A bifurcation analysis of stage-structured density dependent integrodifference equations

Suzanne L. Robertson [a],[*],[1], J.M. Cushing [a],[b]

[a] *Interdisciplinary Program in Applied Mathematics, University of Arizona, Tucson, AZ 85721, USA*
[b] *Department of Mathematics, University of Arizona, Tucson, AZ 85721, USA*

ARTICLE INFO

ABSTRACT

There is evidence for density dependent dispersal in many stage-structured species, including flour beetles of the genus *Tribolium*. We develop a bifurcation theory approach to the existence and stability of (non-extinction) equilibria for a general class of structured integrodifference equation models on finite spatial domains with density dependent kernels, allowing for non-dispersing stages as well as partial dispersal. We show that a continuum of such equilibria bifurcates from the extinction equilibrium when it loses stability as the net reproductive number n increases through 1. Furthermore, the stability of the non-extinction equilibria is determined by the direction of the bifurcation. We provide an example to illustrate the theory.

© 2011 Elsevier Inc. All rights reserved.

1. Introduction

Spatial dispersal can be an important factor affecting the dynamics of populations. There are many reasons an organism may move between different spatial locations, including quality of the environment, competition for resources, and crowding. In populations structured according to factors such as age classes or life-cycle stages, not all classes necessarily disperse in the same way. Food or habitat preference may vary according to age or life-cycle stage. Integrodifference equations were first introduced in population ecology by Kot and Schaffer [15] to model the dynamics of dispersing populations with distinct reproduction and dispersal stages. Alzoubi [1–4] built upon the analysis done by Van Kirk and Lewis [23], Hardin, Takac and Webb [12] and Kot and Schaffer [15] by incorporating structured population dynamics into integrodifference equation models. He examined the existence and stability of equilibria of stage-structured models by extending the modeling methodology of Cushing [6] in a non-spatial setting to include a spatial component.

Dispersal may also be driven by density dependent interactions between age classes or life-cycle stages. For example, vulnerable life-cycle stages of cannibalistic species move to avoid predatory stages [13,17,22]. Here we extend and generalize Alzoubi's results by incorporating density dependent dispersal into stage-structured integrodifference equation models. We assume density (of one or more life stages) may affect the dispersal of a given life stage in two different ways. First, it may influence whether or not an organism disperses. Second, given that an organism does disperse, density may also affect how far it moves. The latter effect results in a density dependent kernel while the former results in an added non-integral term to the model. This method of incorporating density dependence into integrodifference equations was used by Dwyer and Morris [10] in studying the effect of resource density on consumer dispersal.

* Corresponding author.
E-mail addresses: srobertson@mbi.osu.edu (S.L. Robertson), cushing@math.arizona.edu (J.M. Cushing).
[1] Current address: Mathematical Biosciences Institute, The Ohio State University, Columbus, OH 43210, USA.

In this paper we examine the existence and stability of the extinction equilibrium and of non-extinction equilibria for stage-structured density dependent integrodifference equation models, using bifurcation theory based on the inherent net reproductive number n ([6,7], also referred to in the literature as R_0). We relate the stability of non-extinction equilibria near the extinction state to the direction of bifurcation at the critical value $n = 1$. Finally, we illustrate the theory with an example.

2. Background

In the following sections, we develop a general stage-structured integrodifference equation model incorporating density dependent dispersal. We aim to write the equilibrium equations for this model in an abstract operator form and to apply the general bifurcation theorems of Rabinowitz [19] and Dancer [9] to show the existence of a branch of non-extinction equilibria bifurcating from the extinction state. Here we present the main bifurcation results of Rabinowitz and Dancer that we will use in Section 3.

The equilibrium equations of the models we develop will take the general form

$$\vec{x} = A(\lambda, \vec{x}) \tag{1}$$

where $\lambda \in \mathbb{R}$, E is a real Banach space with norm $\| \cdot \|$ and $A : \mathbb{R} \times E \to E$ is compact and continuous. Our goal is to write the operator A in the following form studied by Rabinowitz [19] and Dancer [9]:

$$A(\lambda, \vec{x}) = \lambda L \vec{x} + H(\lambda, \vec{x}) \tag{2}$$

where $H(\lambda, \vec{x})$ is $o(\|\vec{x}\|)$ for $\vec{x}$ near 0 uniformly on bounded λ intervals and L is a compact linear operator on E. We note that $A(\lambda, 0) = 0$ for all $\lambda \in \mathbb{R}$. All potential bifurcation points from the trivial branch of solutions of $\vec{x} = A(\lambda, \vec{x})$ (i.e. solutions of the form $(\lambda, 0)$, $\lambda \in \mathbb{R}$) must be from the set $\{(\mu, 0): \mu \in r(L)\}$, where $r(L)$ denotes the set of characteristic values of L. If μ is a characteristic value of odd (geometric) multiplicity, then $(\mu, 0)$ is a bifurcation point [16].

Theorem 1. *(See Rabinowitz [19].) Let S be the closure of the set of nontrivial solution pairs $(\lambda, \vec{x})$ of Eq. (1). If μ is a characteristic value of odd (geometric) multiplicity, then S has a (maximal) subcontinuum C_λ such that $(\mu, 0) \in C_\lambda$ and C_λ either*

1. *meets infinity in $\mathbb{R} \times E$, or*
2. *meets $(\overline{\mu}, 0)$, where $\mu \neq \overline{\mu} \in r(L)$.*

Furthermore, if a characteristic value of the linear operator L is simple (of multiplicity one) and $A(\lambda, \vec{x})$ is Fréchet differentiable near $(\mu, 0)$, C_λ can be written as $(\lambda(\epsilon), x(\epsilon)) = (\mu + O(1), \epsilon \nu + O(|\epsilon|))$ for $\epsilon \approx 0$, where $\nu \in E$ is an eigenvector corresponding to μ [19]. The continuum C_λ can be broken up into two subcontinua, C_λ^- and C_λ^+ (parametrized by $\epsilon < 0$ and $\epsilon > 0$, respectively).

