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The Net Reproductive Number and Bifurcation in an Integro-Difference System of Equations

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Abstract

A model for structured populations with a two-phase life cycle has been derived in [2], also we proved there the existence of a branch of positive equilibrium points in the positive cone. In this paper we study the stability of the positive equilibria using the inherent net reproductive number n as the bifurcation parameter.

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0.1 INTRODUCTION

One of the most important characteristics of populations is dispersal. It is noticed that individuals move in their habitat for several reasons, including crowding, searching for food, environmental fluctuations, diseases, etc., and this movement can greatly affect the dynamics of the population. Dispersal was incorporated into population models since long time, for examples see $[4-16, 19, 20]$. In the earlier models, dispersal was modeled by reaction-diffusion equations. Recently, many studies emphasized on the fact that in most annual plants populations and many kinds of insects the cycle of life is divided into two distinct stages. In the first stage, the populations grow and produce offsprings, and in the second stage, the newborns disperse within their habitat. This led Kot and Schaffer [10] to model such populations by integro-difference equations that are discrete in time and continuous in space. In Kot-Schaffer model individuals are treated as identical. However, in most populations individuals can vary greatly with respect to characteristics that

affect their growth , reproduction and dispersal. In [2], we introduced a model that based on Kot and Schaffer, but we consider structured populations. In structured models individuals are classified with respect to characteristics such as age, weight, body size, etc. and the resulting classes are tracked dynamically, for a good book on structured populations see [3]. In [2] we proved the existence of a branch of positive equilibria and we studied the stability properties of this branch from the bifurcation point of view.

Our main purpose in this paper is to prove that the bifurcating branch of positive equilibria extends globally by applying the Rabinowitz bifurcation theory using the inherent net reproductive number as the bifurcation parameter.

Now, we outline our model that was derived in [2]: Suppose that the individuals of a population are categorized into a finite number of classes (e.g., by chronological age or some measure of body size). Let $\Omega \in R^n$ be a compact subset which denotes the spatial habitat where the population lives and disperses. Assume that the individuals are not allowed to leave Ω. Let $x_i(t,s)$, for $i = 1, 2, ..., m$, denote the density of individuals at the location $s \in \Omega$ who belong to the $i-$th class at time $t = 0, 1, \cdots$. Let $\overrightarrow{x}(t,s) = (x_1(t,s), ..., x_m(t,s))^T$ where $x_i : I \times \Omega \longrightarrow R^+$, and I is the set of nonnegative integers in the interval $[0, \infty)$. Here the unit of time is equal to the dispersal period. Let $t_{ij}(\overrightarrow{x}(t,\nu), \nu)$ be the expected fraction of $j-$class individuals at position ν who survive and transfer to class i per unit of time. Then at time $t+1$ the density of individuals in class i at position s is

$$\sum_{j=1}^{m} \int_{\Omega} k_{ij}(s,\nu)\, t_{ij}(\overrightarrow{x}(t,\nu), \nu)\, x_j(t,\nu)\, d\nu \ ,$$

where the kernels $k_{ij}(s,\nu)$ give the probability that an individual at position ν at time t will settle at position s by the end of the dispersion period. Let $f_{ij}(\overrightarrow{x}(t,\nu), \nu)$ be the expected number of surviving $i-$class offspring at place ν per $j-$class individuals per unit of time. Then at time $t+1$ the number of offspring in the $i-$class at the position s is

$$\sum_{j=1}^{m} \int_{\Omega} l_{ij}(s,\nu)\, f_{ij}(\overrightarrow{x}(t,\nu), \nu)\, x_j(t,\nu)\, d\nu$$

where $l_{ij}(s,\nu)$ is the probability that an $i-$class newborn of individual in the $j-$class at position ν will settle at position s after the dispersion period. Now at time $t+1$ the total number of individuals in class i at position s is given by the following equation:

