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Equilibria in a Dipersal Model for Structured Populations

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Abstract

We derive a model for structured population with a two-phase life cycle. Growth and reproduction occur during the first phase. The first phase is followed by a dispersal phase in which individuals are allowed to move throughout a habitat. Also, we prove the existence of a branch of positive equilibria using bifurcation results of Rabinowitz.

Key Words: Integro-difference equations, Dynamical systems, Dispersion, Structured populations.

1. Introduction

Dispersal within a population is one of the most notable characteristics of individuals. Individuals move in their habitat for several reasons, including crowding, environmental fluctuations, diseases, etc., and this movement can greatly affect the dynamics of the population. Therefore, it is important to take dispersal into account when studying stability and persistence of populations. Dispersal was incorporated into population models in the pioneering work of Skellam [22], Kierstead and Slobodking [10], Fisher [5], Kolmogrov, Petrovsky and Piscounov [9]. Also, dispersal occurs in studies by Levin [14], McMurtrie [18], Cohen and Murray [3], Hamilton and May [6], MacArthur and Wilson [17], Levin and Segel [16], Vance [23], Ellner [4], Liven, Cohen, and Hastings [15], and Okubo [19].

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In the earlier studies of dispersal there was an emphasis on continuous time growth models based on reaction-diffusion equations. However, the cycle of many populations involves two phases. The year of these populations is divided into two distinct stages: the growth phase, in which the population grows and produces newborns and a dispersal phase, in which the newborns disperse. Examples of such populations include annual plants and many insects. Such life cycle characteristics motivated Kot and Schaffer [11] to model these kinds of populations by integrodifference equations that are continuous in space, but discrete in time. They modeled the growth phase by a nonlinear operator and the dispersal phase by a linear operator. They studied the trivial (or extinction) equilibrium of the model resulting from the composition of these two operators. Harden, Takac and Webb [7, 8] completed the study of the Kot-Schaffer model by proving several results about the existence and stability of nontrivial equilibria. Mathematically, they worked with nonlinear operators defined on the space of continuous functions. Van Kirk and Lewis [24] proved that if the operators involved in Kot-Schaffer model are defined and continuous on L_2, then the results of Hardin et al. remain valid. Moreover, they proved the existence of a branch of positive equilibria that bifurcates from the extinction equilibrium.

In the 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. Therefore, we are motivated to introduce a new model for two-phase life cycle populations considered by Kot-Schaffer and Van Kirk-Lewis. Our model [1] combines a "structured population" model of Jim Cushing [2] with the discrete time dispersal model of Kot-Schaffer. In structured models individuals are classified with respect to characteristics such as age, weight, body size, etc. and the resulting classes are tracked dynamically. Our main purpose in this paper is to prove the existence of a branch of equilibrium points to our model using bifurcation theory techniques. Our results generalize and extend those of Van Kirk and Lewis in two significant directions: our model is more general that includes demographic structure and we prove that the bifurcating branch of positive equilibria extends globally by applying the Rabinowitz bifurcation theory.

2. Preliminaries

In this section, we introduce some definitions and results from the theory of functional analysis that represent the main tools in our study.

Let $\mathcal{F} : E_1 \to E_2$, where E_1 and E_2 are real Banach spaces and $\mathcal{F}$ is a continuous operator. Suppose the equation $\mathcal{F}(U) = 0$ is satisfied by a curve of solutions $C = \{U(t) : t \in [a, b]\}$. If for some $s \in (a, b)$, $\mathcal{F}$ has zeros not lying on C in every neighborhood of $U(s)$, then $(s, U(s))$ is said to be a *bifurcation point* for $\mathcal{F}$ with respect to the curve C. If $\mathcal{F}(f_n)$ has a convergent subsequence in $\mathcal{F}(E_1)$ for every bounded sequence f_n in E_1, then $\mathcal{F}$ is called a *compact operator*. Equivalently, $\mathcal{F}$ is compact if $\mathcal{F}(C)$ is relatively compact in E_2 whenever C is a bounded subset of E_1. $\mathcal{F}(C)$ is relatively compact in E_2 if $\mathcal{F}(C)$ is compact.

