# Spreading speeds of spatially periodic integro-difference models for populations with non-monotone recruitment functions.

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**Abstract**

An idea used by H. R. Thieme [T79b] is extended to show that a class of integro-difference models for a periodically varying habitat has a spreading speed and a formula for it, even when the recruitment function $R(u, x)$ is not nondecreasing in $u$, so that overcompensation occurs. Numerical simulations illustrate the behavior of solutions of the recursion whose initial values vanish outside a bounded set.

# 1 Introduction.

We shall consider integro-difference, that is, integral recursion, models of the form

$$u_{n+1}(x) = Q[u_n](x) := \int_{-\infty}^{\infty} k(x, y) R(u_n(y), y) dy, \ x \in \mathcal{R} \tag{1.1}$$

for the growth and spread of a single species in a periodically varying environment. Here $R(v, y)$ is the recruitment function at the location $y$, and $k(x, y)dx$ is the probability that an individual which starts at $y$ migrates to the interval $[x, x+dx]$. The fact that the habitat is periodic means that there is a period $L$ such that the functions $R(v, y)$ and $k(x, y)$ have the periodicity properties

$$\begin{aligned} R(v, y + L) = R(v, y) \text{ and } k(x + L, y + L) = k(x, y) \\ \text{for all } v \geq 0 \text{ and all } x \text{ and } y. \end{aligned} \tag{1.2}$$

This condition implies that if $u_n$ in (1.1) is $L$-periodic, the same is true of $u_{n+1}$. For instance, the recruitment function $R(v, x) := ve^{3+\cos x - v}$, which is of Ricker type, and the dispersal kernel

$$k(x, y) := [1 + (1/2) \cos x] e^{-|2x + \sin x - 2y - \sin y|}$$

have these properties with $L = 2\pi$.

The notion of periodically varying habitats was introduced in [SKT86], and extended in [SK97], [W02], [KKTS03], and [BHR05]. It was shown in these papers that when the habitat is periodic and the growth and spread of a single population is modelled either by a recursion $u_{n+1} = Q[u_n]$ in which the operator $Q$ is order-preserving, or by a reaction-diffusion equation, which can be formulated in terms of such a recursion (see [W02]), then there is an asymptotic spreading speed $c^*$ with which an invasion of the species into new territory spreads. Other approaches can be found in [GF79], [Fr84], [PX91], [X00], [BH02], [LLM06], [RL06] and [KKS06].

These results are extensions of known results (see, e. g., [D79, T79a, W78, W82]) for a homogeneous habitat, which is characterized by the properties that $R(v, x)$ is independent of $x$, and that $k(x, y)$ is a function of $x - y$ only.

All these results assume that the population dynamics are either governed by a reaction-diffusion equation, or by a recursion with an order-preserving operator $Q$. The operator on the right of the recursion (1.1) is order-preserving if and only if the recruitment function $R(u, x)$ is nondecreasing in $u$.

Simulations in [KS07] showed that there seems to be an asymptotic spreading speed $c^*$ of an invasion of a periodically patchy habitat when the recruitment function is the Ricker function $R(v, x) = ve^{r(x)-v}$, which increases for $v \leq 1$ but decreases for $v \geq 1$. Such a model is said to exhibit **overcompensation.**

Horst Thieme [T79b] proved that for a spatially homogeneous habitat, a spreading speed $c^*$ can be defined for a class of recruitment functions with overcompensation which includes the Ricker function. It is the purpose of the present work to extend Thieme's result to the case of periodic habitats. That is, we shall show that under suitable hypotheses on the functions $R$ and $k$, the recursion (1.1) has an asymptotic spreading speed $c^*$.

The equilibria of a recursion model with a single patch in the presence of overcompensation were investigated by R. W. Van Kirk and M. A. Lewis [VKL97].

The present work establishes the existence of a spreading speed for a class of integro-difference models in which both the growth and dispersal properties may vary periodically in the habitat, and overcompensation may occur. Section 2 contains our hypotheses and our main result, Theorem 2.1. Section 3 contains two theorems on equilibrium solutions and a theorem on how the invadabilty of a domain whose migration lies in a restricted class is affected by a change in the period $L$. Section 4 presents the results of numerical simulations of a model for a periodically patchy habitat. Section 5 is a discussion of the results and of possible extensions. All proofs are contained in the Appendix, which is Section 6.

# 2 Periodically varying habitats.

In order to obtain our spreading results, we shall need some definitions and hypotheses about the functions $R$ and $k$ in (1.1). We shall assume that $R(0, x) = 0$ for all $x$ so that there is no spontaneous generation of population, and that $R(v, x) \geq 0$ for all $v$ and $x$. We also assume that for each $x$, the function $R(v, x)$ is $L$-periodic in $x$, that it has the right partial derivative

$$m(x) := [\partial R/\partial v](0, x) \tag{2.1}$$

at $v = 0$, and that

$$R(v, x) \leq m(x)v. \tag{2.2}$$

Clearly, $m(x)$ is nonnegative and periodic of period $L$.

In order to find a formula for the spreading speed, we first consider the eigenvalue problem

$$M_\mu[w] := \int_{-\infty}^{\infty} k(x,y)e^{\mu(x-y)}m(y)w(y)dy = \lambda w(x), \text{ with } w(x+L) = w(x). \tag{2.3}$$

By writing the integral as the sum of integrals over intervals of length $L$ and using the periodicity properties of $k$, $m$, and $w$, we can write this equation as

$$\int_{-L/2}^{L/2} K_\mu(x,y)m(y)w(y)dy = \lambda w(x), \tag{2.4}$$

where we have defined the function

$$K_\mu(x,y) := \sum_{j=-\infty}^{\infty} k(x, y+jL)e^{\mu(x-y-jL)}. \tag{2.5}$$

The periodicity condition on $w$ follows from the fact that $K_\mu(x,y)$ is $L$-periodic in both of its variables. Thus (2.4) is a standard eigenvalue problem for an integral operator with the nonnegative kernel $K_\mu(x,y)m(y)$ on the finite interval $[-L/2, L/2]$. We shall assume in Hypothesis 2.1.ix that there is a power $G$ of the operator $M_\mu$ which takes every continuous function which is positive somewhere on the set where $m(x) > 0$ into a strictly positive function. It is known (see, e. g., Theorem 1 of Section 21.3 of [L02]) that the problem (2.3) has a positive principal eigenvalue $\tilde{\lambda}(\mu)$ with an associated eigenfunction $\tilde{w}(x)$ which is continuous, positive and $L$-periodic, and that all other eigenvalues have absolute values smaller than $\tilde{\lambda}(\mu)$. Moreover, the Krein-Rutman inequalities

$$\min_x \left\{ \frac{M_\mu[w](x)}{w(x)} \right\} \le \tilde{\lambda}(\mu) \le \max_x \left\{ \frac{M_\mu[w](x)}{w(x)} \right\} \tag{2.6}$$

are satisfied for every continuous positive $L$-periodic function $w(x)$. (See, e. g., Theorem 2.12 of [CC03].) We shall obtain our spreading speed $c^*$ by applying the formula

$$c^* = \inf_{\mu>0}\{(1/\mu)\ln\tilde{\lambda}(\mu)\}, \tag{2.7}$$

with $\tilde{\lambda}(\mu)$ this principal eigenvalue. This formula is known when $R(v,x)$ is nondecreasing in $v$ and $R(v,x) \le m(x)v$. (See, e .g ., Corollary 2.1 of [W02] or [KKTS03].)

We shall use the following hypotheses to show that this $c^*$ is the asymptotic spreading speed of (1.1) in the sense of Thieme [T79b].

**Hypotheses 2.1.**

*i.* $R(v,x) \geq 0$, $R(0,x) = 0$ *for all* $x$, *and the periodicity condition in (1.2) is satisfied. Moreover,*

*a.* $R(v,x)$ *is continuous in* $v$, *uniformly in* $v$ *and* $x$; *and*

*b.* $R(v,x)$ *is lower semicontinuous in* $x$, *uniformly in* $v$. *That is, for every* $x_0$ *and every positive* $\epsilon$ *there is a number* $\delta(\epsilon, x_0)$ *such that* $R(v,x) \geq R(v,x_0) - \epsilon$ *whenever* $|x - x_0| \leq \delta(\epsilon, x_0)$.

*ii. The dispersal kernel* $k(x,y)$ *has the following properties.*

*a. For each fixed* $y$, $k(x,y)$ *is a probability density. That is,* $k(x,y) \geq 0$, *and*

$$\int_{-\infty}^{\infty} k(x,y)dx = 1.$$

*b.* $k(x,y)$ *is lower semicontinuous. That is, for each* $(x_0, y_0)$ *and each* $\epsilon > 0$ *there is a positive number* $\delta(x_0, y_0, \epsilon)$ *such that* $k(x,y) \geq k(x_0,y_0) - \epsilon$ *when* $|x - x_0| + |y - y_0| \leq \delta(x_0, y_0, \epsilon)$.

