_2 = \|L_r\|/\alpha$ we arrive at

\[ c_1 N \leq L_r N \leq c_2 N \text{ for all } N \in C_\alpha. \]

We apply $(G'1)$ to conclude that the set $F_r(C_\alpha)$ is bounded. Hence, in contrast to the proof of Theorem 3.3, we must take $C = C_\alpha$.

To verify (21) we observe that, by (25), the function $\Theta_r(x, N, L) = g_r(x, N, L)/g_r(x, 0, 0)$ maps the set $[0, \infty) \times [0, \infty)$ into $[0, 1]$. We set

\[ \eta(s) = \inf \{\Theta_r(x, N, L) \mid 0 \leq t \leq p - 1, x \in \Omega, 0 \leq N \leq s, 0 \leq L \leq \|L_r\| s\} \]

(for $s \equiv 0$) with $\eta(s) \rightarrow 1$ as $s \rightarrow 0$, and

\[ \eta(s) \cdot g_r(x, 0, 0) \leq g_r(x, N, L) \leq g_r(x, 0, 0) \]

whenever $x \in \Omega$, $0 < N \leq s$ and $0 < L \leq \|L_r\| s$. Since also $c_1 N \leq L_r N \leq \|L_r\| \|N\|_\infty 1$ for every $N \in C_\alpha$, the inequalities above imply those in (24) for all $0 \neq N \in C_\alpha$. Hence, (21) follows by the same arguments as in the proof of Theorem 3.3. The rest of this proof is identical to the proof of Theorem 3.3. □

The following two corollaries of Theorems 3.3 and 3.4 cover the cases when the growth of the population is modeled by the logistic or the Ricker function, and crowding and dispersion by integral operators.
COROLLARY 3.5. Let \( \lambda_i, \kappa_i \in C_+(\Omega) \) with \( \lambda_i \gg 0 \) and \( \kappa_i \gg 0 \) \((i = 0, 1, \cdots, p - 1)\), and let the map \( F_i \) be defined by either (2) or (3). Assume that \( K \) is an integral operator on \( C(\Omega) \) defined by (11) with a nonnegative continuous kernel \( k(x, y) \) satisfying (20), and let the interior of \( \Omega \) be connected in \( \mathbb{R}^n \). Finally, let \( \Phi_i = K \circ F_i \). Then the map \( \Psi_p \) has a fixed point \( N^* \in C_+(\Omega) \setminus \{0\} \) if and only if \( r = \text{spr} \left( \Psi_p'(0) \right) > 1 \).

**Proof.** We can apply Theorem 3.3 directly. Note that Arzelà-Ascoli's theorem implies that \( K \) is completely continuous. The irreducibility of \( K \) was proved after (20).

COROLLARY 3.6. Let \( \lambda_i, \kappa_i \in C_+(\Omega) \) with \( \lambda_i \gg 0 \) and \( \kappa_i \gg 0 \) \((i = 0, 1, \cdots, p - 1)\), and let \( L_i \) be an integral operator on \( C(\Omega) \) defined by (7) with a nonnegative continuous kernel \( l_i(x, y) \) satisfying

\[
\int_\Omega l_i(x, y) \, dy > 0 \quad \text{for all} \ x \in \Omega.
\]

(For example, (20) with \( l \), in place of \( k \) implies (26).) Let \( F_i \) be defined by either (5) or (6). Assume that \( K \) is an integral operator on \( C(\Omega) \) defined by (11) with a continuous kernel \( k(x, y) \) satisfying

\[
k(x, y) > 0 \quad \text{for all} \ x, y \in \Omega.
\]

Finally, let \( \Phi_i = K \circ F_i \). Then the map \( \Psi_p \) has a fixed point \( N^* \in C_+(\Omega) \setminus \{0\} \) if and only if \( r = \text{spr} \left( \Psi_p'(0) \right) > 1 \).

**Proof.** Inequality (26) means \( L_i 1 > 0 \). By (27) and the continuity of \( k \) over the compact set \( \Omega \times \Omega \) we have

\[
0 < m_1 = \min_{\Omega \times \Omega} k \leq m_2 = \max_{\Omega \times \Omega} k < \infty.
\]

It follows from (11) that

\[
m_1 \int_\Omega N(y) \, dy \leq KN(x) \leq m_2 \int_\Omega N(y) \, dy
\]

for all \( x \in \Omega \) and \( N \in C_+(\Omega) \). Hence, hypothesis \((K')\) in Theorem 3.4 is satisfied with \( \alpha = m_1/m_2 \). Now we may apply Theorem 3.4. \( \square \)

**Example 3.7.** Let \( \lambda_0 = \lambda \) and \( \kappa_0 = \kappa \) be positive constants, and let the map \( F = F_0 \) be defined by (2), i.e., \( F(N) = \lambda N(1 - \kappa^{-1}N)^+ \) for all \( N \in C_+(\Omega) \). Assume that \( K \) and \( \Omega \) are as in Corollary 3.5, and let \( \Phi = K \circ F \). Then \( r = \text{spr} \left( \Pi(0) \right) = \lambda \cdot \text{spr} \left( K \right) \). Hence, the map \( \Phi \) has a fixed point \( N^* \in C_+(\Omega) \setminus \{0\} \) if and only if \( \lambda > 1/\text{spr} \left( K \right) \). In Examples 4.3 and 5.3 we will discuss this local and global stability of this fixed point, respectively.

4. Local stability of \( p \)-periodic solutions. In this section we study local stability of the solution \( N^* \) to the fixed-point equation (17). More precisely, given \( N_0 \in C_+(\Omega) \) and \( N_{n+1} = \Psi_p(N_n) \) for \( n = 0, 1, \cdots \), does the sequence \( \{N_n\}_{n=0}^\infty \) converge to \( N^* \) provided \( N_0 \) is sufficiently close to \( N^* \)? This certainly is the case when the operator \( \Psi_p \) on \( C_+(\Omega) \) is Fréchet differentiable at the point \( N^* \), with \( \text{spr} \left( \Psi_p'(N^*) \right) < 1 \). In this case we can find an equivalent norm \( \| \cdot \| \) on \( C(\Omega) \) under which the operator \( \Psi_p'(N^*) \) is a strict contraction (cf. Deimling [5, Prop. 9.6]). Hence, there exist \( \rho \in (0, 1) \) and \( \delta > 0 \) such that \( \| N_0 - N^* \|_\infty \leq \delta \) implies

\[
\| N_{n+1} - N^* \|_\infty \leq \rho \| N_n - N^* \|_\infty \quad \text{for all} \ n \geq 0.
\]

For the sake of simplicity we will consider only the case when \( p = 1, F_i = F \) and \( K_i = K \) for \( i \geq 0 \). We also assume that \( F \) is a Nemytskii operator defined by (4) with \( g_i = g \).
Theorem 4.1. Let $g : \Omega \times [0, \infty) \to [0, \infty)$ be a continuous function which is continuously differentiable with respect to the second variable in a set $\{(x, N) | x \in \Omega \text{ and } 0 \leq N \leq M_0(x)\}$ with some $M_0 \in C_+(\Omega)$. In addition, suppose that $g$ has the following properties:

(G1) There exists $M \in C_+(\Omega)$ such that

$$f(x, N) = Ng(x, N) \equiv M(x) \quad \text{for all } x \in \Omega, \quad N \geq 0.$$  

(G3) $g(x, 0) > 0$ for all $x \in \Omega$, and there exist $\delta > 0$ and $M_\delta \in C_+(\Omega)$ such that $M_\delta \equiv M_0$, and

$$g(x, N) \geq \left| \frac{\partial f}{\partial N} (x, N) \right| + \delta N \quad \text{for all } x \in \Omega \text{ and } 0 \leq N \leq M_\delta(x).$$

(28)

Let $K$ be a completely continuous and irreducible positive operator on $C(\Omega)$ which satisfies $KM \equiv M_\delta$. Finally, let $F$ be defined by (4), and $\Phi = K \circ F$. Then every fixed point $N^* \in C_+(\Omega) \setminus \{0\}$ of the map $\Phi$ satisfies $\text{spr}(\Phi(N^*)) < 1$. In particular, $N^*$ is locally stable.

Proof. Let $N^* = \Phi(N^*)$ for $N^* \in C_+(\Omega) \setminus \{0\}$. Then (G1) implies

$$N^* = Kf(\cdot, N^*(\cdot)) \equiv KM \equiv M_\delta.$$

Hence, we may apply (28) to obtain

$$f(x, N^*(x)) \equiv \left( \left| \frac{\partial f}{\partial N} (x, N^*(x)) \right| + \frac{1}{2} \delta N^*(x) \right) N^*(x) + \frac{1}{2} \delta N^*(x)^2,$$

for all $x \in \Omega$. We set for all $N \in C(\Omega)$,

$$AN = K \left( \left| \frac{\partial f}{\partial N} (\cdot, N^*(\cdot)) \right| + \frac{1}{2} \delta N^* \right) N.$$

Clearly, $A$ is a completely continuous, positive operator on $C(\Omega)$. We claim that $A$ is also irreducible. In fact, by (G3) there exists $\gamma > 0$ such that $f(x, N) \equiv \gamma N$ for all $x \in \Omega$ and $0 \leq N \leq M_\delta(x)$. Consequently, $N^* = Kf(\cdot, N^*(\cdot)) \equiv \gamma KN^*$. But $K$ is positive irreducible, and therefore $N^* > 0$. Thus, $\beta = \frac{1}{2} \delta \cdot \min N^* > 0$, and so $AN \equiv \beta KN$, for all $N \in C_+(\Omega)$, shows that $A$ is also irreducible.