$$\begin{aligned} x_i(t+1,s) &= \sum_{j=1}^{m} \int_{\Omega} k_{ij}(s,\nu)\, t_{ij}\left(\overrightarrow{x}(t,\nu),\nu\right) x_j(t,\nu)\, d\nu \\ &\quad + \sum_{j=1}^{m} \int_{\Omega} l_{ij}(s,\nu)\, f_{ij}\left(\overrightarrow{x}(t,\nu),\nu\right) x_j(t,\nu)\, d\nu \end{aligned} \tag{3.1}$$

where $i = 1, 2, ..., m$. The system of equations (3.1) may be put in the matrix system

$$\begin{aligned} \overrightarrow{x}(t+1,s) &= \int_{\Omega} T\left(s,\nu,\overrightarrow{x}(t,\nu)\right) \overrightarrow{x}(t,\nu)\, d\nu + \\ &\quad \int_{\Omega} F\left(s,\nu,\overrightarrow{x}(t,\nu)\right) \overrightarrow{x}(t,\nu)\, d\nu \end{aligned} \tag{3.2}$$

where $T = (k_{ij}t_{ij})$ and $F = (l_{ij}f_{ij})$ for $1 \leq i, j \leq m$. The functions t_{ij} and f_{ij} have $[0,\infty) \times \Omega$ as their domains, and their ranges lie in $[0,\infty)$ and $(0,1]$ respectively.

To this end, we mention some definitions and facts; A kernel of an integral operator is called *admissible* if it generates a compact linear operator. A nonnegative admissible kernel $k(s,t)$ is said to be *of positive type* if for each nonnegative continuous function $\phi(s)$, not identically zero, there exist an iterated kernel $k^{(n)}(s,t)$ such that $\int_G k^{(n)}(s,t)\,\phi(t)\,dt > 0$, $(s \in G)$. Here $k^{(n)}$ is defined as follows:

$$k^{(n)}(s,t) = \int_G \cdots \int_G k(s,t_1) \cdots k(t_{p-1},t)\, dt_1 \cdots dt_{p-1}$$

where t_1, ...,t_{p-1} are from G. A sufficient condition for the kernel $k(s,t)$ to be of positive type is that $k^{(n)}(s,s) > 0$; for some $n \geq 1$. So, every Fredholm linear operator with positive kernel is of positive type.

The nonlinear operator $A : L_2(\Omega) \to L_2(\Omega)$ is *of Hammerstein type* if it has the form

$$A(x(v)) = \int_{\Omega} k(u,v)\, f(x(v),v)\, dv$$

where $f : R \times \Omega \to R$, and $k : \Omega \times \Omega \to R$. This operator may be considered as a composition of the Fredholm linear operator

$$B = \int_{\Omega} k(u,v)\,\phi(v)\,dv$$

and the nonlinear substitution operator $F(x) = f(x(v), v)$, where $B, F : L_2(\Omega) \to L_2(\Omega)$, and $f : R \times \Omega \to R$. A necessary and sufficient condition for the substitution operator F to act from $L_2(\Omega)$ to itself is that f is continuous and $|f(x,v)| \leq a(v) + b|x|$ for some $a(v) \in L_2(\Omega)$ and constant $b > 0$. Moreover, if F acts from $L_2(\Omega)$ to itself, then it is bounded and continuous.

Since in biological applications we are interested in solutions that belong to the positive cone K_+ of $L_2(\Omega)^m$ we will restrict our domain to an open set of $L_2(\Omega)^m$ that contains the positive cone K_+.

1 MAIN RESULTS

Let X be a real Banach space with a total ordered cone X_+ and $L : X \to X$ be a linear operator. L is called *strongly positive if* $Lx > 0$ whenever $x > 0$. Let us denote by $\rho(L)$ the spectral radius of L, which is the radius of the smallest circle that contains all the eigenvalues of L. *The Krein-Rutman Theorem* states that a compact, strongly positive linear operator T has a positive, strictly dominant, algebraically simple eigenvalue $\rho(T)$ associated with a positive eigenvector, and no other eigenvalue has a nonnegative eigenvector. Moreover, *the dual operator* T^* also has $\rho(T)$ as an algebraically simple eigenvalue associated with a strictly positive eigenvector x^*. Also, if $S : X \to X$ is another compact linear operator with $Sx \geq Tx$ for all $x \geq 0$, then $\rho(S) \geq \rho(T)$, and if $Sx \geq Tx$ for all $x > 0$, then $\rho(S) > \rho(T)$. This is called *the comparison principle*. For proofs of all these results (see [21]) (pp. 291-293). let $A, B : H \to H$ be linear operators and X a Banach space, then we have