*c.* $k$ *has the periodicity property in (1.2).*

*iii. There is a positive continuous* $L$*-periodic function* $\hat{\alpha}(x)$ *such that the operator*

$$Q[u](x) := \int_{-\infty}^{\infty} k(x,y)R(u(y),y)dy,$$

*which appears on the right side of (1.1), satisfies the inequality*

$$0 \leq Q[u] \leq \hat{\alpha} \quad \textit{whenever } 0 \leq u \leq \hat{\alpha}.$$

*That is, if* $u_n \leq \hat{\alpha}$, *the recursion (1.1) shows that* $u_m \leq \hat{\alpha}$ *for all* $m \geq n$.

*iv.* $k(x,y)$ *is uniformly* $L_1$*-continuous in* $x$. *That is,*

$$\lim_{h \to 0} \int_{-\infty}^{\infty} |k(x+h,y) - k(x,y)|dy = 0, \ \textit{uniformly in } x,$$

*so that the family of functions* $Q[u]$ *with* $0 \leq u \leq \hat{\alpha}$ *is equicontinuous.*

*v. There is a function* $m(x)$ *with the following properties*

*a.* $m(x)$ *is nonnegative,* $L$*-periodic, bounded, and lower semicontinuous.*

*b.*

$$0 \leq R(v,x) \leq m(x)v \ \textit{for all } 0 \leq v \leq \hat{\alpha}(x) \ \textit{and all } x. \tag{2.8}$$

*c. For every positive number* $\delta$ *there is a positive number* $\epsilon_\delta$ *such that*

$$R(v,x) \geq (1-\delta)m(x)\min\{v, \epsilon_\delta\} \ \textit{for all } 0 \leq v \leq \hat{\alpha}(x) \ \textit{and all } x. \tag{2.9}$$

vi. *One has a continuous positive L-periodic function $\ell(x)$ and a number $\eta$ with the properties*

$$\eta > 1 \quad \text{and} \quad \int_{-\infty}^{\infty} k(x,y)m(y)\ell(y)dy \geq \eta\ell(x) \text{ for all } x. \tag{2.10}$$

vii. *The functions $k(x,y)$ and $R(v,x)$ have the evenness properties*

$$k(-x,-y) = k(x,y) \quad \text{and } R(v,-x) = R(v,x) \text{ for all } x,\ y, \text{ and } v. \tag{2.11}$$

*This implies that, if the function $u_n$ in (1.1) is even, then the same is true of $u_{n+1}$.*

viii. *There is at least one positive number $\mu$ such that the L-periodic function*

$$\int_{-\infty}^{\infty} k(x,y)e^{\mu(x-y)}m(y)dy$$

*is bounded. That is, the tail of the product $k(x,y)m(y)$ is exponentially thin.*

ix. *There are an integer $J$ and a positive integer $G$ with the following property: For every $a$ with $|a| \leq L/2$ and $m(a) > 0$, and for every $b$ with $|b - JL| \leq L$ there is a $G+1$-tuple of numbers $x_0, x_1, \cdots, x_G$ such that*

   a. *$x_0 = a$ and $x_G = b$;*

   b. *$k(x_j, x_{j-1})m(x_{j-1}) > 0$ for $j = 1, \cdots, G$.*

*This implies that the descendants in the $G$th generation of an individual located in the interval $[-L/2, L/2]$ who survives to the end of the first growth period have positive population density on an interval of length $2L$ centered at an integer multiple of $L$.*

**Remarks.** 1. Because we wish to treat habitats which consist of uniform patches with jumps across their boundaries, we have required $R(v,x)$ and $k(x,y)$ to be semicontinuous rather than continuous.

2. Hypotheses 2.1.v.b and c show that $m(x) = 0$ if and only if the environment at $x$ is lethal in the sense that $R(v,x) = 0$ for all $v$.

3. If $k(x,y) > 0$ for all $x$ and $y$, Hypothesis 2.1.ix is certainly satisfied with $G = 1$ and any integer $J$.

4. If $s(y) := \int_{-\infty}^{\infty} k(x,y)dx < 1$ for some $y$ so that death may occur during migration, we can replace $R$ by $\hat{R}(v,y) := s(y)R(v,y)$ and $k$ by

$\hat{k}(x,y) := k(x,y)/s(y)$ in (1.1) to obtain an equivalent system for which Hypothesis 2.1.ii is satisfied.

Thieme [T79b] obtained his results on spreading with overcompensation in a spatially homogeneous habitat by bounding the recruitment function above and below by nondecreasing functions with the same derivative at zero. We shall show that this idea can be extended to the case of a periodic habitat.

We define the nondecreasing function

$$R^+(v,x) := \max_{0\le w\le v} R(w,x),$$

and the order-preserving operator

$$Q^+[u] := \int_{-\infty}^{\infty} k(x,y)R^+(u(y),y)dy.$$

The following Lemma asserts the existence of a smallest positive $L$-periodic equilibrium solution of the recursion

$$u_{n+1}^+ = Q^+[u_n^+]. \tag{2.12}$$

**Lemma 2.1.** *If the Hypotheses 2.1 are satisfied, then there is a continuous $L$-periodic solution, which we shall call $\alpha(x)$, of the equilibrium equation $Q^+[u] = u$ with the following property: If the sequence $u_n^+$ is a solution of the recursion (2.12), and if $u_0^+(x)$ is any positive continuous $L$-periodic function with $u_0^+(x) \le \alpha(x)$, then $u_n^+(x)$ converges to $\alpha(x)$ uniformly.*

We now define the nondecreasing function

$$R^-(v,x) := \min_{v\le w\le \alpha(x)} R(w,x), \tag{2.13}$$

and the order-preserving operator

$$Q^-[u] := \int_{-\infty}^{\infty} k(x,y)R^-(u(y),y)dy.$$

The following Lemma is analogous to Lemma 2.1.

**Lemma 2.2.** *There is a positive continuous $L$-periodic solution, which is denoted by $\sigma(x)$, of the equilibrium equation $Q^-[u] = u$ with the following property: If the sequence $u_n^-$ is a solution of the recursion*

$$u_{n+1}^- = Q^-[u_n^-], \tag{2.14}$$

*and if $u_0^-(x)$ is any positive continuous $L$-periodic function with $u_0^-(x) \le \sigma(x)$, then $u_n^-(x)$ converges to $\sigma(x)$ uniformly.*

These lemmas will be proved in the Appendix.

We have the following extension of Theorem 2.6 of [T79b] to the case of a periodic habitat.

**Theorem 2.1.** *Suppose that the recruitment function $R(v, x)$ and the dispersal kernel $k(x, y)$ satisfy the Hypotheses 2.1. Define $c^*$ by the formula (2.7) with $\tilde{\lambda}(\mu)$ the principal eigenvalue of (2.3). If $u_0(x)$ is continuous, the solution $u_n(x)$ of the recursion (1.1) has the following properties*

*i. If $0 \le u_0(x) \le \alpha(x)$ for all $x$, then*

$$u_n(x) \le \alpha(x) \text{ for all } n \text{ and } x. \tag{2.15}$$

*ii. If $0 \le u_0(x) \le \alpha(x)$ and $u_0(x) = 0$ whenever $|x|$ is sufficiently large, then*

$$\lim_{n\to\infty} \left\{ \sup_{|x|\ge nc} u_n(x) \right\} = 0 \text{ when } c > c^*. \tag{2.16}$$

*iii. If $0 \le u_0(x) \le \alpha(x)$ and $m(x)u_0(x) \not\equiv 0$, then*

$$\liminf_{n\to\infty} \left\{ \min_{|x|\le nc} [u_n(x) - \sigma(x)] \right\} \ge 0 \text{ when } 0 < c < c^*. \tag{2.17}$$

*iv. If $R(v, x)$ has the additional property that $R(v, x)$ is nondecreasing in $v$ for all $0 \le v \le \alpha(x)$ and all $x$, then $\alpha(x) \equiv \sigma(x)$, the function $u^*(x) := \alpha(x)$ is a solution of the equilibrium equation $Q[u^*] = u^*$, and*

$$\lim_{n\to\infty} \left\{ \max_{|x|\le nc} |u^*(x) - u_n(x)| \right\} = 0$$

*when $0 < c < c^*$, $m(x)u_0(x) \not\equiv 0$, and $u_0(x) \le u^*(x)$.*

**Remarks.** 1. We see from Hypothesis 2.1.vi and from (2.6) that

$$\tilde{\lambda}(0) > 1.$$

This inequality implies that the equilibrium $u \equiv 0$ is unstable for the recursion (1.1), so that the extinction state is invadable. Conversely, if $\tilde{\lambda}(0) > 1$, then setting $\ell(x)$ equal to the corresponding positive eigenfunction gives Hypothesis 2.1.vi. If, on the other hand $\tilde{\lambda}(0) < 1$, the formula (2.7) shows that $c^* = -\infty$, so that no spreading occurs.

2. The symmetry condition (2.11) can be replaced by the assumption that the integral in Hypothesis 2.1.viii is bounded for at least one positive

and one negative value of $\mu$. One then finds the forward spreading speed $c^*(1)$ from the formula (2.7), and the backward spreading speed $c^*(-1)$ from

$$c^*(-1) = \inf_{\mu>0}\{(1/\mu)\ln\tilde{\lambda}(-\mu)\}. \tag{2.18}$$

In this case, the inequality (2.17) must be modified by taking the minimum over the interval $-nc_1 \le x \le nc_2$, where $c_1$ and $c_2$ are any numbers such that $c_1 < c^*(-1)$ and $c_2 < c^*(1)$. The supremum in (2.16) is taken over the exterior of the interval $(-nc_1, nc_2)$ with $c_1 > c^*(-1)$ and $c_2 > c^*(1)$.