As in the proof of Theorem 3.1, we have $\mu = \text{spr}(A) > 0$, and $\mu$ is an eigenvalue of $A$ with a strictly positive spectral projection $P$ of rank one. To conclude our proof we first observe that (29) implies

$$N^* = Kf(\cdot, N^*(\cdot)) \equiv AN^* + \frac{1}{2} \delta \cdot K(N^*)^2.$$

But the irreducibility of $K$ and $N^* \gg 0$ entail $K(N^*)^2 > 0$, and so $N^* > AN^*$. Thus, $PN^* > PAN^* = \mu PN^*$, and consequently, $\mu < 1$. Finally, the inequality

$$|\Phi(N^*)N| \equiv \left| K \left[ \frac{\partial f}{\partial N} (\cdot, N^*(\cdot)) N \right] \right| \leq A|N|$$

implies $|\Phi(N^*)^nN| \equiv A^n|N|$, for all $N \in C(\Omega)$ and $n = 1, 2, \cdots$, whence $\|\Phi(N^*)^n\|^{1/n} \leq \|A^n\|^{1/n}$. By Gelfand’s formula we let $n \to \infty$ to obtain $\text{spr}(\Phi(N^*)) \leq \mu < 1$. □

The following corollary of Theorem 4.1 covers the case when the growth of population is modeled by the logistic or the Ricker function, and dispersion by an integral operator.

Corollary 4.2. Let $\lambda, \kappa \in C_+(\Omega)$ with $\lambda \gg 0$ and $\kappa \gg 0$, and let the map $F$ be defined by (2) or (3). Assume that $K$ is an integral operator on $C(\Omega)$ defined by (11) with a
nonnegative continuous kernel \( k(x, y) \) satisfying (20), and let the interior of \( \Omega \) be connected in \( \mathbb{R}^n \). Again, let \( \Phi = K \circ F \). Finally, we set \( \varepsilon = 8/3 \) if \( F \) is defined by (2), and \( \varepsilon = 2e \) if \( F \) is defined by (3). (Here \( e = 2.71828 \ldots \).

Then the inequality \( K(\lambda \kappa) \ll \varepsilon \kappa \) implies that every fixed point \( N^* \in C_+(\Omega) \setminus \{0\} \) of the map \( \Phi \) satisfies \( \text{spr}(\Phi'(N^*)) < 1 \). In particular, \( N^* \) is locally stable.

**Proof.** (a) Let \( F \) be defined by (2), and \( g(x, y) = \lambda(x)(1 - \kappa(x)^{-1} N)^* \) for \( x \in \Omega, \ N \geq 0 \). Then hypothesis (G1) of Theorem 4.1 is satisfied with \( M = \frac{1}{\lambda} \kappa \). Next we may choose \( M_0 = \kappa \). Hypothesis (G3) is satisfied for every \( M_0 \in C_+(\Omega) \) with \( M_0 \ll \frac{3}{2} \kappa \), provided \( \delta > 0 \) is small enough. In particular, we may take \( M_0 = \frac{1}{2} K(\lambda \kappa) \ll \frac{1}{2} \varepsilon \kappa = \frac{3}{2} \kappa \), in which case \( KM = M_0 \). Consequently, Theorem 4.1 applies to our situation.

(b) The case when \( F \) is defined by (3) is completely analogous. We have to take \( M = (1/e) \lambda \kappa \), \( M_0 = 2 \kappa \) and \( M_0 = (1/e) K(\lambda \kappa) \ll 2 \kappa \).

We illustrate Corollary 4.2 with the following continuation of Example 3.7.

**Example 4.3.** Suppose that all hypotheses of Example 3.7 are satisfied. Then \( K(\lambda \kappa) = \lambda \kappa \cdot K \) is \( \lambda \kappa \| K \| \). Hence, the inequality \( \lambda < \frac{3}{2} \| K \|^{-1} \) implies that every fixed point \( N^* \in C_+(\Omega) \setminus \{0\} \) of the map \( \Phi \) satisfies \( \text{spr}(\Phi'(N^*)) < 1 \).

We do not know whether the constant \( \frac{3}{2} \) in the inequality above can be replaced by a number \( \varepsilon \in (\frac{3}{2}, 3] \). Namely, let us take \( K \) to be the average operator

\[
KN(x) = |\Omega|^{-1} \int_{\Omega} N(y) \, dy \quad \text{for } x \in \Omega, \ N \in C(\Omega),
\]

where \( |\Omega| = \int_{\Omega} dy \) is the \( n \)-dimensional Lebesgue measure of the set \( \Omega \subset \mathbb{R}^n \). Then the map \( \Phi \) has a unique nontrivial fixed point \( N^* = (1 - 1/\lambda) \kappa \). Furthermore, \( N^* > 0 \) if and only if \( \lambda > 1 \). A straightforward computation yields \( \text{spr}(\Phi'(N^*)) = |2 - \lambda| \). Thus, \( N^* \) is locally stable if and only if \( 1 < \lambda < 3 \). Note that \( \| K \| = 1 \). Hence, in this special case we may replace \( \frac{3}{2} \) by \( 3 \).

5. **Global stability of \( p \)-periodic solutions.** In this section we study global stability of the solution \( N^* \) to the fixed-point equation (17). As in \( \S 4 \), we consider a sequence \( \{N_n\}_{n=0}^{\infty} \) defined by \( N_0 \in C_+(\Omega) \) and \( N_{n+1} = \Psi_p(N_n) \) for \( n = 0, 1, \ldots \). Does this sequence converge to \( N^* \) provided \( N_0 > 0 \)? If it does, then \( N^* \) is the unique solution of equation (17). To prove this convergence we need to impose certain monotonicity and weak concavity assumptions on the restriction of the map \( \Psi_p \) to an order interval containing the image of \( \Psi_p \) (cf. Krasnoselski and Zabreiko [13, \S 47.6]).

To formulate our global stability theorem we need the following concepts. Given \( f, g \in C(\Omega) \) with \( f \leq g \), the set \( \{f, g\} = \{h \in C(\Omega) | f \leq h \leq g\} \) is called an order interval in \( C(\Omega) \). An operator \( \Phi : [0, g] \to C(\Omega) \) is called monotone if \( \Phi(f) \leq \Phi(g) \) whenever \( f \leq g \), and \( \Phi \) is \( \Phi \) a weakly concave if \( \Phi(r \phi) \geq r \Phi(\phi) \) whenever \( 0 \leq \phi \leq [0, g] \) and \( 0 < r < 1 \).

For the sake of simplicity we will consider only the case when \( p = 1 \) and \( \Phi_t = \Phi = K \circ F_t \) for \( t \geq 0 \). We start with the following abstract form of our global stability result.

**Theorem 5.1.** Let \( \Phi : C_+(\Omega) \to C_+(\Omega) \) be continuous such that for some \( M \in C_+(\Omega) \), \( \Phi(C_+(\Omega)) \) is a relatively compact subset of \( [0, M] \), and the restriction of \( \Phi \) to \( [0, M] \) is monotone and weakly concave. In addition, suppose that, given \( 0 < N \in [0, M] \), there exists an integer \( j \geq 1 \) such that

\[
\Phi^j(N) = \Phi \circ \cdots \circ \Phi(N) > 0.
\]

Finally, let \( 0 < N_0 \in C_+(\Omega) \) and \( N_{n+1} = \Phi(N_n) \) for \( n \geq 0 \). Then the limit

\[
N^* = \lim_{n \to \infty} N_n \text{ exists in } C(\Omega)
\]
and satisfies \( N^* = \Phi(N^*) \). Moreover, if \( \Phi \) has a nontrivial fixed point in \( C_+(\Omega) \setminus \{0\} \), then this fixed point is unique and equal to \( N^* \).

Proof. Let \( M_0 = M \) and \( M_{n+1} = \Phi(M_n) \) for \( n \geq 0 \). Since \( \Phi \) is bounded above by \( M \) and monotone, we have \( M_{n+1} \leq M_n \) for \( n \geq 0 \). Hence, the compactness of \( \Phi \) implies that the limit \( N^* = \lim_{n \to \infty} M_n \) exists in \( C(\Omega) \). Clearly, \( \Phi(N^*) = N^* \) by the continuity of \( \Phi \). So we are done if \( N^* = 0 \). Thus, from now on we will assume that \( N^* > 0 \). Since \( \Phi \) satisfies (30), we even have \( N^* > 0 \).

In the rest of this proof we compare \( N_n \) to \( M_n \) and \( N^* \). Since \( N_0 = \Phi(N_0) \leq M \), we may assume that already \( N_0 = M \). Also, (30) shows that there exists an integer \( j \geq 0 \) such that \( N_j > 0 \). Hence, we may assume that \( 0 \leq N_0 \leq M \). The monotonicity of \( \Phi \) implies

\[
N_n \leq M_n \quad \text{for all} \quad n \geq 0.
\]

Let us set \( r_n = \min_{\Omega}(N_n/N^*) \), \( n \geq 0 \). We need to show that

\[
r_n \to 1 \quad \text{as} \quad n \to \infty.
\]

Then (31) follows from (32) and (33).