$$(AB)^* = B^* A^* \qquad (a)$$

$$(A+B)^* = A^* + B^* \qquad (b)$$

$$\left(A^{-1}\right)^* = (A^*)^{-1} \ . \qquad (c)$$

We will use these properties in the proof of the following Theorem.

Theorem 2.1. *Let X be a real Banach space, and N, $M : X \to X$ be compact linear operator. Assume $I-N$ is invertible. Then, under the following assumptions*

1. *$M(I-N)^{-1}$ and its dual have positive simple, dominant eigenvalue n that associated*

with positive eigenvectors $y \geq 0$, $\omega^* > 0$,

2. *$N + cM$ is strongly positive for all real numbers $c > 0$, we have $n < 1$ if and only if*

$r < 1$, and $n > 1$ if and only if $r > 1$. (Therefore, $n = 1$ if and only if $r = 1$). Here

$r = \rho(N + M)$.

Proof. By Krain-Rutman Theorem $N + M$ has a positive, strictly dominant, algebraically simple eigenvalue $r = \rho(N + M)$, which is associated with a unique (up to a constant multiple) positive eigenvector. From (1), $\omega^* > 0$ is an eigenvector associated with n so that $(M(I-N)^{-1})^* = n\omega^*$. The dual properties (a), (c) and (b) imply

$$(I - N^*)^{-1} M^* \omega^* = n\omega^*.$$

Apply $I - N^*$ to both sides of this equation and divide by n to get $\frac{1}{n}M^*\omega^* = (I - N^*)\omega^*$ or

$$\left(N^* + \frac{1}{n}M^*\right)\omega^* = \omega^*$$

which is equivalent to

$$\left(N + \frac{1}{n}M\right)^* \omega^* = \omega^*. \qquad (i)$$

By assumption (2), $N + \frac{1}{n}M$ is strongly positive compact linear operator, so by Krain-Rutman Theorem it has a positive eigenvector associated with a simple strictly dominant positive eigenvalue. Moreover, $\left(N + \frac{1}{n}M\right)^*$ has the same simple dominant eigenvalue associated with a strictly positive eigenvector. Since $\omega^* > 0$, and from equation (1), it is associated with the eigenvalue 1, then 1 is the dominant eigenvalue of $\left(N + \frac{1}{n}M\right)^*$. Thus, 1 is the dominant eigenvalue of $N + \frac{1}{n}M$ and $\rho\left(\frac{M}{n} + N\right) = 1$. For the first case; if $n < 1$, then $\frac{1}{n} > 1$. Since for all $x > 0$, $\left(\frac{M}{n} + N\right)x > (N + M)x$, we have $1 = \rho\left(\frac{M}{n} + N\right) > \rho(N + M) = r$. Conversely, if $r < 1$, then $\frac{M}{n} + N < \frac{M+N}{n}$,

and $r < 1 = \rho\left(\frac{M}{n} + N\right) < \rho\left(\frac{M+N}{n}\right) = \frac{1}{n}\rho\left(N + M\right) = \frac{r}{n}$. Thus, $n < 1$. The second case can be proved the same way. This completes the proof.