Theorem 2. *(See Dancer [9].) If $\mu \in r(L)$ is a simple characteristic value, then each of the subcontinua C_λ^- and C_λ^+ meet $(\mu, 0)$ and either*

1. *meet infinity in $\mathbb{R} \times E$, or*
2. *$C_\lambda^+ \cap C_\lambda^- \neq \{(\mu, 0)\}$.*

3. Model development and existence of equilibria

Let $\Omega \subseteq \mathbb{R}^n$ be the closure of an open, bounded subset of $\mathbb{R}^n$ representing the spatial habitat of a species that can be divided into distinct categories or classes, such as age groups, size categories or life-cycle stages. We assume that population dynamics (reproduction and class transitions) occur first, followed by dispersal. Dispersing individuals cannot leave Ω. Let $x_i(t, s)$, $i = 1, 2, \ldots, m$ represent the density of individuals at the location $s \in \Omega$ who are in the ith class at time t (unit of time equal to dispersal period) and let $\vec{x}(t, s) = (x_1(t, s), \ldots, x_m(t, s))^T$. Let $\tau_{ij}(\vec{x}(t, \cdot), v)$ be the expected fraction of individuals in class j at spatial position v who survive and move into class i in one unit of time. This notation indicates (as it similarly does in subsequent occurrences) that τ_{ij} is a functional acting on $\vec{x}(t, s)$ as a function of s. Surviving individuals might also disperse, and we let $k_{ij}(s, v, \vec{x}(t, \cdot))$ denote the dispersal kernel, or the fraction of individuals at position v at time t that settle at position s by the end of the dispersal period. As indicated, these quantities may depend on the density of any or all classes at any or all spatial locations.

Let $f_{ij}(\vec{x}(t, \cdot), v)$ be the expected number of surviving i-class offspring at position v per j-class individual per unit of time. Let the dispersal kernel $l_{ij}(s, v, \vec{x}(t, \cdot))$ denote the fraction of i-class offspring of a j-class individual at position v settling at position s after one time unit. The total number of i-class individuals at position s at time $t + 1$ is

$$x_i(t+1, s) = \int_\Omega \sum_{j=1}^m \big[k_{ij}\big(s, v, \vec{x}(t, \cdot)\big) \tau_{ij}\big(\vec{x}(t, v), v\big) + l_{ij}\big(s, v, \vec{x}(t, \cdot)\big) f_{ij}\big(\vec{x}(t, v), v\big) \big] x_j(t, v) \, dv.$$

To be more general, we can also consider the case where only a fraction of the population disperses at any given time. This fraction may be spatially or density dependent, and we denote it by $\gamma_{ij}(\vec{x}(t,\cdot), v)$. The number of i-class individuals at spatial location s at time $t+1$ is now

$$x_i(t+1, s) = \int_\Omega \sum_{j=1}^m \left[k_{ij}\big(s, v, \vec{x}(t,\cdot)\big)\tau_{ij}\big(\vec{x}(t,v), v\big) + l_{ij}\big(s, v, \vec{x}(t,\cdot)\big)f_{ij}\big(\vec{x}(t,v), v\big)\right]\gamma_{ij}\big(\vec{x}(t,\cdot), v\big)x_j(t,v)\,dv$$
$$+ \sum_{j=1}^m \big(1 - \gamma_{ij}\big(\vec{x}(t,\cdot), s\big)\big)\left[\tau_{ij}\big(\vec{x}(t,s), s\big)x_j(t,s) + f_{ij}\big(\vec{x}(t,s), s\big)x_j(t,s)\right].$$

Using the $m \times m$ matrices $T = (k_{ij}\tau_{ij}\gamma_{ij})$, $F = (l_{ij}f_{ij}\gamma_{ij})$, $T^* = (\tau_{ij}(1 - \gamma_{ij}))$ and $F^* = (f_{ij}(1 - \gamma_{ij}))$, we can write the above equation in matrix form:

$$\vec{x}(t+1, s) = \int_\Omega \left[T\big(s, v, \vec{x}(t,\cdot)\big) + F\big(s, v, \vec{x}(t,\cdot)\big)\right]\vec{x}(t, v)\,dv + \left[T^*\big(s, \vec{x}(t,\cdot)\big) + F^*\big(s, \vec{x}(t,\cdot)\big)\right]\vec{x}(t, s). \tag{3}$$

The equilibrium equation is then

$$\vec{x}(s) = \int_\Omega \left[T\big(s, v, \vec{x}(\cdot)\big) + F\big(s, v, \vec{x}(\cdot)\big)\right]\vec{x}(v)\,dv + \left[T^*\big(s, \vec{x}(\cdot)\big) + F^*\big(s, \vec{x}(\cdot)\big)\right]\vec{x}(s). \tag{4}$$

We will assume the domain of the operator defined by the right-hand side of (4) is a Banach space E of integrable functions defined on Ω (such as $C(\Omega)$ or $C^1(\Omega)$).

Note 1. Only nonnegative valued solutions of the equilibrium equation (4) are biologically relevant. Let K_+ denote an open cone in E consisting of nonnegative valued functions. In cases where the operator defined by the right-hand side of (4) is defined on an open set $G \subseteq E$ containing $\overline{K}_+$, the closure of the cone K_+, any re-definition of singularities outside the positive cone are irrelevant to a biological application. We therefore assume that one may redefine any nonlinearities outside the cone in such a way as to make the operator globally defined on E.

Note 2. In certain applications it is appropriate to impose boundary conditions on our problem. Rather than working in a restrictive subspace of E, we will carefully choose our kernel in these applications so as to hold the boundary conditions invariant.

We will denote the integral operators of Eq. (4) with kernels $T(s, v, \vec{x}(\cdot))$ and $F(s, v, \vec{x}(\cdot))$ by T and F respectively and the last two operators on the right side of Eq. (4) by T^* and F^*, respectively.

Assumption 1. Let E be an ordered Banach space of integrable functions defined on Ω. The operators $T, F, T^*, F^* : E \to E$ are continuous and Fréchet differentiable.