Let R denotes the set of real numbers. We are interested in equations of the form

$$u = \mathcal{A}(\lambda, u), \tag{2.1}$$

where $\lambda \in R$, E is real Banach space with norm $\| \, . \, \|$ and $\mathcal{A} : R \times E \to E$ is compact and continuous. Moreover, we assume $\mathcal{A}(\lambda, u) = \lambda\mathcal{L}(u) + \mathcal{H}(\lambda, u)$, where $\mathcal{H}(\lambda, u)$ is $o(\|u\|)$ for u near 0 uniformly on bounded λ intervals and $\mathcal{L}$ is a compact linear operator on E. Note that $\mathcal{A}(\lambda, u) = 0$ for all $\lambda \in R$. Solutions of equation (2.1) of the form $(\lambda, 0)$ with $\lambda \in R$ are called *trivial solutions*. Let $r(\mathcal{L}) = \{\mu \in R : \nu = \mu\mathcal{L}(\nu) \text{ for some } \nu \in E\backslash\{0\}\}$ be the set of all reciprocals of the nonzero eigenvalues of $\mathcal{L}$.

All possible bifurcation points of equation (2.1) with respect to the curve of trivial solutions are from the set $\{(\mu, 0) : \mu \in r(\mathcal{L})\}$. Moreover, it is proved in Krasnosel'skii [12] that if μ is a characteristic value of odd (geometric) multiplicity, then $(\mu, 0)$ is a bifurcation point. Later on Rabinowitz [20] proved that the bifurcating branch of positive equilibria from the bifurcation point $(\mu, 0)$ extends globally and connects to the boundary of the domain of the operator $\mathcal{A}$. We denote by S, the closure of the set of nontrivial solution pairs (μ, u) of equation (2.1) Now, we list the main bifurcation theorems of Rabinowitz [20].

Theorem 2.1. *(Rabinowitz) If μ is a characteristic value of odd (geometric) multiplicity, then S has a maximal subcontinuum C_μ such that $(\mu, 0) \in C_\mu$ and C_μ either*

1) *meets infinity in $R \times E$, or*

2) *meets $\left(\bar{\mu}, 0\right)$, where $\mu \neq \bar{\mu}$ is a characteristic value of odd multiplicity.*

If the operator $\mathcal{A}$ is not globally defined then we have the following result.

Theorem 2.2. *(Rabinowitz) If $\Omega \subseteq R \times E$ is a bounded open subset containing $(\mu, 0)$, and $\mathcal{A}(\lambda, u)$ is compact and continuous on $\bar{\Omega}$, and μ is a characteristic value of odd (geometric) multiplicity, then S has a maximal subcontinuum $C_\mu \in \bar{\Omega}$ such that $(\mu, 0) \in C_\mu$ either*

1) *meets $\partial\Omega$, or*

2) *meets $\left(\bar{\mu}, 0\right)$ where $\mu \neq \bar{\mu} \in r(\mathcal{L})$, and $\left(\bar{\mu}, 0\right) \in \Omega$.*

It is well-known that it is not an easy matter to find the geometric multiplicity of a characteristic value of a linear operator $\mathcal{L}$, but in most applications, the characteristic values of interest are those of multiplicity one. In the case of a simple characteristic value μ, if $\mathcal{A}(\lambda, u)$ is Fre'chet differentiable in u, near $(\mu, 0)$, then C_μ is given by the parametrization $(\lambda(\epsilon), u(\epsilon)) = (\mu + O(1), \epsilon v + O(|\epsilon|))$ for $\epsilon \approx 0$, where v is an eigenvector corresponding to μ. For a proof of the existence of this parametrization (which is called the Liapunov-Schmidt expansion) see E. Zeidler [25] (pp. 375–381) or Jim Cushing [2]. Also, the curve C_μ has two portions parametrized by $\epsilon \geq 0$ and $\epsilon \leq 0$. Using this parametrization Rabinowitz proved, in the case μ is a simple characteristic value, C_μ can be decomposed into subcontinua C_μ^+ and C_μ^-, which near $(\mu, 0)$ have only $(\mu, 0)$ as a common point.