3. It is difficult to find the functions $\alpha$ and $\sigma$ exactly. It is easily seen that the function $\alpha$ in Statement i can be replaced by any positive continuous $L$-periodic function $a(x)$ which satisfies the inequality $Q^+[a] \le a$. The function $\hat{\alpha}(x)$ in Hypothesis 2.1.iii is an example of such a function. Of course, replacing $\alpha$ by $a$ in the definition (2.13) may lower the values of $R^-$, and hence also the function $\sigma$. Clearly, Statements ii and iii are still correct if $\alpha$ is replaced by a lower bound for $\alpha$. The proof of Lemma 2.1 provides many such lower bounds.

# 3 Periodic equilibria.

While Theorem 2.1 gives rather precise information about how the solution $u_n(x)$ of the recursion (1.1) behaves well ahead of the front, it gives little information about what happens well behind the front. Theorem 2.1 of [W02] shows that when $R(v, y)$ is nondecreasing in $v$, there is convergence to a positive periodic equilibrium behind the front. This raises the question of whether or not such a result is valid in the presence of overcompensation. However, this only makes sense if there is exactly one $L$-periodic solution of the equilibrium equation $u = Q[u]$. In this section we shall discuss additional conditions on the recruitment function $R(v, y)$ and the migration kernel $k(x, y)$ which imply that the periodic equilibria $\alpha$, $\sigma$, and $u^*$ are uniquely defined.

We begin with a theorem which shows that $\alpha$ and $\sigma$ are the only solutions of their equilibrium equations.

**Theorem 3.1.** *Suppose that the Hypotheses 2.1 are satisfied, and that, in addition, for each $x$ the specific growth rate $R(v, x)/v$ is either strictly decreasing in $v$ or zero for all $v$. Then the following statements are valid.*

*i. If $u(x)$ and $v(x)$ are two distinct positive $L$-periodic solutions of the equilibrium equation $u = Q[u]$, then $u - v$ must be positive at some values of $x$ and negative at others.*

*ii. There is exactly one positive $L$-periodic solution $\alpha(x) \le \hat{\alpha}(x)$ of the equilibrium equation $u = Q^+[u]$, and it is even in $x$.*

iii. *There is exactly one positive $L$-periodic solution $\sigma(x) \leq \hat{\alpha}(x)$ of the equilibrium equation $u = Q^-[u]$, and it is even in $x$.*

**Remarks.** 1. The facts that $\alpha$ is the only positive solution of the recursion $u = Q^+[u]$ and that $Q^+$ is monotone imply that the sequence $u_n$ obtained by the iteration process $u_{n+1} = Q^+[u_n]$ with $u_0 = \hat{\alpha}$ decreases to $\alpha$. Thus we obtain a sequence of arbitrarily close upper bounds. If, instead, we start the iteration with a suitably small multiple of the function $\ell$ in Hypothesis 2.1.vi, we obtain an increasing sequence of arbitrarily close lower bounds. The difference between one of the upper bounds and one of the lower bounds gives a bound for the error in either one. Similar comments apply to approximating $\sigma$ by iteration.

2. Remark 1 and induction show that if $u_0 \leq \hat{\alpha}$, then

$$\limsup_{n\to\infty} u_n(x) \leq \alpha(x). \tag{3.1}$$

This means that the statements of Theorem 2.1 but with the inequality $u_n \leq \alpha$ replaced by (3.1) are valid under the weaker assumption $u_0 < \hat{\alpha}$ rather that $u_0 < \alpha$. In fact, if $\limsup_{v\to\infty}[R(v,x)/v] < 1$ uniformly in $x$, $\hat{\alpha}$ can be taken to be any sufficiently large constant, so that $u_0$ may be any bounded function.

We have only been able to prove the uniqueness of a positive $L$-periodic solution $u^*(x) \leq \hat{\alpha}$ of the equilibrium equation $u = Q[u]$ for a special class of migration kernels. Choose any positive constant $\beta$ and any odd one-periodic smooth function $\phi(x)$ with the properties

$$\phi(x+1) = \phi(x),\ \phi(-x) = -\phi(x),\ \text{and } \phi'(x) > -1 \text{ for all } x, \tag{3.2}$$

and define the $L$-periodic kernel

$$k(x,y) = (\beta/2)[1 + \phi'(x/L)]e^{-\beta|x+L\phi(x/L)-y-L\phi(y/L)|}. \tag{3.3}$$

It is easily verified that $x$-integral of this kernel is 1, and that the periodicity condition $k(x+L, y+L) = k(x,y)$ and the evenness condition $k(-x,-y) = k(x,y)$ are satisfied. The advantage of this kernel is given by the following theorem.

**Theorem 3.2.** *Let the kernel $k$ in the recursion (1.1) be of the form (3.3) where $\beta$ is any positive constant and $\phi$ has the properties (3.2). If for each $x$ the specific growth rate $R(v,x)/v$ is either strictly decreasing in $v$ or zero for all $v$, then there is exactly one positive $L$-periodic solution $u^*(x)$ of the equilibrium equation $u = Q[u]$ with $0 \leq u \leq \hat{\alpha}$, and it is even in $x$.*

For the above kernel, we can also obtain information about how the eigenvalue $\tilde{\lambda}(0)$ varies with a change of the period $L$.

**Theorem 3.3.** *Let the migration kernel have the form (3.3), where $\phi(x)$ has the properties (3.2). Let the function $\hat{R}(v,x)$ be one-periodic and even in $x$, and let*

$$R(v,x) := \hat{R}(v,x/L),$$

*so that*

$$m(x) = \hat{m}(x/L) := \hat{R}_v(0,x/L).$$

*Suppose that the Hypotheses 2.1 with the possible exception of Hypothesis 2.1.vi are satisfied. Then the principal eigenvalue $\tilde{\lambda}(0)$ of the problem (2.3) with $\mu = 0$ is increasing in the parameter $L$. In particular,*

*i. if*

$$\int_{-1/2}^{1/2} \hat{m}(x)[1+\phi'(x)]dx \geq 1,$$

*Hypothesis 2.1.vi is satisfied for all positive values of $L$;*

*ii. if*

$$\int_{-1/2}^{1/2} \hat{m}(x)[1+\phi'(x)]dx < 1 \text{ and } \max \hat{m}(x) > 1,$$

*there is a positive number $\hat{L}$ such that Hypothesis 2.1.vi is satisfied when $L \geq \hat{L}$, but no spreading occurs when $L < \hat{L}$;*

*iii. if $m(x) \leq 1$, then no spreading occurs for any positive value of $L$.*

We note that when $k(x,y)$ has the form (3.3), it is easy to find an explicit formula for the kernel $K_\mu(x,y)$ defined in (2.5). Namely, when $0 \leq \mu < \beta$, $|x| \leq L/2$, and $|y| \leq L/2$,

$$\begin{aligned} K_\mu(x,y) = &\frac{\beta[1+\phi'(x/L)]e^{\mu(x-y)}}{2}\Big\{e^{-\beta|x+L\phi(x/L)-y-L\phi(y/L)|} \\ &+ \frac{e^{\beta(x+L\phi(x/L)-y-L\phi(y/L))}}{e^{(\beta+\mu)L}-1} + \frac{e^{-\beta(x+L\phi(x/L)-y-L\phi(y/L))}}{e^{(\beta-\mu)L}-1}\Big\}. \end{aligned}$$

This kernel is useful in finding the eigenvalue $\tilde{\lambda}(\mu)$, which can be used to calculate the spreading speed. The kernel

$$K_0(x,y) = \frac{\beta[1+\phi'(x/L)]\cosh\beta[(L/2) - |x+L\phi(x/L)-y-L\phi(y/L)|]}{2\sinh[\beta L/2]}$$

is particularly useful, because one can write the operator $Q$ on the right-hand side of (1.1) as

$$Q[u](x) = \int_{-L/2}^{L/2} K_0(x,y)R(u(y),y)dy$$

for any $L$-periodic function $u(x)$. This means that each step of the iterative approximation of $u^*$ involves approximating an integral over a finite interval. In fact, if $u$ is also even in $x$, one obtains the formula

$$Q[u](x) = \int_0^{L/2} [K_0(x,y) + K_0(x,-y)]R(u(y),y)dy,$$

which only involves an integral over the interval $[0, L/2]$. Because the operators $Q^+$ and $Q^-$ have the same migration kernel, the same comments apply to the iterations used to approximate $\alpha$ and $\sigma$.

