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Small Perturbations in Nonlinear Age-Structured Population Equations

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Foreword

A nonlinear age-structured population dynamic model described by partial integro-differential equation is considered, where the nonlinear term reflects the interaction among individuals. This non-linear model is interpreted as a perturbed one. An approximation method based on the ideas of averaging, of a slow time transformation and a power series expansion is suggested. The asymptotic properties of the approximate solution are analyzed. It is shown that the approximate solution remains close to the explicit one as $t \to \infty$.

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SMALL PERTURBATIONS IN NONLINEAR

AGE-STRUCTURED POPULATION EQUATIONS

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Key words: Population age structure -Nonlinear partial integro-differential equation - averaging - small perturbations.

Introduction

The continuous time evolution of age-structured populations is usually modeled by the partial differential equations with integral-type boundary conditions. Such linear models are relevant for many applications and have been much studied [Keyfitz 1977, McKendrick A.G. 1926, von Foerster 1959, Webb 1984]. The key parameter for such models is called "the net reproduction function". Its value determines the asymptotic properties of the solution. If this parameter is equal to one then in accordance to the well-known Sharpe-Lotka result [Sharpe and Lotka 1911, Samuelson 1976, Webb 1984] the equation has a stationary solution. Note that this stationary solution has an interesting property: it depends on the initial age distribution of the population. When net reproduction function is greater then 1 the linear model produces the infinite population growth.

More realistic models include the stabilizing factors in the right hand sides of population's equations. The populations' interaction or interaction of individuals within a population often play such a stabilizing role [Prüss 1981,1983]. Other effects of age-structured interaction among the individuals are related to studies of epidemic process [Andreasen 1989, Busenberg, Ianelli and Thieme 1991, Hoppensteadt 1974] and population cycles [Swick 1983, Frauenthal 1975]

The analysis of interacting age-structured populations leads to non-linear partial integro-differential equations with integral-type boundary conditions [Gurtin and MacCamy 1974, Murray 1989]. The existence and uniqueness of the solutions of such equations were proved under rather general conditions [Gurtin and MacCamy 1974, Webb 1985]. However, an explicit expression for the solutions was not found in the general case. Additional assumptions concerning the equation coefficients provide an ability to obtain the structure of the solutions and to analyze their properties [Gurtin and Levin 1982, Bulanzhe 1988]. Less restrictive conditions allow us to find the approximate solutions of this equation and to analyze their properties [Boulanger 1984].

When the interaction term is relatively small and the net reproduction function is close to one the resulting non-linear equation can be interpreted as an perturbed linear one. It seems intuitively plausible that the smaller the perturbation is, and the closer the net reproduction function is to one, the better solution of the linear equation resembles the solution of the perturbed one. It turns out that this assertion is true only on the finite time interval. Asymptotic properties of the perturbed equation are completely different from those of the linear one. This situation is important when constructing the approximate solution of the perturbed equation. It turns out that the approximation produced by the direct implementation of the small perturbation method [Cole and Kevorkian 1981] coincides with the solution of the linear equation and hence does not guarantee the appropriate asymptotic properties of the approximate solution.

In this paper the technique which provides "good" asymptotic properties of the approximate solution is developed. The approach combines three ideas widely used in the analysis of nonlinear dynamical systems: slow time transformation, averaging and power series expansion with respect to a small parameter. It turns out that the constructed approximate solution has one additional property. It coincides with the explicit solution of a special case of the general equation considered in [Bulanzhe, 1988]. The asymptotic properties of this solution are analyzed. It is shown that the approximate solution remains close to the solution of perturbed equation when $t \to \infty$.