Theorem 2.3. *(Rabinowitz) If μ is a simple characteristic value, then each of C_μ^+ and C_μ^- meets $(\mu, 0)$ and either*

1) *meets infinity in $R \times E$,* or

2) *meets $\left(\bar{\mu}, 0\right)$, where $\mu \neq \bar{\mu} \in r(\mathcal{L})$.*

3. Main Results

The Model Derivation: 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 $t = 0, 1, ...$ 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 $t_{ij}\left(\overrightarrow{x}\left(t, \nu\right), \nu\right)$ 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

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

where the kernels $k_{ij}\left(s, \nu\right)$ 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 $f_{ij}\left(\overrightarrow{x}\left(t, \nu\right), \nu\right)$ 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

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

where $l_{ij}\left(s, \nu\right)$ 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:

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

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

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

where $T = \left(k_{ij} t_{ij}\right)$ and $F = \left(l_{ij} f_{ij}\right)$ 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.

In order to study the dynamical system defined by equation (3.2) we begin by studying the existence of solutions of the following autonomous equilibrium equation:

$$\overrightarrow{x}(s)=\int_{\Omega}T(s,\nu,\overrightarrow{x}(\nu))\overrightarrow{x}(\nu)\,d\nu+\int_{\Omega}F(s,\nu,\overrightarrow{x}(\nu))\overrightarrow{x}(\nu)\,d\nu. \tag{3.3}$$

Since biologically only nonnegative solutions are of interest, we focus on solutions lying in the positive cone K_+ of $\mathrm{L}_2^m(\Omega)$. So we assume that the domain of the operator defined by the right hand side of equation (3.3) is an open set G containing K_+. We denote the integral operator with kernels $T(s,\nu,\overrightarrow{x}(\nu))$ and $F(s,\nu,\overrightarrow{x}(\nu))$ by T and F respectively. We assume the operator $I-\bar{T}$ is invertible, where

$$\bar{T}\left(\overrightarrow{y}\right)=\int_{\Omega}T\left(s,\nu,\overrightarrow{0}\right)\overrightarrow{y}(v)\,d\nu.$$

The inverse of the operator $I-\bar{T}$ is called the resolvent of $\bar{T}$. It is well known that the resolvent of a linear operator of integral type is a linear operator of integral type, see Riesz and Nagy [21]. Let R denotes the resolvent of the Fredholm linear integral operator $\bar{T}$, then R is given by the linear integral operator $R\left(\overrightarrow{y}\right)=\int_{\Omega}r(s,\nu)\overrightarrow{y}(v)\,d\nu$. Let $\bar{F}\left(\overrightarrow{y}\right)=\int_{\Omega}F\left(s,\nu,\overrightarrow{0}\right)\overrightarrow{y}(v)\,d\nu$. We normalize the f_{ij}'s in such a way that $f_{ij}=n\phi_{ij}$, and write $\bar{F}=n\bar{\Phi}$, where $n\in R^1$ is the so-called "inherent net reproductive number" (i.e., the expected number of offspring per newborn per its lifetime). This number is defined as follows: Assume the operator $\bar{F}\left(I-\bar{T}\right)^{-1}$ has a positive, strictly dominant, simple eigenvalue n with nonnegative eigenvector $v\geq 0$, then n is called *the inherent net reproductive number*. This definition of n is a generalization of the definition for the non-spatial case given in [1]. Note that $\bar{\Phi}\left(I-\bar{T}\right)^{-1}$ has a dominant eigenvalue equal to 1. If we expand both of T and Φ about $\overrightarrow{x}=\overrightarrow{0}$, we can rewrite equation (3.3) as follows:

$$\overrightarrow{x}(s)-\int_{\Omega}T\left(s,\nu,\overrightarrow{0}\right)\overrightarrow{x}(\nu)\,d\nu=$$