**Example 3.1.** We consider the recursion

$$\begin{aligned} u_{n+1}(x) =& [1 + (\pi/4)\cos(2\pi x/L)] \\ & \int_{-\infty}^{\infty} e^{-2|x+(L/8)\sin(2\pi x/L)-y-(L/8)\sin(2\pi y/L)|} u_n(y) e^{3+4\cos(2\pi y/L)-u_n(y)} dy. \end{aligned} \tag{3.4}$$

(3.4) is the recursion (1.1) in which $R(v,y) = \hat{R}(v, y/L)$ where $\hat{R}$ is the one-periodic Ricker function

$$\hat{R}(v,y) = ve^{3+4\cos(2\pi y)-v},$$

and the migration kernel is (3.3) with $\beta = 2$, and $\phi(x) = (1/8)\sin 2\pi x$. Since $R(v,x)/v = e^{3+4\cos(2\pi x/L)-v}$ which is decreasing in $v$, we may apply Theorems 3.1, 3.2, and 3.3 to see that the $L$-periodic equilibrium solutions $\sigma$, $u^*$, and $\alpha$ are uniquely defined and even, and that $\tilde{\lambda}(0)$ is increasing in $L$.

The special form (3.3) of the migration kernel also permits us to find methods for calculating the equilibrium $u^*$. We shall use the following property.

**Lemma 3.1.** *Suppose that the Hypotheses 2.1 are satisfied, that $k(x,y)$ has the form (3.3), and that $R(v,x)$ is differentiable in $v$, and satisfies the inequality $[R(v,x)/v]_v < 0$ for all positive $v$ and all $x$ for which $m(x) > 0$. Then the eigenvalues of the operator*

$$\mathcal{L}[\eta](x) := \int_{-L/2}^{L/2} K_0(x,y) R_v(u^*(y),y)\eta(y)dy, \tag{3.5}$$

*which is the linearization of the operator $Q$ in (1.1) at the equilibrium $u^*$, are all real and uniformly less than 1.*

**Remark.** Because the operator may have eigenvalues less than $-1$, Lemma 3.1 does not show that the equilibrium $u^*$ is an attractor for the iteration (1.1). However, it does show that $u^*$ is an attractor for the relaxed iteration scheme

$$u_{n+1} = (1-\rho)u_n + \rho Q[u_n]$$

when $\rho$ is positive and sufficiently small. Thus, $u^*$ can be approximated by using this iteration.

## 4 A spatially periodic example and its simulation.

In this Section we present the results of numerical simulations of the recursion

$$u_{n+1}(x) = \int_{-\infty}^{\infty} (1/2)e^{-|x-y|} u_n(y) e^{r(y)-u_n(y)} dy, \tag{4.1}$$

where $r(x)$ is the even $L$-periodic piecewise constant function which is defined by the formula

$$r(x) = \begin{cases} r_1 & \text{for } |x| < L_1/2 \\ r_2 & \text{for } L_1/2 \leq |x| \leq L/2. \end{cases}$$

We shall assume that $r_1 \geq r_2$, so that $R(v, x)$ is lower semicontinuous in $x$. The migration kernel is, of course, of the form (3.3) with $\beta = 1$ and $\phi(x) \equiv 0$.

The secular equation to determine the principal eigenvalue $\tilde{\lambda}(\mu)$ of the problem (2.3) is given in equation (23) of [KS07]. In our notation, this equation is

$$\cos(q_1 L_1)\cosh(q_2 L_2) + [(q_2^2 - q_1^2)/(2q_1 q_2)]\sin(q_1 L_1)\sinh(q_2 L_2) = \cosh(\mu L), \tag{4.2}$$

where $L_2$, $q_1$ and $q_2$ are defined by

$$L_2 := L - L_1,\ q_2 := \sqrt{1 - (e^{r_2}/\lambda)},\ \text{and } q_1 := \begin{cases} \sqrt{(e^{r_1}/\lambda) - 1} & \text{when } \lambda < e^{r_1} \\ i\sqrt{1 - (e^{r_1}/\lambda)} & \text{when } \lambda > e^{r_1}. \end{cases} \tag{4.3}$$

This formula was used in [KS07] to compute the spreading speed $c^*$ by means of the formula (2.7). The formula comes from constructing a positive eigenfunction of the equation (2.3). The construction shows that one must have $q_1 L_1 < \pi$ when $\lambda = \tilde{\lambda}(\mu)$ and $q_1$ is real, which yields the lower bound

$$\tilde{\lambda}(\mu) > e^{r_1}/[1 + (\pi/L_1)^2] \tag{4.4}$$

for all $\mu$.

The Krein-Rutman inequalities (2.6) show that $\tilde{\lambda}(\mu)$ increases when the linearization $m(x)u$ of the recruitment function is increased. In particular, we see that $\tilde{\lambda}(\mu)$ is an increasing function of $r_1$, $r_2$, and $L_1$ when $L$ is kept constant, and hence that the spreading speed $c^*$ has the same properties. By letting $r_1$ decrease to $r_2$ and by letting $r_2$ increase to $r_1$, we obtain the bounds

$$e^{r_2}/(1 - \mu^2) < \tilde{\lambda}(\mu) < e^{r_1}/(1 - \mu^2). \tag{4.5}$$

when $r_1 > r_2$. These inequalities show that $\tilde{\lambda}(\mu)$ approaches infinity as $\mu$ increases to 1, and that when $r_1 > r_2$, $r_1 > 0$, and $\lambda = \tilde{\lambda}(\mu)$, $q_1$ is real for sufficiently small $\mu$ and imaginary when $\mu$ is sufficiently near 1.

As mentioned in Remark 1 after Theorem 2.1, Hypothesis 2.1.vi is equivalent to the condition $\tilde{\lambda}(0) > 1$, which, in turn is equivalent to the statement that a local invasion always succeeds. It was shown in [KS07] that if $r_1 > 0$, this condition is satisfied if and only if

$$\begin{aligned} & r_2 \geq 0, \text{ or } L_1 \geq \pi/\sqrt{e^{r_1}-1}, \text{ or} \\ & \sqrt{e^{r_1}-1}\tan(\sqrt{e^{r_1}-1}L_1/2) > \sqrt{1-e^{r_2}}\tanh(\sqrt{1-e^{r_2}}L_2/2). \end{aligned} \tag{4.6}$$

We have chosen the parameters $L = 30$, $L_1 = 20$ and $r_2 = -0.1$. Figures 4.1–4.4 show the parts with $x \geq 0$ of the graphs of the even functions $u_n(x)$ with large $n$ generated by the recursion (3.4) with the even initial function

$$u_0 = \begin{cases} 0.4r_1[1-(|x|/100)] & \text{for } |x| \leq 100 \\ 0 & \text{for } |x| > 100. \end{cases}$$

In addition to the graph of $u_n$, we show the graphs of the three functions $\sigma(x)$, $u^*(x)$, and $\alpha(x)$. Because these three graphs are very close to each other when their values are low, we have labeled them near their maximum values. The functions $\alpha$ and $\sigma$ were computed by means of the iterations outlined in the Remark after the statement of Theorem 3.1. The function $u^*$ cannot be calculated in this fashion when it is an unstable equilibrium. We know that when $r_1 = r_2$ so that the habitat is homogeneous, then $u^* \equiv r_1 = r_2$, and the linearization of the equilibrium equation about $u^*$ has the principal eigenvalue $1-r_1$. This value is always less than 1, but it decreases through the value -1 when $r_1 = r_2$ decreases through the value 2. That is, the equilibrium $r_1$ is stable as long as $r_1 = r_2 < 2$, but it develops an oscillatory instability when $r_1 = r_2$ increases beyond the value 2.

When $r_1 > 2$, we have used the Remark after Lemma 3.1 to determine the equilibrium $u^*$. That is, we have approximated $u^*$ by the solution $u_{200}$ of the relaxed iteration

$$u_{n+1}(x) = (1-\rho)u_n(x) + \rho \int_{-L/2}^{L/2} K_0(x,y)R(u_n(y),y)dy$$

with $\rho = 0.2$ and $u_0 = r_1$.

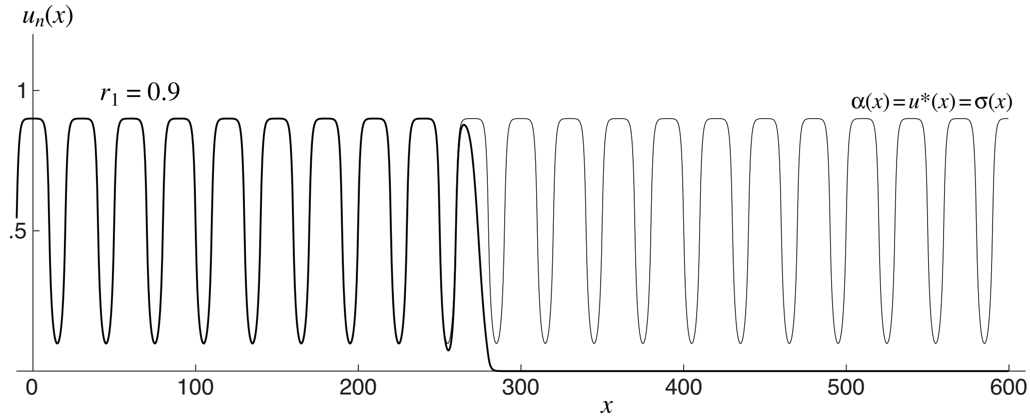


Figure 4.1

In Figure 4.1 $r_1 = 0.9$. In this case, we can take $\hat{\alpha} \equiv r_1$ in Hypothesis 2.1.iii. Since $R(v, y)$ is nondecreasing in $v$ for $0 \leq v \leq r_1$, Statement iv of Theorem 2.1 implies that well behind the front $u_n(x)$ converges to the equilibrium $u^*(x)$. The graphs of $u_{100}(x)$ and of $u^*(x)$ are shown to illustrate this convergence.