To show (33) we first observe that \( r_n N^* \leq N_n \) for all \( n \geq 0 \). In particular, if \( r_n \geq 1 \) for some \( m \geq 0 \), then \( N_n \leq N^* \) for all \( n \geq m \) by the monotonicity of \( \Phi \), and (31) follows from (32). So we may assume that \( r_n < 1 \) for all \( n \geq 0 \). Since \( N^* > 0 \), we have \( 0 < r_n < 1 \). We claim that

\[
0 < r_n < r_{n+1} < 1 \quad \text{for all} \quad n \geq 0.
\]

It remains to prove that, given \( n \geq 0 \), the inequalities \( 0 < r_n < 1 \) imply \( r_n < r_{n+1} \). In fact, the weak concavity and monotonicity of \( \Phi \) imply

\[
r_n N^* = r_n \Phi(N^*) \preceq \Phi(r_n N^*) \preceq \Phi(N_n) = N_{n+1}
\]

which proves \( r_n < r_{n+1} \). Note that \( \Omega \) is compact. Finally, let \( r^* = \lim_{n \to \infty} r_n \). By (34) we have \( 0 < r^* \leq 1 \). If \( r^* = 1 \), then (33) holds. So we may assume that \( 0 < r^* < 1 \).

By the weak concavity of \( \Phi \) we have

\[
r^* \Phi(N^*) + \eta 1 \preceq \Phi(r^* N^*)
\]

for some \( \eta > 0 \), and by the continuity of \( \Phi \) we have the existence of an integer \( n_0 \geq 0 \) such that

\[
\Phi(r^* N^*) \preceq \Phi(r_n N^*) + \eta 1 \quad \text{for all} \quad n \geq n_0.
\]

Combining the last two inequalities we arrive at

\[
r^* N^* = r^* \Phi(N^*) \preceq \Phi(r_n N^*) \quad \text{for each} \quad n \geq n_0.
\]

Since \( r_n N^* \leq N_n \) and \( \Phi \) is monotone, we obtain

\[
\Phi(r_n N^*) \leq \Phi(N_n) = N_{n+1} \quad \text{for each} \quad n \geq 0.
\]

Again, combining the last two inequalities we arrive at \( r^* N^* \leq N_{n+1} \) for each \( n \geq n_0 \). Thus, \( r^* \leq r_{n+1} \) for each \( n \geq n_0 \) which contradicts (34). It follows that \( r^* = 1 \).

The following corollary of Theorem 5.1 covers the case when the growth of population is modeled by the logistic or the Ricker function, and dispersion by an integral operator.

**Corollary 5.2.** Let all hypotheses stated in Corollary 4.2. be satisfied. In addition, assume that the set \( \Omega \) is convex in \( \mathbb{R}^n \). Again, let \( \Phi = K \circ F \). We set \( \epsilon' = 2 \) if \( F \) is defined by (2), and \( \epsilon' = \epsilon \) if \( F \) is defined by (3).
Then the inequality \( K(\lambda \kappa) \geq \varepsilon^\prime \kappa \) implies that the limit (31) exists for every \( 0 < N_0 \in C_+(\Omega) \), and is equal to the unique nontrivial fixed point of \( \Phi \) if there is any.

**Proof.** (a) Let \( F \) be defined by (2), and
\[
\Phi(N) = K[\lambda N(1 - \kappa^{-1}N)^+] \quad \text{for} \quad N \in C_+(\Omega).
\]
Then we may choose \( M = \frac{1}{\kappa} \) in Theorem 5.1. In fact, we have
\[
0 \leq \Phi(N) \leq \frac{1}{2} K(\lambda \kappa) \leq \frac{1}{2} \varepsilon^\prime \kappa = \frac{1}{\kappa} = M
\quad \text{for all} \quad N \in C_+.
\]
Since \( K \) is completely continuous and \( F(C_+(\Omega)) \subseteq [0, \frac{1}{2} \lambda \kappa] \), we conclude that \( \Phi(C_+(\Omega)) \) is a relatively compact subset of \([0, M]\). Since \( F \) is monotone and weakly concave on \([0, M]\), so is \( \Phi \). Note that \( K1 \gg 0 \) which follows from the irreducibility of \( K \) on \( C(\Omega) \).

To verify (30) we first observe that \( F(N) \gg \frac{1}{2} \lambda \kappa = \lambda N \) for \( N \in [0, M] \). Hence, setting \( \beta = \frac{1}{2} \min_\lambda \lambda > 0 \) we obtain
\[
\Phi^j(N) \gg \beta^j K^j N \quad \text{for all} \quad N \in [0, M], \quad j \geq 1.
\]
Since the kernel \( k \) of \( K \) satisfies (20) and the set \( \Omega \) is convex and compact in \( \mathbb{R}^n \), there exists an integer \( j \geq 1 \) such that the kernel \( k_j \) of the operator \( K^j \) is strictly positive on \( \Omega \times \Omega \). (For a proof of this claim, see the proof of the irreducibility of \( K \) after (20).) Consequently, \( 0 < N \in C_+(\Omega) \) implies \( K^j N \gg 0 \), and therefore (30) follows from (35).

Now we may apply Theorem 5.1.

(b) The case when \( F \) is defined by (3) is completely analogous. We have to take \( M = \kappa \). \( \square \)

We illustrate Corollary 5.2 with the following continuation of Examples 3.7 and 4.3.

**Example 5.3.** Suppose that all hypotheses of Example 3.7 are satisfied. In addition, assume that \( \Omega \) is convex. The \( K(\lambda \kappa) = \lambda \kappa \cdot K1 \leq \lambda \kappa \|K\| \). Hence, the inequality \( \lambda \leq 2 \|K\|^{-1} \) implies that the limit (31) exists for every \( 0 < N_0 \in C_+(\Omega) \), and is equal to the unique nontrivial fixed point of \( \Phi \) if there is any.

Again, we do not know whether the constant two in the inequality above can be replaced by a number \( \varepsilon^\prime \in (2, 3] \). The reasons for asking this question are similar to those given in Example 4.3.

6. **Dispersal in time-invariant environment.** In this section we consider a time-invariant environment represented by a nonlinear operator \( F_t = F \) on \( C_+(\Omega) \), for \( t \geq 0 \), which is defined by either (4) or (8). In particular, the map \( F \) is Fréchet differentiable at zero with the Fréchet derivative \( F'(0) \) given by
\[
F'(0)N = \lambda \cdot N, \quad N \in C(\Omega),
\]
where either \( \lambda = g(\cdot, 0) \) or \( \lambda = g(\cdot, 0, 0) \). We assume that also the dispersal strategy of our population is time-invariant and represented by a linear operator \( K_t = K \) on \( C(\Omega) \), for \( t \geq 0 \), which is defined by either (10) or (11). Hence, the evolution of our population is governed by the dynamical system (16) with \( \Phi_t = \Phi = K \circ F \).

A natural question is the following. Given a set \( \mathcal{F} \) of possible environments (or growth conditions) \( F \), which is the best possible dispersal strategy \( K \) that guarantees survival of the population in every environment \( F \in \mathcal{F} \)? Under the concept of *survival* we mean the following situation. Given \( F \in \mathcal{F} \) and \( K \), the fixed-point equation \( N^* = KF(N^*) \) has a nontrivial solution \( N^* \in C_+(\Omega) \). In case the operator \( \Phi = K \circ F \) satisfies the hypotheses of Theorem 3.1 with \( p = 1 \) (see also Theorems 3.3 and 3.4), the existence of a nontrivial fixed point \( N^* \) to the map \( \Phi \) is equivalent to \( r = \text{spr} (\Phi'(0)) > 1 \). In our case we have \( \Phi'(0) = K_1 \), where
\[
K_1N = K(\lambda N) \quad \text{for} \quad N \in C(\Omega),
\]
and either \( \lambda = g(\cdot, 0) \) or \( \lambda = g(\cdot, 0, 0) \). Our rather general concept of survival is supported by our stability results stated as Theorems 4.1 and 5.1. In particular, the limit (30) shows the convergence of the population to a fixed point \( N^* \) of the map \( \Phi \). Moreover, \( N^* > 0 \) if and only if \( r = \text{spr} (\Phi(0)) > 1 \). Hence, the survival of the population depends only on the intrinsic growth rate \( \lambda \). Let \( \Lambda \) denote the set of all \( \lambda \) arising from some \( F \in \mathcal{F} \) through equation (36). In the sequel we assume that \( \Lambda \) is a given subset of \( C_+(\Omega) \backslash \{0\} \). Clearly, if the population is to survive under every intrinsic growth rate \( \lambda \in \Lambda \), then the inequality \( r = \text{spr} (K_\lambda) > 1 \) must hold for every \( \lambda \in \Lambda \). Our task is to find an operator \( K \) that has the best chance to satisfy this inequality. Such an operator \( K \) must maximize the number

\[
(38) \quad s(K, \Lambda) = \inf \{ \text{spr} (K_\lambda) | \lambda \in \Lambda \}.
\]

Moreover, such a maximizer \( K \) should have the form (10) or (11), and it should satisfy also inequality (12), where \( \psi \in C_+(\Omega) \backslash \{0\} \) is a fixed function satisfying also \( \psi \leq 1 \). In order to specify the set of operators \( K \) over which we are going to maximize the number \( s(K, \Lambda) \) we need the following operator-theoretical preliminaries.