$$n\int_{\Omega}\Phi\left(s,\nu,\overrightarrow{0}\right)\overrightarrow{x}(\nu)\,d\nu+h(n,\overrightarrow{x}(\nu)), \tag{3.4}$$

where $h\left(n,\overrightarrow{x}\right)\approxeq o\left(\|x\|\right)$ for $\overrightarrow{x}\approx\overrightarrow{0}$ and uniformly on bounded n intervals. Here, $\|\overrightarrow{x}\|$ is given with respect to $\mathrm{L}_2^m\left(\Omega\right)$ norm. Let $\Phi'\left(\overrightarrow{0}\right)\left(\overrightarrow{x}\right)=\int_\Omega\Phi\left(s,\nu,\overrightarrow{0}\right)\overrightarrow{x}\left(\nu\right)d\nu$, then equation (3.4) may be written in the following equivalent form:

$$\overrightarrow{x}\left(s\right)=n\int_\Omega r\left(s,u\right)\Phi'\left(\overrightarrow{0}\right)\left(\overrightarrow{x}\left(u\right)\right)du+\int_\Omega r\left(s,u\right)h\left(n,\overrightarrow{x}\left(u\right)\right)du,$$

or

$$\overrightarrow{x}=nL\left(\overrightarrow{x}\right)+H\left(n,\overrightarrow{x}\right), \tag{3.5}$$

where

$$L\left(\overrightarrow{x}\right)=\int_\Omega r\left(s,u\right)\Phi'\left(\overrightarrow{0}\right)\left(\overrightarrow{x}\right)du$$

$$H\left(n,\overrightarrow{x}\right)=\int_\Omega r\left(s,u\right)h\left(n,\overrightarrow{x}\right)du.$$

The nonlinear eigenvalue problem (3.5) is of the form that studied by Rabinowitz. Our goal is to verify that this equation satisfies all the conditions that allow us to use the Rabinowitz Theorems stated in section 2. To this end, we mention some definitions and facts: A kernel of an integral operator is said to be *admissible* if it generates a compact linear operator. A nonnegative admissible kernel $k\left(s,t\right)$ is said to be *of positive type* if for each nonnegative continuous function $\phi\left(s\right)$, not identically zero, there exist an iterated kernel $k^{(n)}\left(s,t\right)$ such that $\int_G k^{(n)}\left(s,t\right)\phi\left(t\right)dt>0$, $\left(s\in G\right)$. Here, $k^{(n)}$ is defined as

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

where t_1,...,t_{p-1} are from G. A sufficient condition for the kernel $k\left(s,t\right)$ to be of positive type is that $k^{(n)}\left(s,s\right)>0$; for some $n\geq 1$. So, every Fredholm linear operator with positive kernel is of positive type. The nonlinear operator $A:L_2\left(\Omega\right)\to L_2\left(\Omega\right)$ is *of Hammerstein type* if it has the form

$$A\left(x\left(v\right)\right)=\int_\Omega k\left(u,v\right)f\left(x\left(v\right),v\right)dv,$$

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 $|f(x,v)| \le a(v) + b|x|$ 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. These facts can be found in Krasnoselśkii [12]. We conclude that $q(x) = F(x)\,x$, $x \in L_2(\Omega)$ is bounded and continuous operator, whenever $|f(x,v)| \le C$, C is a constant, $f : R \times \Omega \to R$ is continuous, and for $\Omega \subseteq R^n$ is compact.

We are interested in studying the dynamical system (3.2), of our model, under the following assumptions:

I) The functions $f_{ij} : R_+^m \times \Omega \to R_+$ are bounded and C^k for some $k \ge 1$, and all i and j, where $1 \le i, j \le m$,

II) The functions $t_{ij} : R_+^m \times \Omega \to (0,1]$ are C^k for some $k \ge 1$, and all i and j, where $1 \le i, j \le m$,

III) The kernels k_{ij} and l_{ij} belong to the functional space $L_2(\Omega \times \Omega)$ for all i and j where $1 \le i, j \le m$,

IV) The kernels k_{ij} and l_{ij} are of positive type.