In order to write the equilibrium equation

$$\vec{x} = \big(T + T^*\big)\vec{x} + \big(F + F^*\big)\vec{x}$$

in Rabinowitz form [19], we expand T, F, T^* and F^* around $\vec{x} = \vec{0}$ and rewrite the equilibrium equation as follows

$$\vec{x}(s) - T^*(\vec{0})\vec{x}(s) - \int_\Omega T(s, v, \vec{0})\vec{x}(v)\,dv = \int_\Omega F(s, v, \vec{0})\vec{x}(v)\,dv + F^*(\vec{0})\vec{x}(s) + h\big(\vec{x}(s)\big) \tag{5}$$

where $h(\vec{x}) \equiv o(\|\vec{x}\|)$ for $\vec{x} \approx \vec{0}$. We define $\overline{F}(\vec{y}) = \int_\Omega F(s, v, \vec{0})\vec{y}(v)\,dv$ and $\overline{T}(\vec{y}) = \int_\Omega T(s, v, \vec{0})\vec{y}(v)\,dv$ and make the following assumptions:

Assumption 2. The operator $(I - T^*(\vec{0}) - \overline{T})^{-1}$ exists and is continuous on E.

Assumption 3. Let K_+ be an *open* cone of nonnegative valued functions from E. The operator $(I - T^*(\vec{0}) - \overline{T})^{-1}(\overline{F} + F^*(0))$ has a simple, positive, strictly dominant eigenvalue n with an associated eigenvector $\vec{v} \in K_+$. Furthermore, no other eigenvalue has an eigenvector in the closure $\overline{K}_+$ of K_+.

Note 3. Following [1,6,7] we call n the inherent net reproductive number. It is also commonly denoted by R_0.

Note 4. The Krein–Rutman Theorem (see Appendix A) can be invoked to verify Assumption 3 under certain conditions, namely when we have a *strongly positive* operator. This is done in Alzoubi [3,4]. An operator A is strongly positive if its kernel is of *positive type*, or if there exists an integer n such that A^n maps any vector in the cone into the interior of the cone [16]. It is not true in general, however, that the linear operator L in our applications is strongly positive. In fact, L cannot be strongly positive if we work on a space such as $L_2(\Omega)$ where the cone of positive valued functions on Ω has an empty interior. Nonetheless, Assumption 3 is still often true in applications and can be shown directly in certain cases, eliminating the need to use sufficiency theorems such as the Krein–Rutman Theorem. An example is given in Section 5.

Note 5. Assumptions 2 and 3 are generalizations of those used in [6,7] for non-spatial models.

Following [6], we choose n as our bifurcation parameter. To do this we use n to normalize the f_{ij}. Let $f_{ij} = n\phi_{ij}$, so $\overline{F} = n\overline{\Phi}$ and $F^* = n\Phi^*$. With this normalization $(I - T^*(\vec{0}) - \overline{T})^{-1}(\overline{\Phi} + \Phi^*(\vec{0}))$ has a dominant eigenvalue equal to one.

The equilibrium equation (5) can be written as

$$\vec{x}(s) - T^*(\vec{0})\vec{x}(s) - \int_{\Omega} T(s, v, \vec{0})\vec{x}(v)\,dv = n\int_{\Omega} \Phi(s, v, \vec{0})\vec{x}(v)\,dv + n\Phi^*(\vec{0})\vec{x}(s) + h(n, \vec{x}(s)) \tag{6}$$

where $h(n, \vec{x}) \equiv o(\|\vec{x}\|)$ for $\vec{x} \approx \vec{0}$ uniformly on bounded n intervals, or by Assumption 2 as

$$\vec{x} = nL\vec{x} + H(n, \vec{x}) \tag{7}$$

where

$$L\vec{x} = (I - T^*(\vec{0}) - \overline{T})^{-1}\int_{\Omega} \overline{\Phi}(\vec{0})\vec{x}(u)\,du + (I - T^*(\vec{0}) - \overline{T})^{-1}\Phi^*(\vec{0})\vec{x}$$

and

$$H(n, \vec{x}) = (I - T^*(\vec{0}) - \overline{T})^{-1}h(n, \vec{x}).$$

Eq. (7) has the form (1)–(2) of the nonlinear eigenvalue problem studied by Rabinowitz [19] and Dancer [9]. In order to apply Theorems 1 and 2, we need the operator on the right-hand side of Eq. (7) to be compact and continuous on E. Sufficient for this is the following assumption:

Assumption 4. The operators T, F, T^* and F^* are compact on E.

Note 6. Several theorems from Krasnosel'skii [16] can be used to verify operators are completely continuous (satisfying Assumptions 1 and 4) when working in certain Banach spaces such as $C(\Omega)$ (Theorem 3.1) or $L_P(\Omega)$ (Theorem 3.2). For example, if all the terms t_{ij}, f_{ij}, etc. are continuous functions of their arguments, then Assumptions 1 and 4 hold on the Banach space $E = C(\Omega)$.

By Assumption 1, $(I - T^*(\vec{0}) - \overline{T})^{-1}$ is continuous, and it follows that L and H are completely continuous (i.e. continuous and compact). Moreover, $H(n, \vec{x})$ is $o(\|\vec{x}\|)$ near 0 uniformly on bounded n intervals. In summary, under Assumptions 1–4, Eq. (7) satisfies the conditions needed to apply the bifurcation theory of Rabinowitz and Dancer. The following theorem is a generalization to (7) of Theorem 3.3 of Alzoubi [2].

Theorem 3. *Consider equilibrium equation* (7) *under Assumptions* 1–4. *There exists a continuum* C_n^+ *of solution pairs* $(n, \vec{x})$ *such that* $(1, \vec{0}) \in C_n^+$ *and one of the following alternatives holds*:

1. C_n^+ *lies in* $R \times K_+$ *and is unbounded.*
2. C_n^+ *contains a non-extinction solution pair* $(n^*, \vec{x}^*) \in \mathbb{R} \times \partial K_+, \vec{x}^* \neq \vec{0}$.