First of all, we imbed the space \( C(\Omega) \) into its dual \( M(\Omega) \) by identifying a function \( f \in C(\Omega) \) with the measure \( \mu \in M(\Omega) \) defined by \( d\mu(x) = f(x) \, dx \). This imbedding is a homomorphism of Banach lattices that is also bounded. Keeping this imbedding in mind we write \( C(\Omega) \subset M(\Omega) \). Next, we note that \( C(\Omega) \) is a sequentially weakly-star dense subset of \( M(\Omega) = C(\Omega)^* \), i.e., given \( \mu \in M(\Omega) \), there exists a sequence \( \{f_n\} \subset C(\Omega) \) such that, for every \( f \in C(\Omega) \), we have \( \langle f, f_n \rangle \to \langle f, \mu \rangle \) as \( n \to \infty \) (cf. (19)). This claim is an easy consequence of a regularization argument (cf. Hörmander [9, Thms. 2.1.9, 4.1.5]).

Now it is clear that the operator \( K \) on \( C(\Omega) \) defined by (10) or (11) can be extended to a bounded linear operator \( \tilde{K} \) on \( M(\Omega) \) in a unique way. In fact, if \( K \) is defined by (10), then \( d(\tilde{K} \mu)(x) = \phi(x) \, d\mu(x) \) for \( \mu \in M(\Omega) \), and if \( K \) is defined by (11), then

\[
\tilde{K} \mu(x) = \int_\Omega k(x, y) \, d\mu(y) \quad \text{for} \quad \mu \in M(\Omega)
\]

is still in \( C(\Omega) \). In either case, the spectra of the operators \( K \) on \( C(\Omega) \) and \( \tilde{K} \) on \( M(\Omega) \) coincide. In particular, the same is true of their spectral radii:

\[
(39) \quad \text{spr} (K) = \text{spr} (\tilde{K}).
\]

Similarly, \( \text{spr} (K_\lambda) = \text{spr} (\tilde{K}_\lambda) \) for all \( \lambda \in C_+(\Omega) \).

More generally, let \( K \) be a positive operator on \( C(\Omega) \), and let \( K^* \) denote its adjoint on \( M(\Omega) \), i.e., \( \langle f, K^* \mu \rangle = \langle Kf, \mu \rangle \) for all \( f \in C(\Omega) \) and \( \mu \in M(\Omega) \). Furthermore, let us assume that \( K^* \) maps \( C(\Omega) \) into itself and satisfies also

\[
(40) \quad K^* 1 \leq \psi.
\]

This is the case if \( K \) is defined either by (10) with \( \phi \leq \psi \), or by (11) with (12). Note that (40) coincides with (12) in the latter case. We denote by \( L = K^*|_{C(\Omega)} \) the restriction of \( K^* \) to its invariant subspace \( C(\Omega) \). Note that \( L \geq 0 \). Let \( L^* \) denote its adjoint on \( M(\Omega) \). It is easy to see that \( L^* f = K f \) for all \( f \in C(\Omega) \), and that \( L^* \) is the unique bounded linear extension of \( K \) to an operator on \( M(\Omega) \), because \( C(\Omega) \) is \( w^* \)-dense in \( M(\Omega) \). We set \( \tilde{K} = L^* \). Analogously, given \( \lambda \in C_+(\Omega) \), we denote by \( \tilde{K}_\lambda \) the unique extension of \( K_\lambda \). However, in this case we have no relation between \( \text{spr} (K) \) and
spr (\vec{K}). Instead of (39) we will only require spr (K) \leq spr (\vec{K}), and similarly for K_\lambda and \vec{K}_\lambda. Namely, (40) implies
\[
\text{spr (K)} \leq \text{spr (\vec{K})} = \text{spr (L)} = \|L\|_\infty = \|\psi\|_\infty,
\]
and similarly, the inequality K_\lambda^* 1 \leq \lambda \psi implies
\[
(41) \quad \text{spr (K_\lambda)} \leq \text{spr (\vec{K}_\lambda)} = \|\lambda \psi\|_\infty \quad \text{for all } \lambda \in C_+(\Omega).
\]
Hence, inequality (40) provides an upper bound for the number s(K, \Lambda) defined by (38), i.e., through (41).

By \mathcal{H}(\psi) we denote the set of all positive operators K on C(\Omega) whose adjoint K^* on M(\Omega) maps C(\Omega) into itself with K^* 1 \equiv \psi, and the unique extension \vec{K} of K to a bounded linear operator on M(\Omega) satisfies
\[
(42) \quad \text{spr (K_\lambda)} \leq \text{spr (\vec{K}_\lambda)} \quad \text{for all } \lambda \in C_+(\Omega).
\]
Now we are ready to define optimal dispersion.

**Definition 6.1.** Let \Lambda \subset C_+(\Omega) \setminus \{0\} be nonempty, and let \psi \in C(\Omega) satisfy 0 < \psi \leq 1. We say that an operator K \in \mathcal{H}(\psi) represents optimal dispersion relative to (\Lambda, \psi) if K maximizes the number s(K, \Lambda) over the set \mathcal{H}(\psi).

Our next result states that the stay-in-place strategy K defined by (10) is at least as good as any other dispersal strategy in case the environment is time-invariant.

**Theorem 6.2.** Let \lambda, \psi \in C(\Omega) satisfy \lambda > 0 and 0 < \psi \leq 1. Then the operator K given by KN = \psi N, for N \in C(\Omega), maximizes the spectral radius s(K, \lambda) = \text{spr (K_\lambda)} over the set \mathcal{H}(\psi). The maximum is equal to \|\lambda \psi\|_\infty.

**Proof.** Let K \in \mathcal{H}(\psi) be arbitrary. We set r = \text{spr (K_\lambda)} and \bar{r} = \text{spr (\vec{K}_\lambda)}. By (41) we have r \leq \bar{r} \leq \|\lambda \psi\|_\infty. In particular, if K is given by KN = \psi N, for N \in C(\Omega), then r = \|\lambda \psi\|_\infty since K_\lambda N = \lambda \psi N, for N \in C(\Omega). \quad \Box

Notice that the maximizing operator K from Theorem 6.2 does not depend on the intrinsic growth rate \lambda. However, this maximizer does not have to be unique in \mathcal{H}(\psi). For instance, if the product \lambda \psi is a constant, say \lambda \psi = m > 0, then also the operator K = \phi \otimes \psi defined by
\[
(\phi \otimes \psi)(N) = \phi \int_\Omega \psi N \, dy \quad \text{for } N \in C(\Omega),
\]
maximizes spr (K_\lambda) over the set \mathcal{H}(\psi), provided \int_\Omega \phi \, dx = 1 where \phi \in C_+(\Omega) (cf. (15)). However, if a dispersal strategy K has to be optimal in a large variety of environments \lambda \in \Lambda, it may happen that it is also unique. Namely, we have the following result.

**Theorem 6.3.** Let \psi \in C(\Omega) satisfy 0 < \psi \leq 1, and assume that \Lambda \subset C_+(\Omega) \setminus \{0\} has the following property:
\[
(43) \quad m = \inf \{\|\lambda \psi\|_\infty | \lambda \in \Lambda\} > 0,
\]
and there exists a dense subset \Omega' \subset \Omega such that, given \lambda \in \Omega', there is \lambda \in \Lambda satisfying
\[
\lambda(x)\psi(x) = m \quad \text{and} \quad \lambda(y)\psi(y) < m \quad \text{for all } y \neq x.
\]
Then the operator K given by KN = \psi N, for N \in C(\Omega), is the unique maximizer for the number s(K, \Lambda) over the set \mathcal{H}(\psi). The maximum is equal to m.

**Proof.** Let K \in \mathcal{H}(\psi) be a maximizer for s(K, \Lambda) over \mathcal{H}(\psi). By Theorem 6.2 we must have
\[
(44) \quad s(K, \Lambda) = m.
\]
Next we choose $x \in \Omega'$ and $\lambda \in \Lambda$ such that $\lambda(x) \psi(x) = m > \lambda(y) \psi(y)$ for all $y \neq x$. Again, let $r = \text{spr} (K)$ and $\tilde{r} = \text{spr} (\tilde{K})$. By the Krein–Rutman Theorem (cf. Schaefer [24, Appendix, Cor. 2.4]), $\tilde{r}$ is an eigenvalue of the operator $\tilde{K}$ with a corresponding eigenvector $\phi \in M_+(\Omega) \setminus \{0\}$, i.e., $\tilde{K} \phi = \tilde{r} \phi$. In particular, we have
\[
(\lambda \cdot K^* \mathbf{1}, \phi) = (\mathbf{1}, \tilde{K} \phi) = \tilde{r}(\mathbf{1}, \phi).
\]
Hence, (40) shows that $(\lambda \psi - \tilde{r} \mathbf{1}, \phi) \geq 0$. This inequality is possible only if $\tilde{r} \leq m$. But (42) and (44) imply $m \leq r \leq \tilde{r}$, and therefore we must have $m = r = \tilde{r}$. By our choice of $\lambda$, the inequality $(\lambda \psi - m \mathbf{1}, \phi) \geq 0$ forces that the measure $\phi > 0$ be supported in the set $\{x\}$, i.e., $\phi = c \delta_x$ where $c > 0$ is a constant and $\delta_x$ is the Dirac measure at the point $x$. Hence, we have $\tilde{K} \delta_x = m \delta_x$. Given $N \in C(\Omega)$, this equality implies
\[
\lambda(x) \cdot K^* N(x) = (\lambda \cdot K^* N, \delta_x) = (N, \tilde{K} \delta_x) = m(N, \delta_x) = m N(x) = \lambda(x) \psi(x) N(x),
\]
and consequently, $K^* N(x) = \psi(x) N(x)$. Since $x \in \Omega'$ was arbitrary from a dense subset of $\Omega$, we conclude that $K^* N = \psi N$ for every $N \in C(\Omega)$. Furthermore, the $w^*$-density of $C(\Omega)$ in $M(\Omega)$ implies $d(K^* \mu)(x) = (\psi(x) d\mu(x)$ for each $\mu \in M(\Omega)$, and so $KN = \psi N$ for all $N \in C(\Omega)$. $\square$