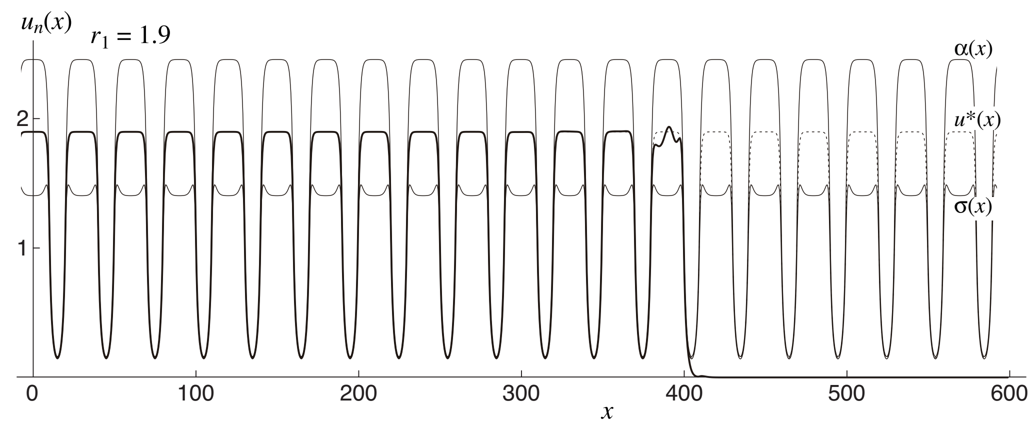


Figure 4.2

In Figure 4.2 $r_1 = 1.9$. In this case, we have $\sigma(x) < u^*(x) < \alpha(x)$, and we have shown the graph of $u_{100}(x)$ superimposed on the graphs of these three functions to show that the solution still seems to converge to $u^*$ well inside the front.

In the case of the spatially homogeneous Ricker function where $r_2 = r_1$, we have $u^* \equiv r_1$. A simple stability analysis shows that this equilibrium is stable for $r_1 < 2$ but unstable for $r_1 > 2$. The work of Oster and May [MO80] shows that as $r_1$ increases above 2, there is a Hopf bifurcation into a stable equilibrium two-cycle, which means that there is a solution of the recursion (1.1) with $u_{n+2} = u_n$ but $u_{n+1} \neq u_n$ for all $n$. At a higher value of $r_1$ this two-cycle bifurcates into a four-cycle, and this process continuous until chaotic behavior is reached for some value of $r_1$. We can expect similar behavior with increasing $r_1$ in the present problem, even though the value of $r_2$ is kept fixed.

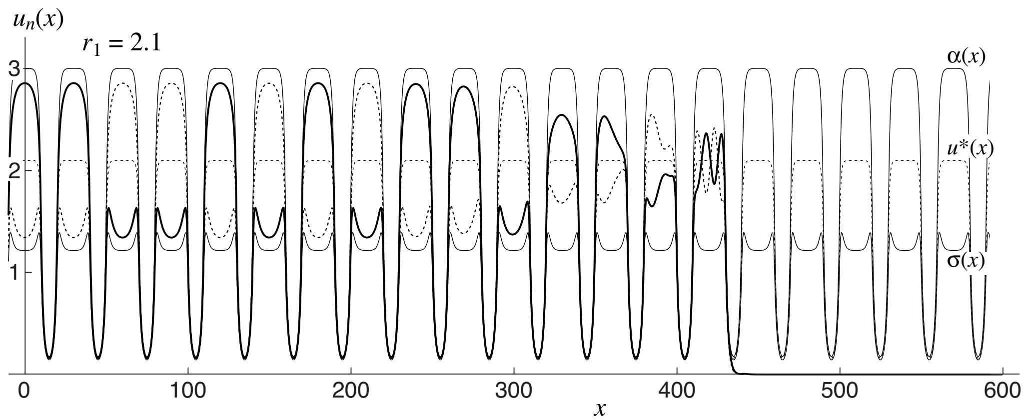


Figure 4.3

In Figure 4.3 $r_1 = 2.1$. We show the graphs of $u_{100}(x)$ (dotted line) and $u_{101}(x)$ (solid line) superimposed on the graphs of $\sigma(x) < u^*(x) < \alpha(x)$ to illustrate the development of an oscillation of period 2 about $u^*$ well behind the front. The equilibrium $u^*$ is unstable for this value of $r_1$.

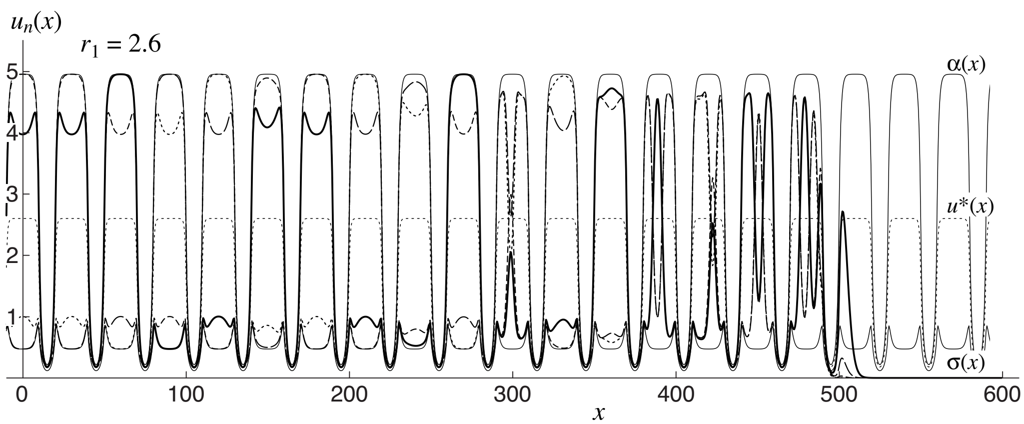


Figure 4.4

In Figure 4.4 $r_1 = 2.6$. We have drawn the graphs of $u_{100}$ (dotted line), $u_{101}$ (dashed line), $u_{102}$ (long-dashed line), and $u_{103}$ (solid line) superimposed on those of $\sigma$, $u^*$, and $\alpha$ to illustrate the development of an oscillation of period 4 around the equilibrium $u^*$.

M. Kot[K92] has found similar behavior in simulations of a spatially homogeneous problem with overcompensation.

Theorem 3.3 shows that if $r_1 > 0 > r_2$ and

$$L_2/L_1 \leq [e^{r_1} - 1]/[1 - e^{r_2}],$$

or if $r_1 > r_2 \geq 0$, then for every positive $L$ $\tilde{\lambda}(0) > 1$, so that spreading occurs. If, on the other hand, $r_1 > 0 > r_2$ but $L_2/L_1 > [e^{r_1} - 1]/[1 - e^{r_2}]$, then there is a positive number $\hat{L}$ such that spreading occurs if and only if $L = L_1 + L_2 \geq \hat{L}$.

# 5 Discussion.

We have shown that, under certain hypotheses, the formula (2.7), which is known to give the spreading speed when the recruitment function is monotone, still works even when overcompensation occurs.

Thieme [T79b] applied his method of treating a nonmonotone spatially homogeneous recruitment function to a more general spatially homogeneous integral equations model, and pointed out that such a model occurs not only in the Kermack-McKendrick theory of epidemics (see, e. g., [D79]), but also in a model for the growth and spread of the adults of a population in which the juveniles do not move. The methods of the present work may well permit one to extend these ideas to obtain a spreading speed for a spatially periodic version of the integral equation model, and perhaps even to a spatially periodic version of the more general integral equation model of Thieme and Zhao [TZ03].

D. Mollison ([M72], Theorem 2.ii) showed that for the simple epidemic model

$$v_t = (1 - v) \int_{-\infty}^{\infty} k(x - y) v(y, t) dy$$

in a homogeneous habitat, the spreading speed is infinite when Hypothesis 2.1.viii is violated. M. Kot, M. A. Lewis, and P. van den Driessche [KLvdD96] showed that for a large class of spatially homogeneous integro-difference models of the form (1.1), the spreading speed is infinite when Hypothesis 2.1.viii is violated.

Theorem 3.3 states that if one wishes to prevent spreading of an invading species by making a certain proportion of the environment unfavorable to its growth, it is better to chop the environment into a sequence of many small unfavorable regions than to use fewer large regions. This is related to a result of [RS07] on the effect of patchiness in random environments. Numerical simulation seems to indicate that the spreading speed increases with increasing $L$ when $L_2/L_1$ is fixed, but we have not been able to prove this.