Proof. We have already shown that Eq. (7) satisfies the conditions necessary for the application of Theorem 2 with subcontinua C_n^+ and C_n^-. Because $\vec{v}$ lies in the open cone K_+, near the bifurcation point $(1, \vec{0})$ the points $(n, \vec{x}) = (1 + O(\epsilon), \epsilon\vec{v} + O(\epsilon^2))$ from C_n^+ and C_n^-, corresponding to $\epsilon > 0$ and $\epsilon < 0$ respectively, lie in $\mathbb{R} \times K_+$ and $\mathbb{R} \times K_-$ where $K_- \triangleq \{\vec{x}: -\vec{x} \in K_+\}$. Note that K_+ and K_- are open and disjoint.

Alternative 1 of Theorem 2 implies C_n^+ is unbounded in $\mathbb{R} \times E$. Either C_n^+ remains (and is unbounded) in $\mathbb{R} \times K_+$ or it meets $\mathbb{R} \times \partial K_+$ at a point $(n^*, \vec{x}^*)$. The point $\vec{x}^* \in \partial K_+$ is not the origin by Assumption 3. This proves the asserted alternatives in the case of Alternative 1 in Theorem 2.

Alternative 2 of Theorem 2 implies the intersection $C_n^+ \cap C_n^-$ contains a point other than the bifurcation point $(1, \vec{0})$. Since both K_+ and K_- are open, this common point cannot lie in $\mathbb{R} \times K_+$ (or $\mathbb{R} \times K_-$) and, as a result, C_n^+ must leave

$\mathbb{R} \times K_+$ at a point $(n^*, \vec{x}^*)$ on the boundary $\mathbb{R} \times \partial K_+$ other than the bifurcation point $(1, \vec{0})$. Moreover, $\vec{x}^*$ cannot be the origin by Assumption 3. This proves the second alternative of the theorem holds. □

In applications, one can often rule out alternative 2 of Theorem 3. For example if we are working in a space with a solid positive cone and can show L is a strongly positive operator (maps vectors on the closure of the cone to the interior of the cone), then there cannot be an equilibrium $\vec{x} \neq \vec{0}$ on the boundary of the positive cone, ∂K_+.

Theorem 3 generalizes Theorem 3.3 of Alzoubi [2] to more general stage-structured integrodifference equations, that include for example density dependent dispersal, formulated on more general Banach spaces and cones (which permits more flexibility in applications).

4. Equilibrium stability

4.1. Extinction equilibrium

In Section 3 we introduced the integrodifference equation (3) and studied its equilibrium equation

$$\vec{x}(s) = A\big(n, \vec{x}(s)\big) \tag{8}$$

where

$$A\big(n, \vec{x}(s)\big) = \int_{\Omega} \big[T\big(s, v, \vec{x}(\cdot)\big) + n\Phi\big(s, v, \vec{x}(\cdot)\big)\big]\vec{x}(v)\,dv + \big[T^*\big(s, \vec{x}(s)\big) + n\Phi^*\big(s, \vec{x}(s)\big)\big]\vec{x}(s).$$

In this section we investigate the stability of the extinction equilibrium $\vec{x} = \vec{0}$, a solution of (8) for all n.

The Fréchet derivative of A with respect to x at $\vec{x} = \vec{0}$ has the following matrix form:

$$A'\big(n, \vec{0}\big)\big(\vec{h}\big)(s) = \int_{\Omega} \big(T(s, v, \vec{0}) + n\Phi(s, v, \vec{0})\big)\vec{h}(v)\,dv + \big[T^*(\vec{0}) + n\Phi^*(\vec{0})\big]\vec{h}(s).$$

Assumption 5. The linear operator $A'(n, \vec{0})$ has a simple, positive, strictly dominant eigenvalue λ_0 associated with a unique eigenvector $\varphi_0 \in K_+$.

Note 7. In certain applications, the Krein–Rutman Theorem can be used to prove the existence of λ_0.

The extinction equilibrium is locally asymptotically stable if the dominant eigenvalue of $A'(\vec{0}, n)$, $\lambda_0 < 1$, and unstable if $\lambda_0 > 1$ (this is the familiar linearization principle; see [11]). We proved in Section 3 that a continuous branch of non-extinction equilibria bifurcates from the extinction equilibrium at $n = 1$. Theorem 7 (see Appendix A) relates the inherent net reproductive number n to the dominant eigenvalue λ_0 of $A'(n, \vec{0})$, asserting $n > 1$ ($n < 1$) if and only if $\lambda_0 > 1$ ($\lambda_0 < 1$). So $n = 1$ if and only if $\lambda_0 = 1$. From this relationship between n and λ_0, we obtain the following theorem:

Theorem 4. *Under Assumptions* 1–5, *the extinction state is stable for* $n < 1$ *and unstable for* $n > 1$.

4.2. Stability and direction of bifurcation

In this section we examine the stability of the branch of non-extinction equilibria whose existence was proved in Theorem 3. Finding a formula for these non-extinction equilibria is in general impossible. However, it is usually possible to relate stability to the direction of bifurcation, at least near the bifurcation point. That relationship follows from the exchange of stability principle for transcritical bifurcations [5,14].

Formula (9) below provides the relationship between the stability of equilibria and direction of bifurcation near the bifurcation point $(n, \vec{x}) = (1, \vec{0})$, where the branch of nontrivial equilibria is parameterized by $(n(\epsilon), x(\epsilon))$, for $|\epsilon|$ small. Let $\hat{\lambda}(\epsilon)$ denote the dominant eigenvalue of the linearization at the nontrivial equilibrium. Then the eigenvalue perturbation along the branch of equilibria is given by $\hat{\lambda}(\epsilon)$, and

$$\lambda'(n_0)\dot{n}(0) = -\dot{\hat{\lambda}}(0) \tag{9}$$

where $' = \frac{d}{dn}$ and $\dot{} = \frac{d}{d\epsilon}$ (see [14, p. 27]). In Eq. (9), $\dot{n}(0)$ determines the direction of bifurcation. If $\dot{n}(0) > 0$, then the bifurcation parameter n increases as ϵ increases and we say the bifurcation is to the right (also called supercritical or forward bifurcation). If $\dot{n}(0) < 0$, n decreases as ϵ increases and the bifurcation is to the left (also called subcritical or backward bifurcation). The sign of $\lambda'(n_0)$ tells us whether the dominant eigenvalue λ_0 increases or decreases through 1 as n increases through the bifurcation point $n = 1$. The signs of these two quantities determine the sign of $\dot{\hat{\lambda}}(0)$ in (9).