We define the positive continuum C^+ by the (connected) intervals

$$\sigma\left(C^+\right) \doteq \left\{n \mid (n,\vec{x}) \in C^+\right\} \subset R^1,$$

$$\rho\left(C^+\right) \doteq \left\{\vec{x} \mid (n,\vec{x}) \in C^+\right\} \subset R_+^m,$$

respectively. We are interested in investigating the spectrum of the equation

$$\vec{x}\left(t+1,v\right) = T\left(\vec{x}\left(t,v\right)\right) + F\left(\vec{x}\left(t,v\right)\right), \tag{6.1}$$

where, $\vec{x} \in L_2\left(\Omega\right)^m$. And T and F are nonlinear integral operators that are defined by the following system of equations:

$$\begin{aligned} x_i\left(t+1,s\right) &= \sum_{j=1}^{m} \int_\Omega k_{ij}\left(s,\nu\right) t_{ij}\left(\overrightarrow{x}\left(t,\nu\right),\nu\right) x_j\left(t,\nu\right) d\nu \\ &\quad + \sum_{j=1}^{m} \int_\Omega l_{ij}\left(s,\nu\right) f_{ij}\left(\overrightarrow{x}\left(t,\nu\right),\nu\right) x_j\left(t,\nu\right) d\nu \end{aligned}$$

where $i = 1, 2, ..., m$. This system of equations can be written in the following matrix system:

$$\begin{aligned} \overrightarrow{x}\left(t+1,s\right) &= \int_\Omega T\left(s,\nu,\overrightarrow{x}\left(t,\nu\right)\right) \overrightarrow{x}\left(t,\nu\right) d\nu \\ &\quad + \int_\Omega F\left(s,\nu,\overrightarrow{x}\left(t,\nu\right)\right) \overrightarrow{x}\left(t,\nu\right) d\nu \end{aligned}$$

where $T = (k_{ij}t_{ij})$ and $F = (l_{ij}f_{ij})$ for $1 \leq i,j \leq m$. The functions t_{ij} and f_{ij} have $[0,\infty) \times \Omega$ as their domains, and their ranges lie in $[0,\infty)$ and $(0,1]$ respectively.

Assume that $F\left(\vec{x}\right)\left(I - T\left(\vec{x}\right)\right)^{-1}$ has a positive, strictly dominant, simple eigenvalue $n\left(\vec{x}\right)$ with nonnegative eigenvector $\upsilon\left(\vec{x}\right) \geq 0$; then $n\left(\vec{x}\right)$ is called *the net reproductive number* at $\vec{x}$. Note that $n = n\left(\vec{0}\right)$ is the inherent net reproductive number n. Assume f_{ij} are scaled to the inherent net reproductive number n such that $f_{ij} = n\phi_{ij}$. Then, we have $F = n\Phi$, where Φ is the

normalized operator in the sense that $\overline{T}\left(\vec{0}\right)+\overline{\Phi}\left(\vec{0}\right)$ has 1 as the dominant eigenvalue.

For some integer $k \geq 0$, consider equation (6.1) under the following assumptions:

1. $t_{ij} \in C^{k+1}\left(R_+^1 \times \Omega, [0,1]\right)$, $\phi_{ij} \in C^k\left(R_+^1 \times \Omega, R_+^1\right)$ and all ϕ_{ij}'s are bounded,

2. $I - T\left(\vec{x}\right)$ is invertible for all $\vec{x} \in K_+^m$, where K_+^m is the positive cone of L_2^m,

3. k_{ij}'s, l_{ij}' and all the kernels at the linearization of (6.1) are $L_2\left(\Omega \times \Omega\right)$ and are

admissible of positive type,

4. for all $\vec{x} \in K_+^m$, $\Phi\left(\vec{x}\right)\left(I-\overline{T}\left(\vec{x}\right)\right)^{-1}$ and its dual have a positive, strictly dominant,

simple eigenvalue $\upsilon\left(\vec{x}\right)$, $\upsilon\left(\vec{0}\right)=1$, with eigenvectors $u\left(\vec{x}\right) \geq 0$, $w^* > 0$.