# 6 Appendix: Proofs of the lemmas and theorems.

**Proof of Lemma 2.1.** We choose a positive $\delta$ so small that

$$(1-\delta)\eta > 1, \tag{6.1}$$

where $\eta > 1$ is the constant in Hypothesis 2.1.vi. We see from Hypothesis 2.1.v.c that if $\epsilon$ is positive and so small that

$$\epsilon\ell(x) \le \epsilon_\delta \text{ for all } x, \tag{6.2}$$

then

$$R(\epsilon\ell) \ge (1-\delta)m\epsilon\ell.$$

Therefore,

$$Q^+[\epsilon\ell] \ge Q[\epsilon\ell] \ge (1-\delta)M_0[\epsilon\ell] > \epsilon\ell. \tag{6.3}$$

We define the sequence $p_n^+$ of $L$-periodic continuous positive functions by means of the recursion

$$p_{n+1}^+ = Q^+[p_n^+] \text{ with } p_0^+ = \epsilon\ell, \tag{6.4}$$

where $\epsilon$ satisfies the inequality (6.2). Then (6.3) shows that $p_1^+ \ge p_0^+$. Because $Q^+$ is order-preserving, that is, because $R^+(v,x)$ is nondecreasing in $v$, we find that $p_2^+ \ge p_1^+$. By repeating this argument we find that the sequence $p_n^+$ is nondecreasing and bounded above by $\hat{\alpha}$. Therefore, $p_n^+(x)$ converges to a limit function, which we call $\alpha(x)$. Hypothesis 2.1.iv shows that the family of functions is equicontinuous, and therefore $\alpha$ is continuous and $L$-periodic, and the convergence is uniform. We let $n$ approach infinity in (6.4) to obtain the equilibrium equation $Q^+[\alpha] = \alpha$.

The sequence $p_n^+$ depends on the parameter $\epsilon$ in (6.4), and it is nondecreasing in $\epsilon$. To show that the limit $\alpha$ is independent of the choice of $\epsilon$, we observe that

$$Q^+[\{\epsilon/[(1-\delta)\eta]\}\ell] \ge (1-\delta)M_0[\{\epsilon/[(1-\delta)\eta]\}\ell] \ge \epsilon\ell.$$

Thus, if $\epsilon$ is replaced by any number

$$\epsilon' \ge \epsilon/[(1-\delta)\eta], \tag{6.5}$$

then the $p_1^{+\prime}$ of the corresponding sequence is at least the $p_0^+$ of the original sequence. Induction shows that $p_n^{+\prime} \geq p_{n-1}^+$ for all $n \geq 1$. In particular, the new limit is at least as large as the old one. Since this limit is nondecreasing in $\epsilon$, it has the same value for any $\epsilon' \leq \epsilon$ which satisfies the inequality (6.5). One can repeat this process to show that one gets the same limit from any $\epsilon' \leq \epsilon$ as long as there is an integer $k$ such that $\epsilon \leq [(1-\delta)\eta]^k \epsilon'$. We recall that $\delta$ was chosen to make $(1-\delta)\eta > 1$. Hence if $\epsilon' > 0$, there is a $k$ which makes this inequality true. That is, one gets the same limit for all positive $\epsilon' \leq \epsilon$.

Finally, we observe that any positive continuous $L$-periodic function $u_0^+ \leq \alpha$ has a positive lower bound of the form $\epsilon' \ell$. Then if $u_n^+$ satisfies the recursion $u_{n+1}^+ = Q^+[u_n^+]$ with this $u_0^+$, $p_n^{+\prime} \leq u_n^+ \leq \alpha$. Taking limits as $n$ goes to infinity shows that $u_n^+$ converges to $\alpha$. Thus the statements of Lemma 2.1 have been established.

**Proof of Lemma 2.2.** The proof is almost identical to that of Lemma 2.1. We again choose $\delta$ so small that (6.1) is satisfied. We see from Hypothesis 2.1.v.c and the definition of $R^-$ that, if $v \leq \epsilon_\delta$, then

$$R^-(v, x) \geq (1-\delta)m(x)v.$$

Therefore, if $\epsilon$ is so small that the inequality (6.2) is satisfied, then

$$Q^-[\epsilon\ell] \geq (1-\delta)M_0[\epsilon\ell] \geq \epsilon\ell.$$

As in the above proof, the solution of the recursion

$$p_{n+1}^- = Q^-[p_n^-] \text{ with } p_0^- = \epsilon\ell$$

gives a bounded nondecreasing equicontinuous sequence of positive $L$-periodic functions, and hence the sequence converges uniformly to a limit $\sigma$. We show as in the preceding proof that $\sigma$ is an equilibrium, that it is unchanged if $\epsilon$ is replaced by any smaller positive number, and that every solution of the recursion

$$u_{n+1}^- = Q^-[u_n^-]$$

for which $u_0^- \leq \sigma$ is positive, continuous, and $L$-periodic converges to $\sigma$ uniformly. This establishes Lemma 2.2.

**Proof of Theorem 2.1.** Because $Q^+[u] \geq Q[u]$ for all $u \leq \alpha$ and because $Q^+$ is order-preserving, we see that if $u_n$ is a solution of the recursion (1.1), if $u_n^+$ satisfies the recursion (2.12), and if $u_n \leq u_n^+ \leq \alpha$, then

$$u_{n+1} = Q[u_n] \leq Q^+[u_n] \leq Q^+[u_n^+] = u_{n+1}^+ \leq \alpha.$$

Thus if $u_0 \leq \alpha$ and we choose $u_0^+ = u_0$, we see by induction that

$$u_n \leq u_n^+ \leq \alpha \tag{6.6}$$

for all $n$. This gives Statement i of the Theorem.

It is not difficult to check that the recursion (2.12) satisfies the Hypotheses 2.1 of [W02] with $\pi_0 = 0$ and $\pi_1 = \alpha$. Hypothesis 2.1.v.b shows that $Q^+[u] \leq M_0[u]$, and Hypothesis 2.1.v.c shows that the inequality $Q^+[u] \geq (1-\delta)M_0[u]$ when $u \leq \epsilon_\delta$ is valid for any $\delta > 0$. Then Corollary 2.1 of [W02] shows that the spreading speed $c^*$ of the recursion with $Q$ replaced by $Q^+$ is given by the formula (2.7). Because of the symmetry conditions (2.11), the set $\mathcal{S}$ defined by (2.9) of [W02] is the interval $[-c^*, c^*]$. Then Statement 2 of Theorem 2.2 of [W02] with $\pi_0 = 0$ implies that

$$\lim_{n\to\infty} \left\{ \sup_{|x|\geq nc} u_n^+(x) \right\} = 0 \text{ when } c > c^*. \tag{6.7}$$

Combining this equation with the inequality (6.6) immediately gives the equation (2.16), which is the second statement of the Theorem.

In a similar manner, we see that if $u_n^-$ is a solution of the recursion (2.14) with $u_0^-(x) \leq \min\{u_0(x), \sigma(x)\}$, then

$$u_n \geq u_n^- \tag{6.8}$$

for all $n$. We find that the recursion (2.14) satisfies the Hypotheses 2.1 of [W02] with $\pi_0 = 0$ and $\pi_1 = \sigma$. We apply Corollary 2.1 of [W02] to see that the recursion (2.14) again has the spreading speed $c^*$ given by the formula (2.7). We apply Theorem 2.3 of [W02] with $\mathcal{S} = [-c^*, c^*]$ to obtain the formula

$$\lim_{n\to\infty} \max_{|x|\leq nc} [\sigma(x) - u_n^-(x)] = 0 \text{ when } c < c^*, \tag{6.9}$$

under the condition that $u_0 \geq s$ for a positive constant $s$ on an interval of length $R_s$, which is defined in [W02]. To remove this extra condition, which is difficult to verify because $R_s$ is hard to find, we shall imitate the proof of Theorem 6.5 of [W82]. Because of Hypothesis 2.1.v.c, we have $Q^-[u] \geq Q_\delta[u]$, where

$$Q_\delta[u](x) := \int_{-\infty}^{\infty} k(x,y)(1-\delta)m(y)\min\{u(y), \epsilon_\delta\}dy.$$

For any $c < c^*$ we choose $\delta$ so small $(1-\delta)c < c^*$, so that $c$ is also less than the spreading speed of the recursion

$$u_{n+1} = Q_\delta[u_n]. \tag{6.10}$$

The proof of Theorem 2.3 of [W02] applied to this recursion is carried out by constructing the sequence $e_\ell$ in (5.26) of [W02]. This sequence of functions has the properties that (i) $e_0$ vanishes outside a bounded set, (ii) the set where $e_n$ is positive grows with the speed $c$, and (iii) $e_n(x)$ is a subsolution of the recursion in the sense that $e_{n+1} \leq Q_\delta[e_n]$. Theorem 2.3 of [W02] is then obtained by requiring $u_0$ to lie above a translate of $e_0$, and applying induction to show that $u_n \geq e_n$, which spreads with speed $c$. That is, the invasion succeeds if $u_0$ lies above a translate of $e_0$.

We shall now show that Hypothesis 2.1.ix leads to a hair-trigger effect, which means that the invasion succeeds whenever $m(x)u_0(x) \not\equiv 0$. For this purpose, we observe that if $\gamma$ is any positive number with $\gamma \leq 1$, then

$$\min\{\gamma u, \epsilon_\delta\} \geq \min\{\gamma u, \gamma\epsilon_\delta\} = \gamma \min\{u, \epsilon_\delta\}.$$

Therefore, $Q_\delta[\gamma u] \geq \gamma Q_\delta[u]$. Thus, the fact that $e_n$ is a subsolution shows that

$$\gamma e_{n+1} \leq \gamma Q_\delta[e_n] \leq Q_\delta[\gamma e_n].$$

That is, $\gamma e_n$ is also a subsolution of (6.10). If $u_0$ is positive on an interval which is longer than the interval outside which $e_0$ vanishes, then one can find a positive $\gamma$ such that $u_0$ is bounded below by a translate of $\gamma e_0$, so that the solution spreads with at least the speed $c$. In this way we see that we can take the above $R_s$ independent of $s$. This is an extension of Theorem 6.4 of [W82].