The linearization of the system at the positive equilibrium $(n(\epsilon), x(\epsilon))$ gives the positive operator $A'(n(\epsilon), x(\epsilon))(h(v))$ where $A'(n(\epsilon), x(\epsilon))$ is the Fréchet derivative of the nonlinear operator A. $\hat{\lambda}(\epsilon)$ is the dominant eigenvalue of $A'(n(\epsilon), x(\epsilon))$ along the bifurcating branch of non-extinction equilibria. The sign of $\dot{\hat{\lambda}}(0)$ tells us if the branch of equilibria gains or loses stability as ϵ increases through 0. Since the extinction state loses stability as n increases through 1, we get the following result from Eq. (9) and the exchange of stability principle (see [14, p. 29]).

Theorem 5. *Assume Assumptions* 1–5 *hold. If the bifurcation is to the right* $(\dot{n}(0) > 0)$*, then the branch of non-extinction equilibria are stable near the bifurcation point* $(\dot{\hat{\lambda}}(0) < 0)$*. If the bifurcation is to the left* $(\dot{n}(0) < 0)$*, then the branch of non-extinction equilibria are unstable* $(\dot{\hat{\lambda}}(0) > 0)$*.*

In general, right bifurcations occur when density dependence represents negative feedback effects on vital parameters. Left bifurcations occur when positive feedback density effects (Allee effects) are of sufficient magnitude [6,7].

5. Example of bifurcation theory

In this section we look at an example integrodifference equation model with density dependent dispersal kernels and apply the theory developed in Sections 3 and 4.

We consider populations whose life cycles consist of two stages, and let $\vec{x}(s) = col(x_1(s), x_2(s))$. These stages can be considered to be juveniles and adults. We assume individuals are born into stage x_1 at a rate dependent on the density of x_2 and let $f_{21} = \frac{b}{1+x_2}$. Thus b represents the maximum birthrate of the species. Individuals transit from stage x_1 to stage x_2 at a rate s_1 $(\tau_{12} = s_1)$ and from stage x_2 to stage x_2 at a rate s_2 $(\tau_{22} = s_2)$.

In order to apply Theorem 3 to the resulting dispersal model, Assumptions 1–4 must be satisfied. We take the Banach space $E = C^1(\Omega)$ under the usual norm $sup_{\Omega}(\|x\|) + sup_{\Omega}(\|x'\|)$ where Ω is the interval $[0, \pi]$. We take the open cone K_+ to be the set of $\vec{x}(s)$ such that the components $x_i(s)$ are positive on $(0, \pi)$ and their derivatives $x_i'(s)$ are nonzero at $s = 0$ and $s = \pi$. All terms f_{ij}, t_{ij}, etc. are continuous in their arguments. As a result we need only verify Assumption 3, i.e. we need to show that the operator $(I - T^*(0) - \overline{T})^{-1}(\overline{F} + F^*(0))$ has a simple, positive, strictly dominant eigenvalue n with an associated eigenvector in K_+ and that no other eigenvalue has an associated eigenvector in $\overline{K}_+$. In order to apply Theorems 4 and 5, we must also show that Assumption 5 is satisfied, i.e. that the operator $\overline{T} + \overline{F} + T^*(0) + F^*(0)$ has a simple, positive, strictly dominant eigenvalue λ_0 with an associated eigenvector in K_+.

To illustrate the details of an application of the theory, we consider the case when the first stage, x_1, is sedentary and cannot disperse $(\gamma_{11} = \gamma_{12} = 0)$, while x_2 is mobile and the entire population disperses at all times $(\gamma_{21} = \gamma_{22} = 1)$. In the absence of stage 1 individuals, stage 2 individuals move according to the density independent kernel

$$k(s, v) = \frac{1}{2} \sin s$$

on $\Omega = [0, \pi]$. This kernel imposes hostile boundary conditions. Dispersers prefer the middle of the habitat, as they are more likely to move to the center of the domain than any other location. Note that the integral over s is equal to one, which ensures that individuals are not lost or gained during dispersal, but are simply redistributed in space.

We assume that the presence of stage 1 individuals at a given location decreases the fraction of stage 2 individuals moving to that location at the next time step. We model this density dependent dispersal assumption by setting

$$k_{21} = k_{22} = \exp(-D_2 x_1(s)) \frac{\sin s}{2C_1},$$

where C_1 is a normalization constant to ensure the integral over s remains 1.

Under these assumptions the operators T and F^* are

$$T(s, v, \vec{x}(\cdot)) = \begin{pmatrix} 0 & 0 \\ s_1 \frac{\sin s}{2C_1} \exp(-D_2 x_1(s)) & s_2 \frac{\sin s}{2C_1} \exp(-D_2 x_1(s)) \end{pmatrix},$$

$$F^*(s, v, \vec{x}(\cdot)) = \begin{pmatrix} 0 & \frac{b}{1+x_2(s)} \\ 0 & 0 \end{pmatrix}.$$

Then

$$T(s, v, \vec{0}) = \begin{pmatrix} 0 & 0 \\ s_1 \frac{\sin s}{2} & s_2 \frac{\sin s}{2} \end{pmatrix}$$

and

$$F^*(s, v, \vec{0}) = \begin{pmatrix} 0 & b \\ 0 & 0 \end{pmatrix}.$$

We want to find the dominant eigenvalue n of $(I - \overline{T})^{-1} F^*(\vec{0})$. We start by calculating the resolvent of $\overline{T}$.