7. Dispersal in time-varying environment. In this section we consider a time-varying environment represented by a sequence of nonlinear operators $\{F_t\}$ on $C_+(\Omega)$, for $t \geq 0$, which are defined by either (4) or (8). In particular, (36) holds with $F_t'(0)$ and $\lambda_t$ in place of $F'(0)$ and $\lambda$, respectively. In contrast to the time-varying environment we assume that the dispersal strategy of our population is time-invariant and represented by a linear operator $K_t = K$ on $C(\Omega)$, for $t \geq 0$, which is defined by either (10) or (11). Again, the evolution of our population is governed by the dynamical system (16) with $\Phi_t = K \cdot F_t$.

We ask the same question as in the previous section. Given a set $\mathcal{F}$ of possible environments (or growth conditions) $F_t$, what is the best possible dispersal strategy $K$ which guarantees survival of the population in every sequence of environments $\{F_t\} \in \mathcal{F}$? Under the concept of survival we mean the following situation: Given $\{F_t\}_{t=0}^{p-1} \in \mathcal{F}$ and $K$, the fixed-point equation (17) has a solution for every $p \geq 1$. In case the operators $\Phi_t$ satisfy the hypotheses of Theorem 3.1, the existence of a nontrivial fixed point $N^*$ to the map $\Psi_p$ is equivalent to $r = \text{spr} (\Psi_p^*(0)) > 1$. As in the previous section, we have $\Phi_t^*(0) = K_{\lambda_t}$, where the operator $K_{\lambda_t}$ is defined by (37) with $\lambda_t$ in place of $\lambda$. Thus, (18) entails
\[
\Psi_p^*(0) = K_{\lambda_{p-1}} \cdots K_{\lambda_0} \quad \text{where} \quad \lambda_t \in \Lambda \quad \text{for} \quad 0 \leq t \leq p - 1.
\]
Again, the set $\Lambda$ has the same meaning as in the previous section, and $\Lambda \in C_+(\Omega) \setminus \{0\}$. If the population is to survive under every finite set of intrinsic growth rates $\{\lambda_t\}_{t=0}^{p-1} \in \Lambda$, then the inequality $r = \text{spr} (K_{\lambda_{p-1}} \cdots K_{\lambda_0}) > 1$ must hold for every subset $\{\lambda_t\}_{t=0}^{p-1} \in \Lambda$. Given $p \geq 1$, we set
\[
s_p(K, \Lambda) = \inf \{ (\text{spr} (K_{\lambda_{p-1}} \cdots K_{\lambda_0}))^{1/p} | \lambda_t \in \Lambda, 0 \leq t \leq p - 1 \},
\]
and also
\[
(45) \quad \sigma(K, \Lambda) = \inf_{p \geq 1} s_p(K, \Lambda).
\]
This time we have to find an operator $K$ that maximizes the number $\sigma(K, \Lambda)$. Again, a maximizer $K$ should have the form (10) or (11), and it should also satisfy inequality (12), where $\psi \in C_+(\Omega) \setminus \{0\}$ is a fixed function also satisfying $\psi \equiv 1$. In the case of a
time-varying environment we maximize the number \( \sigma(K, \Lambda) \) over a subset of the set \( \mathcal{H}(\psi) \) defined in the previous section.

We denote by \( \mathcal{J}(\psi) \) the set of all operators \( K \in \mathcal{H}(\psi) \) which satisfy

\[
\text{spr} (K_{1,t-1}, \ldots, K_{m,0}) \leq \text{spr} (\hat{K}_{1,t-1}, \ldots, \hat{K}_{m,0})
\]

for all \( \lambda_i \in C_+(\Omega), 0 \leq t \leq p-1 \) and \( p=1, 2, \ldots \). We do not know whether \( \mathcal{J}(\psi) \neq \mathcal{H}(\psi) \).

Now we are ready to define optimal dispersion.

**Definition 7.1.** Let \( \Lambda \subset C_+(\Omega) \setminus \{0\} \) be nonempty, and let \( \psi \in C(\Omega) \) satisfy \( 0 < \psi \leq 1 \). We say that an operator \( K \in \mathcal{J}(\psi) \) represents optimal dispersion relative to \( (\Lambda, \psi) \) if \( K \) maximizes the number \( \sigma(K, \Lambda) \) over the set \( \mathcal{J}(\psi) \).

Of course, if \( \Lambda = \{ \lambda \} \) is a singleton, then Definition 6.1 (with \( \mathcal{J}(\psi) \) in place of \( \mathcal{H}(\psi) \)) and Definition 7.1 coincide, since \( s(K, \lambda) = \sigma(K, \lambda) \) for all operators \( K \equiv 0 \). However, if \( \Lambda \) is not a singleton, the situation in a time-varying environment is much more complicated. The *stay-in-place* strategy, which is independent of the set \( \Lambda \), is no longer the best one. In fact, we have the following example.

**Example 7.2.** Let \( \psi \in C(\Omega) \) satisfy \( 0 < \psi \leq 1 \). Assume that \( \Lambda \) is a subset of \( C_+(\Omega) \setminus \{0\} \) with the following property:

There exists a finite system of environments \( \lambda_1, \ldots, \lambda_n \in \Lambda \) such that the sets \( \Omega_i = \{ x \in \Omega | \lambda_i(x) = 1, 1 \leq i \leq n \} \) satisfy \( \bigcup_{i=1}^n \Omega_i = \Omega \).

Let the operator \( K \) have the form \( KN = \phi N \) for \( N \in C(\Omega) \), where \( \phi \in C(\Omega) \) satisfies \( 0 \leq \phi \leq \psi \). Then \( K \in \mathcal{J}(\psi) \) and \( \sigma(K, \Lambda) = 0 \).

**Proof.** We have \( K_{\lambda_1} \cdots K_{\lambda_n} 1 = \lambda_1 \cdots \lambda_n \phi^n = 0 \). Thus, (45) yields \( \sigma(K, \Lambda) = 0 \). \( \square \)

It is clear from this example that a population which does not disperse can be destroyed by a sequence of growth periods with bad growth conditions at some places which eventually cover the entire habitat \( \Omega \). Hence, if this situation occurs, only dispersion can save the population. An extreme example of dispersion is the go-everywhere-uniformly strategy which is represented by the integral operator \( K \) on \( C(\Omega) \) defined by (11) with the kernel

\[
k'(x, y) = |\Omega|^{-1} \psi(y) \quad \text{for } x, y \in \Omega.
\]

Our next result states that the go-everywhere-uniformly strategy is at least as good as any other dispersal strategy in case the environment is time-varying.

**Theorem 7.3.** Let \( \psi \in C(\Omega) \) satisfy \( 0 < \psi \leq 1 \), and assume that \( \Lambda \subset C_+(\Omega) \setminus \{0\} \) has the following property:

\[
\lambda = \inf \left\{ |\Omega|^{-1} \int_\Omega \lambda \psi \, dx | \lambda \in \Lambda \right\} > 0,
\]

and \( \bar{\lambda} / \psi \in \Lambda \). Then the operator \( K' \), whose kernel \( k' \) is given by (47), maximizes the number \( \sigma(K, \Lambda) \) over the set \( \mathcal{J}(\psi) \) of operators \( K \). The maximum is equal to \( \bar{\lambda} \).

(Note that the pair of hypotheses (48) and \( \lambda / \psi \in \Lambda \) is stronger than (43) and \( m / \psi \in \Lambda \), since \( \bar{\lambda} \leq m \).)