Statement of the Problem

Let $\rho(a,t)$ be the function defined on $R^{+} \times R^{+}$ that satisfies the following equation

$$\frac{\partial \rho(a,t)}{\partial a} + \frac{\partial \rho(a,t)}{\partial t} = -\rho(a,t) \left[\mu(a) + \int_0^\infty \beta(a,s) \, \rho(s,t) \, ds \right], \tag{1}$$

with boundary condition

$$\rho(0,t) = \int_0^\infty b(a) \, \rho(a,t) \, da, \tag{2}$$

and initial condition

$$\rho(a,0) = \phi(a). \tag{3}$$

Equation (1) with the conditions (2) and (3) is the particular case of the population dynamic model with interaction of generations suggested by Gurtin and McCamy (Webb 1985).

Suppose that the coefficients of equation (1) have the following properties:

1) the functions $\mu = \mu(a)$, $\beta = \beta(a,s)$, $b = b(a)$, $\phi = \phi(a)$ are supposed to be non-negative, continuous;

2)there are $0 \leq a_1 \leq a_2 < \infty$ such that $b(a) \equiv 0$, for $a \notin (a_1, a_2)$;

3) $\lim\limits_{a \to \infty} \int\limits_0^a \mu(s)\, ds = \infty$,

4)there is $A>0$: $a \in [A,\infty[$ *and* $\phi(a)$ is a decreasing function.

Then its non-negative solution exists and is unique (Webb 1985). These conditions are supposed to hold in our case as well.

It was also shown that in the analysis of the asymptotic properties of the solution the constant R known as "net reproduction function" and defined as

$$R = \int\limits_0^\infty b(a)\, e^{-\int\limits_0^a \mu(s) ds}\, da \tag{4}$$

plays a crucial part. In particular,

$$\begin{aligned} &\textit{if} \quad R \leq 1, \textit{ then} \quad \rho(a,t) \to 0 \;, \quad \textit{as } t \to \infty, \\ &\textit{if} \quad R > 1 \;, \textit{ then} \quad \rho(a,t) \textit{ is bounded as } t \to \infty. \end{aligned} \tag{5}$$

The following assumptions will be used in the formulation of the main result of this paper.

(A) The function $\mu(a) = \mu_\varepsilon(a)$ can be represented as follows

$$\mu_\varepsilon(a) = \mu_0(a) - \varepsilon, \tag{6}$$

where $\mu_0(a)$ is such that

$$\int_0^\infty b(a) e^{-\int_0^a \mu_0(s)ds} = 1, \tag{7}$$

and ε is a positive number such that $\varepsilon \le \inf_{a \ge 0} \mu_0(a)$.

(B) The function $\beta(a,s) = \beta_\varepsilon(a,s)$ is proportional to ε:

$$\beta_\varepsilon(a,s) = \varepsilon\, \bar{\beta}(a,s), \tag{8}$$

where $\bar{\beta}(a,s)$ is some function on $R^+ \times R^+$.

The problem is to construct an approximate solution of problem (1),(2),(3), when the functions $\mu_\varepsilon(a)$ *and* $\beta_\varepsilon(a,s)$ undergo small perturbations given by (6) and (8). Note that these perturbations correspond to small changes of R in the neighborhood of $R=1$, *with* $R>1$.

Formulation of Results

Denote by $P(a,t)$ the unique solution of the following linear equation

$$\frac{\partial P(a,t)}{\partial a} + \frac{\partial P(a,t)}{\partial t} = -P(a,t) \quad \mu_0(a), \tag{9}$$

with boundary condition

$$P(0,t) = \int_0^\infty b(a) \; P(a,t) \; da, \tag{10}$$

and initial condition

$$P(a,0) = \phi(a). \tag{11}$$

Let $v_\varepsilon(a,\xi)$ be the solution of the equation

$$\frac{\partial v_\varepsilon(a,\xi)}{\partial a} + \varepsilon \frac{\partial v_\varepsilon(a,\xi)}{\partial t} = - \varepsilon \; v_\varepsilon(a,\xi) \; [\; -1 + p_0 \int_0^\infty \bar{\beta}(a,s) \; v_\varepsilon(s,\xi) \; l_0(s) \quad ds \;], \tag{12}$$