$$(I - \overline{T}) : \begin{pmatrix} x_1(s) \\ x_2(s) \end{pmatrix} \to \begin{pmatrix} x_1(s) \\ x_2(s) \end{pmatrix} - \int_0^\pi \begin{pmatrix} 0 & 0 \\ \frac{s_1 \sin s}{2} & \frac{s_2 \sin s}{2} \end{pmatrix} \begin{pmatrix} x_1(v) \\ x_2(v) \end{pmatrix} dv.$$

We solve the following for $x_1(s)$ and $x_2(s)$:

$$\begin{pmatrix} x_1(s) \\ x_2(s) \end{pmatrix} - \begin{pmatrix} 0 \\ \frac{s_1 \sin s}{2} \int_0^\pi x_1(v)\, dv + \frac{s_2 \sin s}{2} \int_0^\pi x_2(v)\, dv \end{pmatrix} = \begin{pmatrix} y_1(s) \\ y_2(s) \end{pmatrix}.$$

Clearly $x_1(s) = y_1(s)$ and

$$x_2(s) = y_2(s) + \frac{\sin s}{2} \frac{s_1}{1 - s_2} \int_0^\pi y_1(v)\, dv + \frac{\sin s}{2} \frac{s_2}{1 - s_2} \int_0^\pi y_2(s)\, ds.$$

It follows that

$$(I - \overline{T})^{-1} : \begin{pmatrix} y_1(s) \\ y_2(s) \end{pmatrix} \to \begin{pmatrix} y_1(s) \\ y_2(s) + \frac{\sin s}{2} \left[\frac{s_1}{1 - s_2} \int_0^\pi y_1(v)\, dv + \frac{s_2}{1 - s_2} \int_0^\pi y_2(s)\, ds \right] \end{pmatrix}$$

and since $F^*(\vec{0})\vec{x} = \begin{pmatrix} b x_2(s) \\ 0 \end{pmatrix}$ we obtain

$$(I - \overline{T})^{-1} F^*(\vec{0}) : \begin{pmatrix} x_1(s) \\ x_2(s) \end{pmatrix} \to \begin{pmatrix} b x_2(s) \\ \frac{\sin s}{2} \frac{s_1}{1 - s_2} \int_0^\pi b x_2(v)\, dv \end{pmatrix}.$$

The eigenvalue equation is

$$\begin{pmatrix} b x_2(s) \\ \frac{\sin s}{2} \frac{s_1}{1 - s_2} b \int_0^\pi x_2(v)\, dv \end{pmatrix} = n \begin{pmatrix} x_1(s) \\ x_2(s) \end{pmatrix}.$$

Solving for n from the second component equation, we see $n = \frac{b s_1}{1 - s_2} \int_0^\pi \frac{\sin s}{2}\, ds = \frac{b s_1}{1 - s_2}$. The dominant eigenvalue n is simple and positive and an eigenvector is given by

$$\begin{pmatrix} \sin s \\ \frac{s_1}{1 - s_2} \sin s \end{pmatrix}.$$

This eigenvector lies in the cone K_+ and Assumption 3 is satisfied.

Straightforward calculations show that the operator $\overline{T} + F^*(\vec{0})$ has a unique dominant eigenvalue given by

$$\lambda_0 = \frac{s_2}{2} + \frac{1}{2} \sqrt{s_2^2 + 4 b s_1},$$

with associated eigenvector

$$\begin{pmatrix} x_1(s) \\ x_2(s) \end{pmatrix} = \begin{pmatrix} \sin s \\ \left(\frac{s_2}{2b} + \frac{1}{2b} \sqrt{s_2^2 + 4 b s_1} \right) \sin s \end{pmatrix}. \tag{10}$$

This eigenvector lies in K_+ and thus Assumption 5 is satisfied.

It follows from Theorem 4 that the extinction equilibrium $\vec{x}(s) = \vec{0}$ will be stable for $\frac{b s_1}{1 - s_2} < 1$ and unstable for $\frac{b s_1}{1 - s_2} > 1$. From Theorem 3 we know a continuum of non-extinction equilibria bifurcates from the extinction equilibrium at $\frac{b s_1}{1 - s_2} = 1$. Theorem 5 asserts that the stability of this branch of equilibria is determined by the direction of bifurcation.

For this example, we can show that the bifurcation is a forward bifurcation (and therefore the non-extinction equilibria are stable) by showing that all density effects are deleterious, i.e. $0 \leqslant P(s, v, \vec{x}) \leqslant P(s, v, \vec{0})$ and $0 \leqslant P^*(s, v, \vec{x}) \leqslant P^*(s, v, \vec{0})$, $\forall s, v \in \Omega$, where $P = T + F$, $P^* = T^* + F^*$, and $\vec{x} = col(x_1, x_2)$. As we will see, this implies that there cannot be a stable positive equilibrium for $n < 1$.

For our model,

$$P(s, v, \vec{x}(t, \cdot)) = \begin{pmatrix} 0 & 0 \\ (1 - \mu_1) \frac{\sin s}{2} \exp(-D_{21} x_1(t, s)) & (1 - \mu_2) \frac{\sin s}{2} \exp(-D_{21} x_1(t, s)) \end{pmatrix},$$

$$P^*(s, v, \vec{x}(t, \cdot)) = \begin{pmatrix} 0 & \frac{b}{1 + x_2(t, s)} \\ 0 & 0 \end{pmatrix},$$

$$P(s, v, \vec{0}) = \begin{pmatrix} 0 & 0 \\ (1 - \mu_1) \frac{\sin s}{2} & (1 - \mu_2) \frac{\sin s}{2} \end{pmatrix},$$

and

$$P(s, v, \vec{0}) = \begin{pmatrix} 0 & b \\ 0 & 0 \end{pmatrix}.$$

Since $(1 + x_2(t, s))^{-1} \leqslant 1$ and $\exp(-D_{21}x_1(t, s)) \leqslant 1$, it follows that

$$0 \leqslant P(s, v, \vec{x}(t, \cdot)) \leqslant P(s, v, \vec{0})$$

and

$$0 \leqslant P^*(s, v, \vec{x}(t, \cdot)) \leqslant P^*(s, v, \vec{0}), \quad \forall s, v \in \Omega.$$