**Proof.** Let \( \lambda_0, \lambda_1, \ldots, \lambda_{p-1} \in \Lambda \) and \( K \in \mathcal{J}(\psi) \). We set \( H = K_{\lambda_1} \cdots K_{\lambda_t} K_{\lambda_0} \) on \( C(\Omega) \), and \( \hat{H} = \hat{K}_{\lambda_1} \cdots \hat{K}_{\lambda_t} \hat{K}_{\lambda_0} \) on \( M(\Omega) \). By (46) we have \( r = (\text{spr} (H))^{1/p} \leq \bar{r} = (\text{spr} (\hat{H}))^{1/p} \). As in the previous section, we denote by \( L = H^* |_{C(\Omega)} \) the restriction of \( H^* \) to its invariant subspace \( C(\Omega) \). Then \( \hat{H} = L^* \), and we may apply the Krein–Rutman theorem again (cf. Schaefer [23, Appendix, Cor. 2.4]), to conclude that \( \hat{r} \) is an eigenvalue of the operator \( \hat{H} \) with a corresponding eigenvector \( \phi \in M_+ (\Omega) \setminus \{0\} \), i.e., \( \hat{H} \phi = \hat{r} \phi \). In particular, we have

\[
\hat{r} \phi^{1} (\phi) = \langle 1, \hat{H} \phi \rangle = \langle H^* 1, \phi \rangle.
\]
Furthermore, by induction on \( p \), (40) implies
\[
H^* 1 = \lambda_0 K^*(\lambda_1 K^*(\cdots (\lambda_{p-1} K^* 1) \cdots)) \leq \lambda_0 K^*(\lambda_1 K^*(\cdots (\lambda_{p-1} \psi) \cdots))
\]
\[
\leq \|\lambda_{p-1} \psi\|_\infty \cdot \lambda_0 K^*(\lambda_1 K^*(\cdots (\lambda_{p-2} K^* 1) \cdots)) \leq \cdots \leq \prod_{i=0}^{p-1} \|\lambda_i \psi\|_\infty.
\]
It follows from this estimate, (46) and (49) that
\[
r \leq \tilde{r} \leq \left( \prod_{i=0}^{p-1} \|\lambda_i \psi\|_\infty \right)^{1/p}.
\]
Now we take \( \lambda_0 = \lambda_1 = \cdots = \lambda_{p-1} = \tilde{\lambda}/\psi \in \Lambda \) to conclude that \( \sigma(K, \Lambda) \leq \tilde{\lambda} \).
Finally, if \( K = K' \), then (48) entails
\[
r = \left( \prod_{i=0}^{p-1} \|\lambda_i \psi\|_\infty \right) \int_\Omega \lambda_i \psi \, dx \right)^{1/p} \geq \tilde{\lambda}
\]
for all \( \lambda_i \in \Lambda, 0 \leq i \leq p-1 \). Hence, \( \sigma(K', \Lambda) \geq \tilde{\lambda} \). Consequently, \( K' \) maximizes \( \sigma(K, \Lambda) \) over \( J(\psi) \) over \( \mathcal{J}(\psi) \).

Again, as in the previous section, if the set \( \Lambda \) contains sufficiently many environments, then the maximizer \( K' \) from Theorem 7.3 is unique. We do not know how to prove the uniqueness of \( K' \) in the set \( \mathcal{J}(\psi) \), but we are able to show it in a sufficiently large subset of \( \mathcal{J}(\psi) \) which contains all biologically reasonable dispersal strategies \( K \) except for the stay-in-place strategy.

We denote by \( \mathcal{J}(\psi) \) the set of all integral operators \( K \) on \( C(\Omega) \) defined by (11) and also satisfying (12). Clearly, \( K' \in \mathcal{J}(\psi) \subset \mathcal{J}(\psi) \). Note that this inclusion follows from Schauder's spectral theory for compact operators.

Our uniqueness result reads as follows.

**Theorem 7.4.** Let \( \psi \in C(\Omega) \) satisfy \( 0 < \psi \leq 1 \), and assume that \( \Lambda \subset C(\Omega) \setminus \{0\} \) satisfies (48) and has the following property:

There exists a dense subset \( \Omega' \subset \Omega \) such that, given \( x \in \Omega' \), the sequential \( w^* \)-closure of \( \Lambda \) in \( M(\Omega) \) contains the measure \( \tilde{\lambda}/|\Omega| \psi(x)^{-1} \delta_x \) where \( \delta_x \) denotes the Dirac measure concentrated at the point \( x \).

Then the operator \( K' \) whose kernel \( k' \) is given by (47), is the unique maximizer for the number \( \sigma(K, \Lambda) \) over the set \( \mathcal{J}(\psi) \) of operators \( K \). The maximum is equal to \( \tilde{\lambda} \).

(Notate that we do not need the hypothesis \( \tilde{\lambda}/\psi \in \Lambda \) from Theorem 7.3.)

It will be clear from the proof of this theorem that the number \( \sigma(K, \Lambda) \) in this theorem can be replaced by any of the numbers \( s_p(K, \Lambda) \), for \( p \geq 2 \).

**Proof.** Let \( \Lambda^* \) denote the sequential \( w^* \)-closure of \( \Lambda \) in \( M(\Omega) \). By our hypothesis,
\[
\nu_x = \tilde{\lambda}/|\Omega| \psi(x)^{-1} \delta_x \in \Lambda^* \quad \text{for all} \quad x \in \Omega'.
\]
Furthermore, \( 1/\psi \in C(\Omega) \) implies the \( w^* \)-convergence \( \nu_{x_n} \rightharpoonup \nu_x \) in \( M(\Omega) \) whenever \( x_n \to x \) in \( \Omega \) as \( n \to \infty \). Hence, \( \nu_x \in \Lambda^* \) for all \( x \in \Omega \), and therefore we may assume that \( \Omega' = \Omega \).

As in the previous section, we denote by \( \tilde{K} \) the unique extension of \( K \) to a bounded linear operator on \( M(\Omega) \), whenever \( K \in \mathcal{J}(\psi) \). Since \( K \) is defined by (11), we have
\[
\tilde{K}\mu(x) = \int_\Omega k(x, y) \, d\mu(y) = (k(x, \cdot), \mu) \quad \text{for all} \quad x \in \Omega \text{ and } \mu \in M(\Omega).
\]
We claim that the \( w^* \)-convergence in \( M(\Omega) \) of a sequence
\[
(50) \quad \nu_n \rightharpoonup \mu \quad \text{implies} \quad \tilde{K}\nu_n \to \tilde{K}\mu
\]
in the norm of \( C(\Omega) \) as \( n \to \infty \). In fact, since the kernel \( k \) is continuous over the compact set \( \Omega \times \Omega \), the set \( \mathcal{K} = \{ k(x, \cdot) \in C(\Omega) \mid x \in \Omega \} \) is relatively compact in \( C(\Omega) \), by the Arzelà-Ascoli theorem. Consequently, \( \mu_n \rightharpoonup \mu \) in \( M(\Omega) \) implies \( (k(x, \cdot), \mu_n) \rightharpoonup (k(x, \cdot), \mu) \) uniformly with respect to \( x \in \Omega \) as \( n \to \infty \). It follows that (50) is valid.

Next, let us fix \( K \in \mathcal{K}(\psi) \), and consider a set of points \( x_0, x_1, \ldots, x_{p-1} \in \Omega \) and \( x_p = x_0 \) where \( p \equiv 1 \) is an integer. We set
\[
\nu_i = \nu_{x_i} = \tilde{\lambda}|\Omega|\psi(x_i)^{-1}\delta_{x_i} \in \Lambda^* \quad \text{for } 0 \leq i \leq p - 1
\]
and choose a suitable sequence \( \left\{ \lambda_{i,n} \right\}_{n=1}^\infty \subset \Lambda \) such that \( \lambda_{i,n} \rightharpoonup \nu_i \) in \( M(\Omega) \) as \( n \to \infty \), for every \( i = 0, 1, \ldots, p - 1 \). In analogy with the proof of Theorem 7.3 we set \( H_n = K_{\lambda_{p-1,n}} \cdots K_{\lambda_1,n} K_{\lambda_0,n} \) on \( C(\Omega) \), and denote by \( H \) the positive operator on \( C(\Omega) \) defined by
\[
HN(x) = (\tilde{\lambda}|\Omega|)^p k_{\psi}(x, x_{p-1}) \cdots k_{\psi}(x_2, x_1) k_{\psi}(x_1, x_0) N(x_0)
\]
for all \( x \in \Omega \) and \( N \in C(\Omega) \), where
\[
k_{\psi}(x, y) = k(x, y)\psi(y)^{-1} \quad \text{for } x, y \in \Omega.
\]
It is easy to show that, given an integer \( m \equiv 1 \), implication (50) entails
\[
H_m^n \to H_m^1 \quad \text{in } C(\Omega) \quad \text{as } n \to \infty.
\]
But the positivity of all \( H_n \) and \( H \) implies \( \| H_m^n \| = \| H_m^1 \|_\infty \) and \( \| H_m^n \| = \| H_m^1 \|_\infty \), and consequently, we obtain
\[
\| H_m^n \| \to \| H_m^n \| \quad \text{as } n \to \infty, \quad m \equiv 1.
\]
We claim that
\[
\sigma(K, \Lambda) \subseteq r = (\spr(H))^{1/p}.
\]
Recalling (45) we observe that it suffices to show that
\[
\inf_{n \equiv 1} \spr(H_n) \subseteq \spr(H).
\]
The Gelfand formula for the spectral radius of a bounded linear operator \( A \) on \( C(\Omega) \) reads
\[
\spr(A) = \lim_{m \to \infty} \| A^m \|^{1/m} = \inf_{m \equiv 1} \| A^m \|^{1/m}.
\]
Combining this formula with (52) we arrive at (54), since (54) can be rewritten as
\[
\inf_{m, n \equiv 1} \| H_m^n \|^{1/m} \leq \inf_{m \equiv 1} \| H_m^1 \|^{1/m}.
\]
Thus, (53) is valid.