Lemma 3.1. *Given the assumptions I-IV, the matrix operators T and Φ are compact.*

Proof. Assumptions I and II above imply that f_{ij} and t_{ij} are bounded and continuous functions on $R_+^m \times \Omega$ for all i and j, where $1 \le i, j \le m$, so $t_{ij}\left(\overrightarrow{x}(v), v\right) x_j(v)$ and $f_{ij}\left(\overrightarrow{x}(v), v\right) x_j(v)$ are continuous and bounded operators on $L_2(\Omega)^m$ for all i and j where $1 \le i, j \le m$. Also, all of the kernels k_{ij} and l_{ij} satisfy the assumptions III and IV, so they generate compact linear operators. Thus, the operators from $L_2(\Omega)^m$ into $L_2(\Omega)$ that are defined by the integrals

$$\int_{\Omega} k_{ij}(s,\nu)\, t_{ij}\left(\overrightarrow{x}(\nu), \nu\right) x_j(\nu)\, d\nu$$

and

$$\int_{\Omega} l_{ij}\left(s,\nu\right) f_{ij}\left(\overrightarrow{x}\left(\nu\right),\nu\right) x_j\left(\nu\right) d\nu$$

are completely continuous operators of Hammerstein type for all i and j where $1 \leq i, j \leq m$. Therefore, for all i where $1 \leq i \leq m$ the operators

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

are completely continuous, and so the matrix operators

$$T = \int_{\Omega} T\left(s,v,\overrightarrow{x}\right)\overrightarrow{x}\left(v\right) dv \text{ and } \Phi = \int_{\Omega} \Phi\left(s,v,\overrightarrow{x}\right)\overrightarrow{x}\left(v\right) dv$$

are compact. The proof is complete. □

Lemma 3.2. *Given assumptions I-IV, equation (3.5) satisfies all the conditions of Theorem 2.2 of Rabinowitz.*

Proof. The linear operators $\bar{T}$, $\bar{\Phi}$ are completely continuous being they have positive kernels. Then from equation (3.4) we conclude that $h(n, \overrightarrow{x}(s))$ is completely continuous. Since $\bar{T}$ is completely continuous linear operator, the resolvent R is continuous. Thus $R\bar{\Phi}$ is compact because it is a composition of a continuous and a compact operator, and so $R\bar{\Phi}$ is completely continuous. Also, the operator $H\left(n, \overrightarrow{x}\right) = R\left(h(n, \overrightarrow{x})\right)$ is completely continuous because it is a composition of a continuous operator after a completely continuous operator. Moreover, $H \approx o\left(\|\overrightarrow{x}\|\right)$ is higher order than linear near $\overrightarrow{x} \approx \overrightarrow{0}$, uniformly on compact n intervals.

From our assumptions the kernels $T\left(s, v, \overrightarrow{0}\right)$ and $\Phi\left(s, v, \overrightarrow{0}\right)$ are positive, which implies that $\bar{T}$, R and $\bar{\Phi}$ are linear operators of positive type. Thus, $L = R\bar{\Phi}$ is compact and of positive type. By the classical theorem of Krein-Rutman, L has a positive, simple, strictly dominant eigenvalue μ associated with a nonnegative eigenfunction. Moreover, this eigenfunction is the only nonnegative eigenfunction of L. The proof is complete. □

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_+. Now, we state and prove our main result regarding the existence of nonzero equilibrium points for the autonomous equilibrium equation (3.3) utilizing the Rabinowitz Theory.

Theorem 3.3. *Consider the system of equations (3.1) under the assumptions (I-IV). There exist a continuum C_μ^+ of solution pairs $(n, \overrightarrow{x})$ such that $(\mu, \overrightarrow{0}) \in C_\mu^+$* and *$C_\mu^+ \setminus \{R \times K\} \neq \phi$ contains only positive equilibria. Furthermore, one of the following alternatives holds.*

1) $C_\mu^+ \setminus \left\{\left(\mu, \overrightarrow{0}\right)\right\}$ is unbounded in $R \times K_+$ and contains only positive solution pairs,