Let

$$\vec{y}(t + 1, s) = \int_\Omega \begin{pmatrix} 0 & 0 \\ (1 - \mu_1)\frac{\sin s}{2} & (1 - \mu_2)\frac{\sin s}{2} \end{pmatrix} \vec{y}(t, v)\, dv + \begin{pmatrix} 0 & b \\ 0 & 0 \end{pmatrix} \vec{y}(t, s),$$

$$\vec{y}(0, s) = \vec{x}(0, s).$$

Assume $\vec{x}(t, s) \leqslant \vec{y}(t, s)$, $\forall s \in \Omega$. Then

$$\vec{x}(t + 1, s) = \begin{pmatrix} b\frac{x_2(t,s)}{1 + x_2(t,s)} \\ \frac{\sin s}{2} e^{-D_{21}x_1(s)} \int_\Omega (1 - \mu_1)x_1(v) + (1 - \mu_2)x_2(v)\, dv \end{pmatrix}$$

$$\leqslant \begin{pmatrix} by_2(t, s) \\ \frac{\sin s}{2} \int_\Omega (1 - \mu_1)x_1(v) + (1 - \mu_2)x_2(v)\, dv \end{pmatrix} = \vec{y}(t + 1, s).$$

By induction,

$$\vec{x}(t + 1, s) \leqslant \vec{y}(t + 1, s), \quad \forall s \in \Omega, \ \forall t$$

and

$$\lim_{t \to \infty} |\vec{y}(t, s)| = 0 \Rightarrow \lim_{t \to \infty} |\vec{x}(t, s)| = 0.$$

Let λ_0 denote the dominant eigenvalue of $\overline{T} + \overline{F} + T^*(0) + F^*(0)$. By Theorem 7, if $n < 1$ then $\lambda_0 < 1$ and $|y| \to 0$ as $t \to \infty$. Thus the extinction equilibrium $\vec{x} = \vec{0}$ is a global attractor for $n < 1$ and the bifurcation cannot be to the left. (A similar result for non-spatial models is given in [6].) Since the bifurcation is to the right, Theorem 5 guarantees the stability of the non-extinction equilibria near the bifurcation point.

In this section we have utilized the theorem developed in this paper to prove the existence of a stable branch of non-extinction equilibria near $n = 1$ for a relatively simple dispersal model with two life cycle stages. The theory can also be applied to models with any number of life stages as well as dispersal kernels and decision functions with arbitrary spatial and density dependence.

6. Concluding remarks

We developed a general class of stage-structured integrodifference equation models for the dynamics of biological populations subject to density dependent dispersal. These models allow for partial dispersal and non-dispersing stages. The theory developed in this paper addresses the basic question of extinction versus (equilibrium) persistence of the population. It extends and generalizes the basic bifurcation theory of Cushing [6,7] for structured population dynamics in a non-spatial setting and that of Alzoubi [2–4] for stage-structured integrodifference equation models with no density dependent dispersal.

The theory in this paper is valid near the primary bifurcation point $n = 1$ and does not necessarily tell us about the existence or stability of model equilibria for larger values of n. For larger n, simulations show that models of the form (3) with density dependent dispersal can admit spatial patterns. Models of this type have been used to study the spatial patterns formed by several species of the flour beetle *Tribolium*, specifically patterns that involve the spatial separation of life-cycle stages [20,21].

Acknowledgments

Appendix A

A.1. The Krein–Rutman Theorem

Let E be a real Banach space with a total ordered cone K_+, and $L : E \to E$ be a linear operator. L is a *strongly positive* operator if $Lx \gg 0$ whenever $x > 0$ [24]. That is, L maps all nonzero $x \in K_+$ into the interior of the cone, $int(K_+)$. We note that in order for an operator to be strongly positive, the cone K_+ must have a non-empty interior. The Krein–Rutman Theorem may be used in applications to satisfy Assumptions 3 and 5.

Theorem 6 *(Krein–Rutman). (See [24].) Let E be a real Banach space with an order cone K_+ having a non-empty interior. Then a linear, compact, and strongly positive operator $T : E \to E$ has the following properties*:

(1) *T has exactly one eigenvector with $x > 0$ and $\|x\| = 1$. The corresponding eigenvalue is the spectral radius $\rho(T)$ and this is algebraically simple. Furthermore, $x \gg 0$.*
(2) *The dual operator T^* has $\rho(T)$ as an algebraically simple eigenvalue with a strictly positive eigenvector x^*.*

Corollary 1 *(Comparison principle). (See [24].) If $S : E \to E$ is a compact linear operator with $Sx \geqslant Tx$ for all $x \geqslant 0$, then $\rho(S) \geqslant \rho(T)$. If $Sx > Tx$ for all $x > 0$, then $\rho(S) > \rho(T)$.*

A.2. The net reproductive number

Here we prove a theorem relating the inherent net reproductive number n to the dominant eigenvalue λ_0 of $A'(\vec{0}, n)$, asserting $n > 1$ ($n < 1$) if and only if $\lambda_0 > 1$ ($\lambda_0 < 1$). Thus $n = 1$ if and only if $\lambda_0 = 1$. The non-spatial version of this theorem was proved by Cushing [8] and Li and Schneider [18]. Theorem 7 generalizes and offers a completed proof of Theorem 2.1 of Alzoubi [3].

The proof of Theorem 7 will use the following facts from Zeidler [24]. For linear operators $A, B : E \to E$ on a Banach space E, we have the following properties [24]:

(a) $(AB)^* = B^*A^*$;
(b) $(A + B)^* = A^* + B^*$;
(c) $(A^{-1})^* = (A^*)^{-1}$.