From our definition of the operator \( H \) we conclude that
\[
r^n = \spr(H) = (\tilde{\lambda}|\Omega|)^p k_{\psi}(x_0, x_{p-1}) \cdots k_{\psi}(x_2, x_1) k_{\psi}(x_1, x_0).
\]
The key step in the proof of the uniqueness of \( K' \) is as follows: we apply the inequality between the geometric and arithmetic means to estimate
\[
r = \tilde{\lambda}|\Omega| \left[ \prod_{i=0}^{p-1} k_{\psi}(x_{i+1}, x_i) \right]^{1/p} \leq \tilde{\lambda}|\Omega| \frac{1}{p} \sum_{i=0}^{p-1} k_{\psi}(x_{i+1}, x_i)
\]
where equality holds if and only if all summands are pairwise equal, i.e.,
\[
k_{\psi}(x_{i+1}, x_i) = k_{\psi}(x_1, x_0) \quad \text{for all } i = 0, 1, \ldots, p - 1.
\]
We recall that $x_0, x_1, \cdots, x_{p-1} \in \Omega$ are arbitrary while $x_p = x_0$. Hence, $r = r(x_0, x_1, \cdots, x_{p-1})$ is a function of these points. We set

$$s_p^*(K) = \inf\{r(x_0, x_1, \cdots, x_{p-1}) | x_i \in \Omega, 0 \leq i \leq p - 1\}.$$ 

Since $s^*_p(K) \geq s^*_p(K)$ for all $p \geq 2$, we will assume that $p \geq 2$. Integrating (55) with respect to $x_{i+1}$ over $\Omega$, for $i = 0, 1, \cdots, p - 1$, we obtain

$$s^*_p(K)|\Omega|^p \leq \int_\Omega \cdots \int_\Omega r \, dx_0 \cdots dx_{p-1} \equiv \tilde{\lambda}|\Omega|^p \sum_{i=0}^{p-1} \sup_{x_i \in \Omega} \int_\Omega k_{\phi}(x_{i+1}, x_i) \, dx_{i+1} \equiv \tilde{\lambda}|\Omega|^p$$

(57)

where the inequalities become equalities only if the equality (56) holds for all $x_i \in \Omega$, $0 \leq i \leq p - 1$, and also

$$\sup_{y \in \Omega} \int_\Omega k_{\phi}(x, y) \, dx = 1.$$ 

(58)

Note that, by (51), condition (12) can be rewritten as

$$\int_\Omega k_{\phi}(x, y) \, dx \equiv 1 \quad \text{for all } y \in \Omega.$$ 

Combining (53) with (57) we obtain $\sigma(K, \Lambda) \equiv \tilde{\lambda}$ whenever $K \in \mathcal{F}(\psi)$.

Finally, let $K \in \mathcal{F}(\psi)$ satisfy $\sigma(K, \Lambda) = \tilde{\lambda}$. Then also $s^*_p(K) = \tilde{\lambda}$ for every $p \geq 2$, and (56) with $p \geq 4$ yields

$$k_{\psi}(x_3, x_2) = k_{\psi}(x_1, x_0) \quad \text{for all } x_0, x_1, x_2, x_3 \in \Omega.$$ 

Hence, $k_{\psi}$ is a constant, and so (58) implies $k_{\psi} = |\Omega|^{-1}$, i.e., $k = k'$ by (47) and (51).

We conclude that $K'$ is the unique maximizer for $\sigma(K, \Lambda)$ over $\mathcal{F}(\psi)$. Moreover, $\sigma(K', \Lambda) = \tilde{\lambda}$ by the last part of the proof of Theorem 7.3.

Using the Gelfand formula from this proof again we observe that

$$\sigma(K, \Lambda) = \inf\{\|K_{\psi_{p-1}} \cdots K_\psi K_{\Lambda_1} \psi_{\Lambda_1} \|^p_{\infty} \|A_t \|\} \Lambda_t \in \Lambda, 0 \leq t \leq p - 1 \text{ and } p \geq 1$$

for all $K \geq 0$.

Returning to the dynamical system (16) with $\Phi_t = K \circ F_t$, for $t \geq 0$, we know that $\Phi_t(0) = 0$, and $\Phi'_t(0) = K_{\Lambda_t}$ by (36) and (37). Hence, the linear operator $\Psi'_t(0) = K_{\psi_{p-1}} \cdots K_\psi K_{\Lambda_t} \psi_{\Lambda_t}$ approximates the operator $\Psi_{\psi} = \Phi_{\psi_{p-1}} \cdots \Phi_{\psi} \Phi_{\Lambda}$ near zero. It is now clear that if the density of our population stays sufficiently low during its entire evolution (or if we neglect the crowding phenomenon and assume linear growth), then its behavior as $p \to \infty$ is determined by the behavior of the operator $\Psi'_t(0)$ as $p \to \infty$. In particular, if we start with the initial distribution equal to $1$, then we have the distribution $N'_p = \Psi'_t(0)1$ after $p$ growth-dispersal cycles. This consideration justifies our definition of the number of $\sigma(K, \Lambda)$ from the point of view of the asymptotic behavior of the linearization at zero of our dynamical system.

8. Numerical examples of dispersion strategies. In this section we discuss various examples of dispersion kernels. Our goal is not to simulate realistic natural conditions, but rather to illustrate the results of the previous sections with simple examples. For simplicity we take the habitat $\Omega$ to be a closed interval $\Omega = [-L/2, L/2]$ where $0 < L < \infty$. We will emphasize the comparison of various dispersion strategies.
We consider the following four dispersion kernels:

\[ k^{(1)}(x, y) = \delta(x - y) \quad (\delta(\cdot) \text{ is the Dirac delta function,}) \]

\[ k^{(2)}(x, y) = \frac{1}{L}, \quad L > 0, \]

\[ k^{(3)}(x, y) = \frac{1}{\sqrt{2\pi\sigma}} e^{-|x - y|^2/2\sigma^2}, \quad \sigma = 0.5, \]

\[ k^{(4)}(x, y) = \frac{1}{\sqrt{2\pi\sigma}} e^{-|x - y|^2/2\sigma^2}, \quad \sigma = 1. \]

The dispersion operators for these kernels are

\[ (K^{(i)} N)(x) = \int_{-L/2}^{L/2} k^{(i)}(x, y) N(y) \, dy, \quad i = 1, 2, 3, 4. \]

The dispersion operator \((K^{(1)} N)(x) = N(x)\) is the stay-in-place strategy, \((K^{(2)} N)(x) = 1/L \int_{-L/2}^{L/2} N(y) \, dy\) is the go-everywhere-uniformly strategy, and \(K^{(3)}, K^{(4)}\) are diffusion strategies. The strategies (1) and (2) are extremes with the strategies (3) and (4) intermediate between them. Since \(\int_{-L/2}^{L/2} k^{(1)}(x, y) \, dx < 1, \ i = 3, 4\), the diffusion strategies have a small seed (or population) loss through the boundaries.

We next define a class of space-dependent intrinsic growth rates. This set of intrinsic growth rates will be large enough to illustrate interesting phenomena, yet small enough to remain simple. For \(0 \leq c \leq 2\) we define the piecewise linear function \(\lambda^c(y)\) as follows (see Fig. 1):

\[
\lambda^c(y) = \begin{cases} 
   c & \text{if } -L/2 \leq y \leq 0, \\
   c + 16(2 - c)y/L & \text{if } 0 < y \leq L/4, \\
   16 - 7c - 16(2 - c)y/L & \text{if } L/4 < y \leq L/2.
\end{cases}
\]

Notice that \(\int_{-L/2}^{L/2} \lambda^c(y) \, dy = 2L\) (independently of \(c\)). Let \(\lambda^c(y) = \lambda^c(-y), -L/2 \leq y \leq L/2\). For \(c = 0\) there is no growth on one side of the habitat, whereas for \(c = 2\) there is constant growth throughout the habitat. For \(0 \leq c_1 \leq c_2 \leq 2\) set

\[ \Lambda_{c_1, c_2} = \{\lambda^c: c_1 \leq c \leq c_2\} \cup \{\lambda^c: c_1 \leq c \leq c_2\}. \]

Then \(\Lambda_{c_1, c_2}\) is a class of one-sided biased growth conditions for the habitat \([-L/2, L/2]\).

\[ \text{FIG. 1. Space-dependent intrinsic growth rate.} \]
Given these growth conditions, we will compare the four dispersion strategies with one another. We will discuss the extinction and survival of the species in time-invariant and time-periodic environments, as well the nontrivial equilibria for nonlinear logistic models. As in §§6 and 7 we let $K_N = K(AN)$ and
\[
s_p(K^{(i)}, \Lambda_{c_1,c_2}) = \inf\{\text{spr}(K^{(i)}_{\Lambda_{c_1,c_2}})\}^{1/p} | \lambda_j \in \Lambda_{c_1,c_2}, j = 0, \cdots, p - 1\},
\]
\[
\sigma(K^{(i)}, \Lambda_{c_1,c_2}) = \inf\{s_p(K^{(i)}, \Lambda_{c_1,c_2}) | p \geq 1\}.
\]

We first consider extinction and survival of the species in the time-invariant environment case ($p = 1$). By Theorem 3.1 the survival of the species over all possible growth conditions in $\Lambda_{c_1,c_2}$ is equivalent to $s_1(K^{(i)}, \Lambda_{c_1,c_2}) > 1$. For the stay-in-place strategy $s_1(K^{(i)}, \Lambda_{c_1,c_2}) = 8 - 3c_2$ (independently of $L$ and $c_1$), since $\text{spr}(K^{(1)}_{\Lambda}) = \max_y \lambda'(y) = 8 - 3c$. For the go-everywhere-uniformly strategy $s_1(K^{(2)}, \Lambda_{c_1,c_2}) = 2$ (independently of $L$, $c_1$, and $c_2$), since $\text{spr}(K^{(2)}_{\Lambda}) = 1/L \int_{L/2}^{L/2} \lambda'(y) dy = 2$. The graphs of $s_1(K^{(i)}, \Lambda_{c_1,c_2})$, $i = 1, 2, 3, 4$, are given in Fig. 2 for various values of $c_2$ and various habitat sizes. In accordance with the results established in §6 the stay-in-place strategy is more advantageous. Notice that this advantage decreases as the set of growth conditions includes more spatially uniform rates (that is, as $c_2 \to 2$). Notice also that the diffusion strategies approach the stay-in-place strategy as the habitat size $L$ increases and as the diffusion parameter $\sigma$ decreases.