with boundary condition

$$v_\varepsilon(0,\xi) = \int_0^\infty b(a) \; l_0(a) \; v_\varepsilon(a,\xi) \; da, \tag{13}$$

and initial condition

$$v_\varepsilon(a,0) = 1, \tag{14}$$

where p_0 and $l_0(a)$ are given by

$$p_0 = \frac{\int_0^\infty b(s) l_0(s) \int_0^s \frac{\phi(u)}{l_0(u)} du ds}{\int_0^\infty s b(s) l_0(s) ds}, \tag{15}$$

$$l_0(a) = e^{-\int_0^a \mu_0(s) ds}.$$

One more assumption about the function $v_\varepsilon(a,t)$ will be used in formulating the main result:

(C) $v_\varepsilon(a,\xi)$ is an analytical function of ε uniformly in a,ξ.

Let us define the function $\rho_\varepsilon(a,t)$ as

$$\rho_\varepsilon(a,t) = \frac{P(a,t)}{e^{-\varepsilon t}(1-f)+f}, \tag{16}$$

with

$$f = p_0 \frac{\int_0^\infty b(a) l_0(a) \int_0^\infty \int_0^a \bar{\beta}(s,q) l_0(q)\, ds\, dq\, da}{\int_0^\infty s\, b(s)\, l_0(s)\, ds}, \tag{17}$$

where $P(a,t)$ is the solution of equation (9) with conditions (10),(11).

In the sequel we will denote $\rho(a,t)$ to be the solution of the perturbed equation (1) with conditions (2),(3) and assumptions (A),(B). Note that in this case $\rho(a,t)$ depends on ε.

The main result of this paper is stated as follows.

Theorem 1. Let $\rho(a,t)$ satisfy the equation (1) with conditions (2), (3), with assumptions (A), (B), (C) being true. Then for any $0<T<\infty$ and for any $\gamma>0$ there is an $\varepsilon_0(T)>0$ such that for any $\varepsilon<\varepsilon_0(T)$

$$\sup_{\substack{a\geq 0 \\ 0\leq t\leq T}} |\rho(a,t) - \rho_\varepsilon(a,t)| \leq \gamma. \tag{18}$$

An important property of the approximate solution $\rho_\varepsilon(a,t)$ is that it coincides with the explicit solution of equation (1) if the function $\beta(a,s)$ is of a special form. More exactly, let us consider the following equation

$$\frac{\partial x(a,t)}{\partial a} + \frac{\partial x(a,t)}{\partial t} = -x(a,t) \left[\mu_0(a) - \varepsilon + \varepsilon \int_0^\infty F(s,t)\, x(s,t)\, ds \right], \tag{19}$$

with boundary condition

$$x(0,t) = \int_0^\infty b(a)\; x(a,t)\; da, \tag{20}$$

and initial condition

$$x(a,0) = \phi(a), \tag{21}$$

where $F(s,t)$ is given by the formula

$$F(s,t) = p_0 \frac{b(s)\; l_0(s) \displaystyle\int_0^\infty\int_0^s \bar{\beta}(a,q)\; l_0(q)\; da\; dq}{P(a,t) \displaystyle\int_0^\infty a\; b(a)\; l_0(a)\; da}. \tag{22}$$

Here p_0 *and* $l_0(a)$ are given by (15).

The following statement holds:

Theorem 2. Under the conditions of the theorem 1 the function $\rho_\varepsilon(a,t)$ given by (16) is the explicit solution of the problem (19),(20),(21).

Remark. Note that because of the asymptotic property of the function $P(a,t)$

$$\lim_{t\to\infty} P(a,t) = p_0\; l_0(a) \tag{23}$$

(Webb,1984) we have

$$\lim_{t\to\infty} \rho_\varepsilon(a,t) = \hat{\rho}(a), \tag{24}$$

where

$$\hat{\rho}(a) = l_0(a) \frac{\int_0^\infty a\, b(a)\, l_0(a)\, da}{\int_0^\infty b(a)\, l_0(a) \int_0^\infty\int_0^a \bar{\beta}(s,p)\, ds dp da}. \tag{25}$$

Generally speaking, equality (24) does not guarantee that the function $\hat{\rho}(a)$ approximates $\rho(a)$, where $\rho(a) = \lim_{t\to\infty} \rho(a,t)$, since according to theorem 1 function $\rho_\varepsilon(a,t)$ approximates $\rho(a,t)$ only on the finite time interval [0,T]. The next statement asserts that this property of $\hat{\rho}(a)$ is true under some additional condition.