Theorem 7. *Let E be a real Banach space with an order cone K_+ having a non-empty interior and $F, T : E \to E$ are compact linear operators with $I - T$ invertible. Assume*:

1. *$F(I - T)^{-1}$ and its dual have a simple, positive, dominant eigenvalue n associated with positive eigenvectors $y > 0$ and $w^* > 0$.*
2. *$T + cF$ is strongly positive for all real numbers $c > 0$.*

Then one of the following holds:

1. *$r = n = 1$,*
2. *$1 < r < n$,*
3. *$0 < n < r < 1$ where $r = \rho(T + F)$.*

Proof. From Assumption 1, $(F(I - T)^{-1})^* w^* = n w^*$. Then $(I - T^*)^{-1} F^* w^* = n w^*$. Apply $I - T^*$ to both sides of this equation and divide by n. Then $\frac{1}{n} F^* w^* = (I - T^*) w^*$ or $(T^* + \frac{1}{n} F^*) w^* = w^*$. This is equivalent to

$$\left(T + \frac{1}{n} F \right)^* w^* = w^*.$$

We see 1 is the dominant eigenvalue of the strongly positive operator $(T + \frac{1}{n} F)^*$ and also $T + \frac{1}{n} F$. So $\rho(\frac{F}{n} + T) = 1$ We consider three cases.

1. Assume $n = 1$. Then $1 = \rho(\frac{F}{n} + T) = \rho(\frac{F}{1} + T) = \rho(F + T) = r$.
2. Assume $n > 1$. Then using Corollary 1 we have $T + \frac{F}{n} < F + T < nT + F$ and $1 = \rho(\frac{F}{n} + T) < \rho(F + T) = r < \rho(nT + F) = n$. So $1 < r < n$.
3. Assume $0 < n < 1$. Then using Corollary 1 we have $T + \frac{F}{n} > F + T > nT + F$ and $1 = \rho(\frac{F}{n} + T) > \rho(F + T) = r > \rho(nT + F) = n$. So $0 < n < r < 1$. □

References

[1] M.Y. Alzoubi, A dispersal model for structured populations, PhD thesis, University of Arizona, 1999.
[2] M.Y.M. Alzoubi, Equilibria in a dispersal model for structured populations, Turkish J. Math. 31 (2007) 421–433.
[3] M.Y.M. Alzoubi, The net reproductive number and bifurcation in an integro-difference system of equations, Appl. Math. Sci. 4 (4) (2010) 191–200.
[4] M.Y.M. Alzoubi, Stability and bifurcation in a system of integro-difference equations model, Appl. Math. Sci. 4 (64) (2010) 3175–3188.
[5] M.G. Crandall, P.H. Rabinowitz, Bifurcation, perturbation of simple eigenvalues and linearized stability, Arch. Ration. Mech. Anal. 52 (1973) 161–180.
[6] J.M. Cushing, An Introduction to Structured Population Dynamics, CBMS-NSF Regional Conf. Ser. in Appl. Math., vol. 71, SIAM, Philadelphia, 1998.
[7] J.M. Cushing, Matrix models and population dynamics, in: M.A. Lewis, M.A.J. Chaplain, J.P. Keener, P.K. Maini (Eds.), Mathematical Biology, in: IAS/Park City Math. Ser., Amer. Math. Soc., Providence, RI, 2009, pp. 47–150.
[8] J.M. Cushing, Z. Yicang, The net reproductive value and stability in matrix population models, Natur. Resource Modeling 8 (1994) 297–333.
[9] E.N. Dancer, On the structure of solutions of non-linear eigenvalue problems, Indiana Univ. Math. J. 23 (11) (1974) 1069–1076.
[10] G. Dwyer, W.F. Morris, Resource-dependent dispersal and the speed of biological invasions, Am. Nat. 167 (2006) 165–176.
[11] M.I. Gil', Difference Equations in Normed Spaces: Stability and Oscillations, Elsevier, Amsterdam, 2007.
[12] D.P. Hardin, P. Takac, G. Webb, Asymptotic properties of a continuous-space discrete-time population model in a random environment, J. Math. Biol. 26 (1988) 361–374.
[13] V. Jormalainen, S.M. Shuster, Microhabitat segregation and cannibalism in an endangered freshwater isopod, *Thermosphaeroma thermophilum*, Oecologia 111 (1997) 271–279.
[14] H. Kielhöfer, Bifurcation Theory: An Introduction with Applications to PDEs, Springer, New York, 2004.
[15] M. Kot, W. Schaffer, Discrete-time growth-dispersal model, Math. Biosci. 80 (1986) 109–136.
[16] M.A. Krasnosel'skii, Topological Methods in the Theory of Nonlinear Integral Equations, Springer, Berlin, 1964.
[17] K. Leonardsson, Effects of cannibalism and alternative prey on population dynamics of *Saduria entomon* (Isopoda), Ecology 72 (1991) 1273–1285.
[18] C.K. Li, H. Schneider, Applications of Perron–Frobenius theory to population dynamics, J. Math. Biol. 44 (2002) 450–462.
[19] P.H. Rabinowitz, Some global results for nonlinear eigenvalue problems, J. Funct. Anal. 7 (1971) 1291–1313.
[20] S.L. Robertson, Spatial patterns in stage-structured populations with density dependent dispersal, PhD thesis, University of Arizona, 2009.
[21] S.L. Robertson, J.M. Cushing, Spatial segregation in stage-structured populations with an application to *Tribolium*, J. Biol. Dyn. 5 (5) (2011) 398–409.
[22] E. Sparrevik, K. Leonardsson, Effects of large *Saduria entomon* (isopoda) on spatial distribution of their small *S. entomon* and *Monoporeia affinis* (amphipoda) prey, Oecologia 101 (1995) 177–184.
[23] R.W. Van Kirk, M.A. Lewis, Integrodifference models for persistence in fragmented habitats, Bull. Math. Biol. 59 (1997) 107–137.
[24] E. Zeidler, Nonlinear Functional Analysis and its Applications I, Springer, Berlin, 1992.