The condition $m(x)u_0(x) > 0$ means that there is an $a$ such that $m(a)u_0(a) > 0$. Because of the $L$-periodicity of the operator $Q_\delta$, we can assume without loss of generality that $|a| \leq L/2$. We now apply Hypothesis 2.1.ix. Because of the continuity of $u_0$ and the semicontinuity of $k$ and $R$, we see that $u_0 > 0$ in a neighborhood of $a$, and that for $j = 1, \cdots, G$, $k(x,y)m(y) > 0$ for $x$ in a neighborhood of $x_j$ and $y$ in a neighborhood of $x_{j-1}$. Therefore the function $u_G$, which is obtained by applying the operators $Q_\delta$ to $u_0$ $G$ times is positive on the interval $|x - (2J+1)L/2| \leq L$, which has length $2L$. We think of this interval as two adjacent intervals of length $L$ centered on a half-integer multiple of $L$. Because $k$ and $m$ are $L$-periodic, we can apply the same argument to the points of these two intervals where $m > 0$ to see that $u_{2G}$ is positive on the union of an interval of length $2L$ and its translate by $L$, which is an interval of length $3L$. By continuing this argument, we see that $u_{mG}$ is positive on an interval of length $mL$. One now chooses a number $m_0$ so large that a translate by a multiple of $L$ of the above function $e_o$ vanishes outside the resulting interval of length $m_0L$. If one thinks of $u_{m_0G}$ as the initial function for the sequence $u_{m_0G+n}$, the above result implies that (6.9) is valid under our assumptions. This, together with the inequality (6.8) implies the inequality (2.17) of Statement iii of the Theorem.

To obtain Statement iv, we observe that because $R(v,y)$ is nondecreasing in $v$, we have $Q^-[u] = Q[u] = Q^+[u]$ for $u \leq \alpha$. Therefore, $\alpha$ is also the smallest positive equilibrium $\sigma$ of the recursion $u_{n+1} = Q^-[u_n]$ and the smallest positive equilibrium $u^*$ of the recursion $u_{n+1} = Q[u_n]$. The conclusion then follows immediately from (2.15) and (2.17). This completes the proof of Theorem 2.1.

We observe that if the evenness hypotheses (2.11) are not satisfied, then the results of [W02] show that there are a rightward spreading speed given by (2.7) and a leftward spreading speed $c^*(-1)$ given by (2.18). We can then apply Theorems 6.1 and 6.2 of [W02] with the set $\mathcal{S}$ the interval $[-c^*(-1), c^*(1)]$ to obtain the statement of Remark 2 after Theorem 2.1.

**Proof of Theorem 3.1.** Because of the inequalities $(1-\delta)m(x)\min\{v, \epsilon_\delta\} \leq R(v,x) \leq m(x)v$ in Hypotheses 2.1, we see that $R(v,x) = 0$ for all $v$ when $m(x) = 0$, and that $R(v,x)/v$ is strictly decreasing in $v$ when $m(x) > 0$.

Suppose, for the sake of contradiction, that there are two distinct positive $L$-periodic solutions $u$ and $v$ of the equilibrium equation $u = Q[u]$, and that one is never below the other, say $v(x) \geq u(x)$. The $L$-periodic function $v(x)/u(x)$ must take on its maximum value at some point $\hat{x}$. We observe that

$$\begin{aligned}
0 &= v(\hat{x}) - \{v(\hat{x})/u(\hat{x})\}u(\hat{x}) \\
&= \int_{-\infty}^{\infty} k(\hat{x},y)[R(v(y),y) - \{v(\hat{x})/u(\hat{x})\}R(u(y),y)]dy \\
&= \int_{-\infty}^{\infty} k(\hat{x},y)v(y)[\{R(v(y),y)/v(y)\} - \{R(u(y),y)/u(y)\}]dy \\
&\quad + \int_{-\infty}^{\infty} k(\hat{x},y)[\{v(y)/u(y)\} - \{v(\hat{x})/u(\hat{x})\}]R(u(y),y)dy.
\end{aligned} \tag{6.11}$$

Because $R(v,y)/v$ is nonincreasing and $v \geq u$, the integrand in the integral in the next-to-the-last line is nonpositive. The definition of $\hat{x}$ shows that the integrand of the last integral is also nonpositive. The fact that the sum of these two integrals is zero shows that the integrands of both integrals must be zero. Hypothesis 2.1.vi shows that there must be a point $y_0 = y_0(\hat{x})$ such that $k(\hat{x}, y_0)m(y_0) > 0$. Because of the semicontinuity of $k$ and $m$, there is an open interval $\mathcal{I}$ centered at $y_0$ such that $k(\hat{x}, y)$ and $m(y)$ are positive in $\mathcal{I}$. The same is the true of $R(v(y), y)$ and $R(u(y), y)$. Because $R(v,y)/v)$ is strictly decreasing, the fact that the integrands in the last two lines of (6.11) are zero in $\mathcal{I}$ imply that $v(y) \equiv u(y)$ and $v(y)/u(y) \equiv v(\hat{x})/u(\hat{x})$ for $y$ in $\mathcal{I}$. Since $1 = v(\hat{x})/u(\hat{x})$ is the global maximum value of $v/u$, we conclude that $v \leq u \leq v$ everywhere. That is, $v \equiv u$, so that $u$ and $v$ are not distinct. We have shown that if $u$ and $v$ are two distinct positive $L$-periodic solutions of the equilibrium equation, then neither of them can be bounded above by the other one. This yields Statement i of Theorem 3.1.

To obtain Statement ii, we first observe that for any two numbers $v_1 < v_2$

$$\begin{aligned} R^+(v_2, x) &= \max_{0 \le w \le v_2} R(w, x) \\ &= \max\{\max_{0 \le w \le v_1} R(w, x), \max_{v_1 < w \le v_2} R(w, x)\}. \end{aligned} \tag{6.12}$$

The first of the inner maxima is just $R^+(v_1, x)$. Because $R(v, x)/v$ is strictly decreasing when $m(x) > 0$, we can say that when $v_1 < w \le v_2$ and $m(x) > 0$,

$$R(w, x) < (R(v_1, x)/v_1)w \le R^+(v_1, x)(v_2/v_1).$$

Since $v_2 > v_1$, (6.12) shows that $R^+(v_2, x) < R^+(v_1, x)v_2/v_1$. That is, the function $R^+(v, x)/v$ is also strictly decreasing in $v$ when $m(x) > 0$, and zero otherwise. We recall that, by construction, $\alpha$ is a lower bound for any other positive $L$-periodic solution $u(x)$ of the equilibrium equation $u = Q^+[u]$. We apply Statement i, which we have proved above, to see that there is no other solution, so that $\alpha$ is the only positive $L$-periodic solution in the set $0 \le u \le \hat{\alpha}$.

It follows from the symmetry that if $\alpha(x)$ is a solution, the same is true of $\alpha(-x)$. Since there is only one solution, $\alpha(-x) \equiv \alpha(x)$, so that $\alpha$ is even. This completes the proof of Statement ii of Theorem 3.1.

To prove the third statement, we observe that if $v_1 < v_2$, then

$$\begin{aligned} R^-(v_1, x) &= \min_{v_1 \le w \le \alpha(x)} R(w, x) \\ &= \min\{\min_{v_1 \le w < v_2} R(w, x), \min_{v_2 \le w \le \alpha(x)} R(w, x)\}. \end{aligned} \tag{6.13}$$

The second inner minimum is $R^-(v_2, x)$. We observe that when $v_1 \le w < v_2$ and $m(x) > 0$, $R(w, x) > R(v_2, x)w/v_2 \ge R^-(v_2, x)w/v_2 \ge R^-(v_2, x)v_1/v_2$. Thus (6.13) shows that $R^-(v_1, x) > R^-(v_2, x)v_1/v_2$. That is, $R^-(v, x)/v$ is also strictly decreasing in $v$ when $m(x) > 0$, and zero otherwise. Since the positive $L$-periodic equilibrium solution $\sigma$ of the equilibrium equation $u = Q^-[u]$ is constructed so that there all other solutions must lie above it, Statement i shows that there are no other positive $L$-periodic solutions. As in the proof of Statement ii, this establishes Statement iii, and finishes the proof of Theorem 3.1.

**Proof of Theorem 3.2.** Because $\phi' > -1$, the function $\xi = x + \phi(x)$ has a positive derivative, and hence has an inverse function with a positive derivative. Because $\phi$ is 1-periodic, $\xi$ increases by 1 when $x$ is increased by 1. Therefore, the inverse function has the same property, which means that the inverse function has the form $x = \xi + \psi(\xi)$ with $\psi$ 1-periodic. Because the derivative of this function is positive, we have the condition

$\psi' > -1$. The oddness of $\phi$ implies that $\psi$ is also odd. By the chain rule, $[1+\psi'(\xi)][1+\phi'(\xi+\psi(\xi))] = 1$.