Theorem 3. Let $\rho(a)$ be the stationary solution of the equation (1) with the conditions (2) and suppose that the assumptions (A) and (B) hold and that $\rho(a)$ is an analytical function of ε uniformly in a. Then

$$\sup_{a\geq 0} \mid \rho(a) - \hat{\rho}(a) \mid \leq \varepsilon K_1, \tag{26}$$

where K_1 is a positive constant that does not depend on ε .

Proof of the Theorems

The proof of the theorem 1 is based on several auxiliary statements.

Lemma 1. Under the conditions of the theorem 1 the solution of problem (1),(2),(3) can be represented as follows:

$$\rho(a,t) \;=\; P(a,t)\; u_\varepsilon(a,t), \tag{27}$$

where $P(a,t)$ is the solution of problem (9),10),(11) and $u_\varepsilon(a,t)$ satisfy

the equation:

$$\frac{\partial u_\varepsilon(a,t)}{\partial a} + \frac{\partial u_\varepsilon(a,t)}{\partial t} = \varepsilon\; u_\varepsilon(a,t) \left(1 - \int_0^\infty \bar{\beta}(a,s)\; P(s,t)\; u_\varepsilon(s,t) ds \;] \right), \tag{28}$$

with boundary condition

$$u_\varepsilon(0,t) = \frac{1}{P(0,t)} \int_0^\infty b(a)\; P(a,t)\; u_\varepsilon(a,t)\; da, \tag{29}$$

and initial condition

$$u_\varepsilon(a,0) = 1. \tag{30}$$

Proof. Let $P(a,t)$ be the solution of problem (9),(10),(11). Substituting (27) into equation (1)-(3) one can easily find that $u_\varepsilon(a,t)$ satisfy (28)-(30). The proof of the Lemma 1 follows then from the uniqueness of the solutions of the equations (9)-(11) and (28)-(30).

Let $\bar{u}_\varepsilon(a,t)$ satisfy the equation with boundary condition

$$\bar{u}_\varepsilon(0,t) = \int_0^\infty b(a)\ l_0(a)\ \bar{u}_\varepsilon(a,t)\ da, \tag{32}$$

and initial condition

$$\bar{u}_\varepsilon(a,o) = 1. \tag{33}$$

The following statement shows that $\bar{u}_\varepsilon(a,t)$ can be considered as an approximation of $u_\varepsilon(a,t)$.

Lemma 2. Let $u_\varepsilon(a,t)$ be the solution of equation (28) with conditions (29),(30). Then for any $\delta > 0$, $\exists\ \hat{\varepsilon}_0 > 0$, such that for any $\varepsilon < \hat{\varepsilon}_0$

$$\sup_{\substack{a\geq 0 \\ 0\leq t\leq L/\varepsilon}} \left| u_\varepsilon(a,t) - \bar{u}_\varepsilon(a,t) \right| \leq \delta, \tag{34}$$

where L is some positive constant.

Proof. In accordance with the averaging method (see for ex. Mitropolski 1971) the estimate (34) follows from the fact that equation (31) with conditions (32), (33) is the averaged equation for equation (28) with conditions (29), (30) (where property (23) is taken into account).