Suppose that $\vec{x} > 0$ is a positive equilibrium, i.e., $\vec{x} = T\left(\vec{x}\right)+n\Phi\left(\vec{x}\right)$. The kernels of the linearization of the operator in (6.1) at $\vec{x}$ are admissible of positive type (see 3) above. Thus, by Krain-Rutman Theorem we conclude that 1 is the dominant eigenvalue of $T\left(\vec{x}\right)+n\Phi\left(\vec{x}\right)$ at each $\vec{x} > 0$. From Theorem 2.1 above we conclude that

$$n\upsilon\left(\vec{x}\right)=1 \text{ for all equilibria } \vec{x} > 0, \tag{6.2}$$

where $n\left(\vec{x}\right)=n\upsilon\left(\vec{x}\right)$. From the biological point of view this equation means each individual replaces itself over the course of its lifetime when the population held at $\vec{x}$. We have proved that the extinction equilibria $\vec{x}=0$ loses stability as n is increased through the critical value $n=1$. We wish to use (6.2) to study the direction of bifurcation and other properties of the spectrum.

In the following Theorem we denote by C^+ the continuum of positive equilibria that bifurcates from the trivial equilibrium.

Theorem 6. *Consider the operator equations (6.1) under the above assumptions (1-4). Then*

1. *the range* $\rho\left(C^+\right)$ *is unbounded and* $\rho\left(C^+\right)\setminus\{0\}$ *contains only positive equilibria*;

2. *the spectrum* $\sigma\left(C^+\right)$ *contains only positive* n.

Proof. **(1)** Our goal is to rule out alternative 2 of Theorem 5. From assumption 3 above the operator $T\left(\vec{x}\right)+n\Phi\left(\vec{x}\right)$ has no nonnegative eigen-

vectors other than the positive eigenvector associated with the dominant eigenvalue. Since an equilibrium is an eigenvector of $T\left(\vec{x}\right)+n\Phi\left(\vec{x}\right)$ associated with the eigenvalue 1, we conclude that a nonnegative equilibrium must be positive. From alternative (1) of Theorem 5, $\rho\left(C^{+}\right)$ contains only positive equilibria and either $\rho\left(C^{+}\right)$ and $\sigma\left(C^{+}\right)$ is unbounded. If the range $\rho\left(C^{+}\right)$ is bounded then since $n\upsilon\left(\vec{x}\right)=1$ and $\upsilon\left(\vec{x}\right)>0$, the spectrum $\sigma\left(C^{+}\right)$ is bounded, which is a contradiction with alternative (1) of Theorem 5. Therefore, $\rho\left(C^{+}\right)$ is unbounded.

(2). Suppose C^{+} contains a pair $\left(n,\vec{x}\right)$ for which $n\leq 0$. Since C^{+} is connected, there must be an equilibrium pair $\left(n,\vec{x}\right)\in C^{+}$, $\vec{x}\geq 0$. But, by (1) above $\vec{x}>0$ and we have $\vec{x}=T\left(\vec{x}\right)$, which contradicts the invertibility of $I-T\left(\vec{x}\right)$ in assumption 2. Thus, the spectrum contains only positive n.

Theorem 6. *Consider the operator equations (6.1) under the above assumptions (1-4). We*

have the following alternatives:

1. *If* $\upsilon\left(\vec{x}\right)\longrightarrow 0$ *as* $\left\|\vec{x}\right\|\longrightarrow\infty$, *then for each* $n>1$, *there exists at least one positive*

equilibrium.

2. *If* $\upsilon\left(\vec{x}\right)<1$ *for* $\vec{x}>0$ *and* $\vec{x}\approx\vec{0}$, *then the bifurcation is to the right and stable. If*

$\upsilon\left(\vec{x}\right)>1$ *for* $\vec{x}>0$ *and* $\vec{x}\approx\vec{0}$, *then the bifurcation is to the left and unstable.*

3. *If* $\upsilon\left(\vec{x}\right)<1$ *for all* $\vec{x}>0$, *then there is no positive equilibrium for* $n<1$.

Proof. (1). If $\upsilon\left(\vec{x}\right)\longrightarrow 0$ as $\left\|\vec{x}\right\|\longrightarrow\infty$, then from the equation $n\upsilon\left(\vec{x}\right)=1$ and the unboundedness of the range $\rho\left(C^{+}\right)$, we conclude that $\sigma\left(C^{+}\right)\subset(0,\infty)$ is an unbounded interval whose closure contains 1. This implies (1). Parts (2) and (3) are simple consequences of equation (6.2).

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