![Fig. 2. $s_1(K^{(i)}, \Lambda_{c_1,c_2})$, $i = 1, 2, 3, 4$.](image)

We next consider extinction and survival in the time-varying environment case ($p > 1$). By Theorem 3.1 again survival is equivalent to $\sigma(K^{(i)}, \Lambda_{c_1,c_2}) > 1$. For simplicity we take $c_2 = 2$. For the stay-in-place strategy $\sigma(K^{(i)}, \Lambda_{c_1,c_2}) = \min\{2, (c_2(8 - 3c_1))^{1/2}\}$ (independently of $L$). This claim follows from the fact that $\text{spr}(K_{\Lambda}^{(i)}K_{\Lambda}^{(i)}) = (8 - 3c_2)^2 = 4$, $\text{spr}(K_{\Lambda}^{(i)}K_{\Lambda}^{(i)}) = \max\{c(8 - 3c_1), c'(8 - 3c_1)\} = c'(8 - 3c)$ for $c < c'$, and similar calculations. It is easily seen that $\sigma(K^{(2)}, \Lambda_{c_1,c_2}) = 2$ (independently of $L$ and $c_1$). The graphs of $\sigma(K^{(i)}, \Lambda_{c_1,c_2})$, $i = 1, 2, 3, 4$, are given in Fig. 3. As established in §7 the go-everywhere-uniformly strategy is optimal. Notice that its advantage decreases as the set of growth conditions is restricted to more uniform rates ($c_1 \to 2$). Again the diffusion strategies approach the stay-in-place strategy as habitat size $L$ increases and diffusion parameter $\sigma$ decreases. The nontrivial equilibria satisfy
\[
N^{*}(x) = \int_{-L/2}^{L/2} k^{(i)}(x, y) \lambda'(y) f(N^{*}(y)) dy, \quad i = 1, 2, 3, 4
\]
where we take $c = 5/3$ and $f(N) = (1 - N)^{+}$. Observe that, given $x \in [-L/2, L/2]$,

$$
N^{*^{(1)}}(x) = \begin{cases} 
0 & \text{if } \lambda^{c}(x) \leq 1, \\
1 - \frac{1}{\lambda^{c}(x)} & \text{if } \lambda^{c}(x) > 1, 
\end{cases}
$$

$$
N^{*^{(2)}}(x) = \left[ 1 - \left( \frac{1}{L} \int_{-L/2}^{L/2} \lambda^{c}(y) \, dy \right)^{-1} \right]^{+} = \frac{1}{2}.
$$

The nontrivial equilibria for the four strategies and various values of $L$ are graphed in Figs. 4-6. The diffusion strategies approach the stay-in-place strategy as the habitat size increases. Notice that the total population of $N^{*^{(2)}}$ is greater than the total population of $N^{*^{(i)}}$, $i = 1, 3, 4$, that is, $\int_{-L/2}^{L/2} N^{*^{(2)}}(x) \, dx > \int_{-L/2}^{L/2} N^{*^{(i)}}(x) \, dx$.

Consider the example above with $L = 1$ and $c = \frac{5}{3}$ instead of $\frac{5}{2}$ (recall that $\lambda^{3/2}(y)$ has a steeper peak than $\lambda^{5/3}(y)$). The stay-in-place mapping $\Phi_{1,3}^{(i)}$ now has a four-cycle as given in Fig. 7 (the graphs have the constant value $\frac{1}{3}$ for $-0.5 \leq x \leq 0$). The diffusion
dispersion mappings $\Phi_{1.5}^{(i)}$, $i=3,4$, however, still have stable equilibria as graphed in Fig. 8. This example shows that spatial dispersion acts to reduce the likelihood of cycles, which may otherwise be present in certain habitat locations in the absence of dispersion.

Last we consider nontrivial equilibria for the four dispersion strategies for the nonlinear logistic case in a time-periodic environment. Let
\[
(\Phi_{i}^{(i)}N)(x) = \int_{-L/2}^{L/2} k^{(i)}(x,y)\lambda^{(i)}(y)f(N(y)) \, dy, \quad i=1,2,3,4
\]
where $L = 1$ and $f(N) = N(1-N)\,^+$ as before. Consider the case when the period $p$ is $p = 3$ years, and in two of the three years $c = 2$ (so that growth conditions are uniform throughout the habitat, that is, $\lambda^{2}(y) = 2$) and in one of the three years $c = 1.5$ (so that good growth conditions hold on the right side). In this case the mappings $\Phi_{1.5}(\Phi_{2}^{(i)}(\Phi_{1}^{(i)}))$, $\Phi_{2}^{(i)}(\Phi_{1.5}^{(i)}(\Phi_{2}^{(i)}))$, and $\Phi_{2}^{(i)}(\Phi_{2}^{(i)}(\Phi_{1.5}^{(i)}))$ have nontrivial equilibria as graphed in Figs. 9, 10, and 11, respectively.

The periodic environment conditions produce a periodic behavior of the population with period $p = 3$. In the first year (Fig. 9) high growth occurs on the right side. In the second year (Fig. 10) crowding greatly reduces the population on the right side.
In the third year (Fig. 11) the population on the right side begins to increase again. This three-year pattern then repeats. The diffusion strategies behave like the stay-in-place strategy in Fig. 9 (where the most recent influence is one-sided growth) and like the go-everywhere-uniformly strategy in Fig. 11 (where the most recent influence is uniform growth). The effect of dispersion in a time-periodic environment (and thus in a time-varying environment) is to moderate disturbances in growth conditions. In this
example the *stay-in-place* mapping $\Phi_{13}^{(i)}$ has a four-cycle (Fig. 7), but when composed in periodic fashion with $\Phi_2^{(i)}$ (Fig. 9, 10, and 11), $\Phi_{13}^{(i)}$ has a stable equilibrium. The effect of time-periodic environmental conditions with period $p$ (and thus of time-varying environmental conditions) is to reduce the likelihood of cycles of length $\neq p$ due to high growth rate and crowding.

9. **Summary.** We have analyzed a discrete-time model of populations that grow and disperse in separate phases. The growth phase is a nonlinear process that allows for the effects of local crowding. The dispersion phase is a linear process that distributes the population throughout its spatial habitat. Our study quantifies the issues of survival and extinction, the existence and stability of nontrivial steady states, and the comparison of various dispersion strategies. Our results show that all of these issues are tied to the global nature of various model parameters.

The theoretical and numerical analysis of our model demonstrates that dispersion is a mechanism for averaging local behavior. Local conditions may vary greatly in
both place and time. Without dispersion extremes of behavior such as multiple equilibrium states, cycles, and chaos may occur in local situations. With dispersion these local extremes may not be present. The absence of observed cycles and chaos in natural populations may be explained in part by the averaging effects of spatial dispersion. Our results emphasize the view of population behavior as a global phenomenon and the role of spatial dispersion as a stabilizing force.

In our comparison of dispersion strategies we first considered the time-invariant case. We proved that from a suitably chosen class of spatially varying environmental conditions the stay-in-place strategy is always optimal. This result applies to a species that exists in different spatial environments, but environments that are unchanging in time. Here time can be viewed relatively and may be only a few generations, since our examples demonstrate that convergence to steady state is usually fast.

We next compared various dispersion strategies in the case of time-varying environments. Here we modeled environments changing in time by environments changing periodically in time with any possible period. We proved that from a suitably chosen class of periodically varying spatial environments the go-everywhere-uniformly strategy is always optimal. This result applies to a species that exists in a variety of spatial environments that change from generation to generation. The variability in time occurs periodically with any possible period, which may also vary from place to place. Examples demonstrated that typically only a few periods are required for convergence to equilibrium.

The extreme strategies of staying-in-place and going-everywhere-uniformly were compared numerically to diffusion strategies in various contexts. These examples revealed that diffusion is frequently a close approximation to one of these extremes, depending upon factors such as habitat size and diffusion coefficients. In this sense a population must choose between these two extremes as a strategy for dispersion, and therefore as a strategy for survival.

We have approached the mathematical analysis of our model from a functional analysis and an operator theory point of view. Specifically, we have used recent results from the theory of positive operators in Banach lattices. This theory is most useful for analyzing the integrodifference equation formulation of our model, where positivity arises in an essential way. Our investigations have concerned populations of a single species. In a forthcoming work we will treat multiple-species populations using similar methods.
REFERENCES