2) *C_μ^+ contains a nonextinction solution $\left(\mu^*, \overrightarrow{x}^*\right) \in R \times \partial K$, $\overrightarrow{x}^* \neq \overrightarrow{0}$.*

Proof. We have proved that under the assumptions (I-IV) the system of equations (3.1) satisfies all the conditions of Theorem 2.2. From alternative 1 of Theorem 2.2 we conclude that either C_μ^+ meets ∞ in K_+ or meets ∂G. But for C_μ^+ to meet ∂G, it must either contains $\left(\mu^*, \overrightarrow{x}^*\right) \in R \times K_+$, $\overrightarrow{x}^* \neq \overrightarrow{0}$, or $\left(\bar{\mu}, \overrightarrow{0}\right) \in R \times K_+$, where $\mu \neq \bar{\mu} \in r(L)$. Since the eigenfunction associated with the dominant eigenvalue of L is the only nonnegative eigenfunction of L, C_μ^+ cannot contain a point $\left(\bar{\mu}, \overrightarrow{0}\right)$ where $\bar{\mu} \neq 0$ is a characteristic value of L. Also this rules out alternative 2 of Theorem 2.2. The proof is complete. □

In fact, this theorem emphasizes the existence of a branch of positive equilibrium points that bifurcates from the point $\left(\mu, \overrightarrow{0}\right)$ and connects to the boundary of the positive cone of the eigenvalue problem given by equation (3.3) and this boundary cannot contain a point $\left(\bar{\mu}, \overrightarrow{0}\right)$ where $\bar{\mu} \neq 0$ is a characteristic value of L.

4. Concluding Remarks

We modeled the growth and dispersal of populations that are classified into different categories by individual characteristics such as body size, weight, age, etc. Our model is described by a system of integro-difference equations. We proved the existence of a branch of positive solutions that bifurcates from the extinction equilibrium at the critical value $n = 1$ of the inherent net reproductive number. The system of integro-difference equations involves nonlinear integral operators of Hammerstein's type acting from L_2^m to L_2^m. We remark that it is perhaps of mathematical interest to extend our study to integral operators acting from L_p^m to L_q^m, under suitable assumptions on p and q (see [12] or [13]). However, we know of no biological reasons to do this in the applications. Therefore, we restricted our attention to $p = q = 2$.

In our model we assumed that Ω is a compact subset of R^n that represents a homogeneous habitat. An interesting question is: how does the habitat affect the population dynamics? Since the habitat is the place where the population lives, many properties of the habitat can have a significant effect on the population, such as the habitat size, the habitat boundaries, the number of patches in the habitat and the amount of resources available. Many researchers studied such properties and their effect on population dynamics, including; Kierstead and Slobodkin [10], Hardin et al. [7, 8] and Van Kirk and Lewis [24]. A question we can address with our model is how the dynamics of a structured population can be affected by the properties of the habitat and whether results for non-structured populations remain valid for structured populations.

We assumed in our model that individuals are allowed to disperse within a habitat. It is also important to compare among different dispersal strategies and their effect on the survival of spatially heterogeneous populations. Dispersal strategies determine how individuals disperse within the habitat and where they settle at the end of the dispersal period. If we consider a heterogeneous habitat with locations that are unsuitable for survival then clearly all the dispersers who settle in such locations are lost. There are many dispersal strategies to consider, such as stay-in-place, go-everywhere-uniformly and diffusion-type strategies. The modeling of these different strategies in our model is by means of different dispersal kernels. Studies of dispersal strategies of non-structured populations appear in the work of Hardin et al. [8] and Leven, Cohen and Hastings [15] and others.

All the above questions can be addressed using our model. Moreover, since our model is structured we can relate these problems to specific life cycle characteristics, such as maturation periods, maximal body size etc.

Finally, we mention that in [1], we proved that the stability of the positive solutions near the extinction equilibrium is related to the direction of bifurcation in the sense that if the bifurcation is to the right, then these positive solutions are stable, and if it is to the left they are unstable. Also, we showed how the spectrum of positive branch can be studied by means of the inherent net reproductive number at equilibrium.

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