The changes of variables

$$x = L[\xi + \psi(\xi)], y = L[\eta + \psi(\eta)],\ U_n(\xi) = [1+\psi'(\xi)]u_n(L[\xi+\psi(\xi)]) \quad (6.14)$$

take the recursion (1.1) with $k(x, y)$ defined by (3.3) into the equivalent form

$$U_{n+1}(\xi) = \int_{-\infty}^{\infty} (\beta L/2) e^{-\beta L|\xi-\eta|} \tilde{R}(U_n(\eta), \eta) d\eta, \quad (6.15)$$

where we have defined

$$\tilde{R}(V, \eta) := (1+\psi'(\eta)) R(V/[1+\psi'(\eta)], L[\eta+\psi(\eta)]), \quad (6.16)$$

which is 1-periodic in $\eta$ for fixed $V$. The dispersal kernel of this recursion is spatially homogeneous.

The equilibrium equation $U = Q[U]$ corresponding to this recursion is

$$\begin{aligned} U(\xi) = (\beta L/2) \Big\{ & e^{-\beta L \xi} \int_{-\infty}^{\xi} e^{\beta L \eta} \tilde{R}(U(\eta), \eta) d\eta \\ & + e^{\beta L \xi} \int_{\xi}^{\infty} e^{-\beta L \eta} \tilde{R}(U(\eta), \eta) d\eta \Big\}. \end{aligned} \quad (6.17)$$

An exercise in differentiation shows that

$$-U''(\xi) + (\beta L)^2 U = (\beta L)^2 \tilde{R}(U(\xi), \xi). \quad (6.18)$$

An equilibrium is a 1-periodic solution of this equation.

Suppose there is another positive 1-periodic solution $V(\xi)$ of the equilibrium equation (6.17). This function also satisfies the differential equation (6.18). We perform the standard trick of multiplying both sides of (6.18) by $V$ and subtracting $U$ times the corresponding equation for $V$. This gives an equation which can be written in the form

$$-[VU' - UV']' = (\beta L)^2 UV[\tilde{R}(U, \xi)/U - \tilde{R}(V, \xi)/V].$$

The hypothesis that for each $x$ $R(v, x)/v$ is either strictly decreasing or identically zero in $v$ shows that $\tilde{R}(V, \xi)$ has the same property. If $U$ and $V$ are distinct, Theorem 3.1 shows that there must be an interval $(a, b)$ such that $U(a) = V(a)$, $U(b) = V(b)$, and $U(\xi) > V(\xi)$ in the interval $(a, b)$. Then $VU' - UV' = V^2(U/V)'$ must be nonnegative at $a$ and nonpositive at $b$, while $VU' - UV'$ is nondecreasing. This can only happen if $UV' - VU' = 0$ so that $U/V$ is the constant 1 throughout the interval. This contradiction shows that there cannot be two distinct positive periodic equilibrium solutions $U$. Since the transformation from $u_n$ to $U_n$ in (6.14) is one-to-one, this proves that there cannot be more than one equilibrium solution.

It remains to show that there is at least one solution of the equilibrium equation. We observe that if $u(x)$ is any $L$-periodic function such that $\sigma(x) \le u(x) \le \alpha(x)$, then $Q[u] \ge Q^-[u] \ge Q^-[\sigma] = \sigma$, and $Q[u] \le Q^+[u] \le Q^+[\alpha] = \alpha$. That is, the operator $Q$ takes the set $\{u : \sigma \le u \le \alpha,\ u(x+L) = u(x)\}$ into itself. Because of Hypothesis 2.1.iv, the range is equicontinuous. Therefore, the Schauder fixed point theorem (see, e. g. , [CH62], pp. 403-406) shows that the equilibrium equation has at least one solution. The above argument showed that there is at most one such solution. Hence, there is exactly one, and we call it $u^*(x)$. Since the evenness conditions of Hypothesis 2.1.vii show that $u^*(-x)$ is also an equilibrium, $u^*$ must be even.

This proves Theorem 3.2.

**Proof of Theorem 3.3.** As in the preceding proof, we make the changes of variable (6.14) to reduce the problem to the recursion (6.15) with 1-periodic boundary conditions. Because $R(v,x)$ now has the form $\hat{R}(v, x/L)$, we see that

$$\tilde{R}(V,\eta) = \hat{R}(V/[1+\psi'(\eta)], \eta + \psi(\eta)).$$

Linearizing this function about $V = 0$ reduces the eigenvalue problem (2.3) to the form

$$\lambda\{-(\beta L)^{-2}\zeta'' + \zeta\} = \hat{m}(\xi + \psi(\xi))\zeta \tag{6.19}$$

with the boundary conditions that $\zeta$ be 1-periodic. This is a self-adjoint problem, so that we can characterize its largest eigenvalue $\tilde{\lambda}(0)$ by the variational formula

$$\tilde{\lambda}(0) = \max_{\zeta(-1/2)=\zeta(1/2)} \frac{\int_{-1/2}^{1/2} \hat{m}(\xi + \psi(\xi))\zeta(\xi)^2 d\xi}{\int_{-1/2}^{1/2}\{(\beta L)^{-2}\zeta'^2 + \zeta^2\} d\xi}. \tag{6.20}$$

Since the quotient on the right is increasing in $L$, the same is true of its maximum, which proves the first statement of Theorem 3.3.

To obtain the other two statements, we find the limit of $\tilde{\lambda}(0)$ as $L$ goes to 0. The equation (6.19) and the one-periodicity of $\zeta$ show that $\zeta'$ is small of order $L^2$, so that $\zeta$ is a positive constant plus a term of order $L^2$. Then (6.20) shows that the limit of $\tilde{\lambda}(0)$ as $L$ goes to zero is $\int_{-1/2}^{1/2} \hat{m}(\xi+\psi(\xi))d\xi$. If this integral is at least 1, then $\tilde{\lambda}(0) > 1$, so that Hypothesis 2.1.vi is satisfied for all positive $L$. If the integral is strictly less that 1, then this hypothesis is not satisfied when $L$ is sufficiently small. On the other hand, we see from the formula (6.20) that $\tilde{\lambda}(0)$ approaches $\max[\hat{m}(x)]$ as $L$ approaches infinity.

Because the change of variables $X = \xi + \psi(\xi)$ shows that

$$\int_{-1/2}^{1/2} \hat{m}(\xi + \psi(\xi)) d\xi = \int_{-1/2}^{1/2} \hat{m}(X)[1 + \phi'(X)] dX,$$

this completes the proof of Theorem 3.3.

**Proof of Lemma 3.1.** As in the proof of Theorem 3.2, we make the changes of variable (6.14) to reduce the recursion (1.1) to the differential equation obtained from that in (6.18) by replacing $U$ by $U_{n+1}$ on the left and by $U_n$ on the right. We then linearize this problem around the positive equilibrium $U^*$. The stability of $U^*$ is determined by the differential equation eigenvalue problem

$$\gamma\{-\eta'' + (L\beta)^2 \eta\} = (L\beta)^2 \tilde{R}_U(U^*(x), x)\eta \tag{6.21}$$

with 1-periodic boundary conditions. The problem is easily seen to be self-adjoint, so that its eigenvalues are real. Because $\tilde{R}_U$ may change sign, one applies the ideas of Hess and Kato (see [HK80]) to obtain, in general, a set of positive and a set of negative eigenvalues. The largest positive eigenvalue $\gamma_+$, is given by the variational principle

$$\gamma_+ = \max_{\zeta(-1/2)=\zeta(1/2)} \frac{(L\beta)^2 \int_{-1/2}^{1/2} \tilde{R}_U(U^*(x), x)\zeta(x)^2 dx}{\int_{-1/2}^{1/2} \{\zeta'^2 + (L\beta)^2 \zeta^2\} dx}, \tag{6.22}$$

and the corresponding eigenfunction $\zeta_+$ is positive.

The maximizer $\zeta_+$ of this ratio satisfies the Euler equation

$$\gamma_+[-\zeta_+'' + (\beta L)^2 \zeta_+] = (\beta L)^2 \tilde{R}_U(U^*, x)\zeta_+.$$

We multiply both sides of this equation by $U^*$, integrate over the interval $[-1/2, 1/2]$, and use integration by parts and the fact that $U^*$ satisfies the equilibrium equation (6.18) to obtain the equation

$$\int_{-1/2}^{1/2} [\gamma_+ \tilde{R}(U^*(x), x) - U^* \tilde{R}_U(U^*, x)]\zeta_+ dx = 0.$$

The inequality $[\tilde{R}(U, x)/U]_U < 0$ shows that $U^* \tilde{R}_U(U^*, x) < \tilde{R}(U^*, x)$ wherever $\tilde{R}(U^*, x) > 0$. This leads to the conclusion that

$$(\gamma_+ - 1) \int_{-1/2}^{1/2} \tilde{R}(U^*, x)\zeta_+(x) dx < 0.$$

Since $\zeta_+$ is positive, $\gamma_+ - 1$ must be negative, which is the statement of Lemma 3.1.

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