Note that after changing the variable t to ξ, where $\xi = \varepsilon t$, and introducing the notation $v(a,\xi) = \bar{u}_\varepsilon(a,t)$ equation (31) with conditions (32),(33) is transformed into

$$\frac{\partial v(a,\xi)}{\partial a} + \varepsilon \frac{\partial v(a,\xi)}{\partial t} = \varepsilon\, v(a,\xi) \left(1 - p_0 \int_0^\infty \bar{\beta}(a,s)\, v(s,\xi)\, l_0(s)\, ds \right), \tag{35}$$

with conditions

$$v(0,\xi) = \int_0^\infty b(a)\, l_0(a)\, v(a,\xi)\, da, \tag{36}$$

and

$$v(a,0) = 1. \tag{37}$$

This equation plays a crucial part in the following statement.

Lemma 3. Let assumptions (A), (B) and (C) be true. Then there is a $v_0(\xi)$ such that

$$\sup_{\substack{a \ge 0 \\ 0 \le \xi \le L}} |\, v(a,\xi) - v_0(\xi)\, | \le \varepsilon K_2, \tag{38}$$

where

$$v_0(\xi) = \left[e^{-\xi} (1 - f) + f \right]^{-1}, \tag{39}$$

f is defined by (17) and K_2 does not depend on ε.

Proof of Lemma 3.

Note that property 4) for the function $\phi(a)$ implies

$$\sup_{\substack{0 \le a \le A \\ 0 \le t \le T}} \rho(a,t) = \sup_{\substack{a \ge 0 \\ 0 \le t \le T}} \rho(a,t).$$

By assumption (C), a solution of (35)-(37) may be represented in the power series form with respect to ε :

$$v(a,\xi) = \sum_{i=0}^{\infty} \varepsilon^i \; v_i(a,\xi). \tag{41}$$

Substituting (41) into (35), (36) and (37) we get the following equation for $v_0(a,\xi)$

$$\frac{\partial v_0(a,\xi)}{\partial a} = 0, \tag{42}$$

with boundary condition

$$v_0(0,\xi) = \int_0^{\infty} b(s) \; l_0(s) \; v_0(s,\xi) \; ds, \tag{43}$$

and initial condition

$$v_0(a,0) = 1. \tag{44}$$

Condition (42) together with the initial condition (44) yield

$$v_0(a,\xi) \equiv v_0(\xi), \qquad v_0(0) = 1, \tag{45}$$

and the boundary condition (43) holds for any such $v_0(\xi)$.

For $v_1(a,\xi)$ we have

$$\frac{\partial v_1(a,\xi)}{\partial a} + \frac{dv_0(a,\xi)}{d\xi} = v_0(\xi)\left[\, 1 - v_0(\xi)\, p_0 \int_0^\infty \bar{\beta}(a,s)\, l_0(s)\, ds \,\right], \tag{46}$$

with boundary condition

$$v_1(0,\xi) = \int_0^\infty b(a)\, l_0(a)\, v_1(a,\xi)\, da, \tag{47}$$

and initial condition

$$v_1(a,0) = 0. \tag{48}$$

After integrating this equation with respect to a we get

$$v_1(a,\xi) = v_1(0,\xi) - a\frac{dv_0(\xi)}{d\xi} + v_0(\xi)\, a - v_0^2(\xi)\, p_0 \int_0^\infty\!\!\int_0^s \bar{\beta}(\sigma,s) l_0(s)\, d\sigma\, ds. \tag{49}$$

After a substitution of the result into the boundary condition (47) we have

$$\frac{dv_0(\xi)}{d\xi} = v_0(\xi)\big(1 - v_0(\xi)\, f\big), \tag{50}$$

where

$$f = p_0 \frac{\int\limits_0^\infty b(a) l_0(a) \int\limits_0^\infty \int\limits_0^a \bar{\beta}(s,q) l_0(q)\, ds\, dq\, da}{\int\limits_0^\infty s\ b(s)\ l_0(s)\ ds}. \tag{51}$$

The solution of this equation is

$$v_0(\xi) = \left(e^{-\xi}\,(1 - f) + f\,\right)^{-1}. \tag{52}$$

Proof of Theorem 1.

Let $\gamma>0$ be fixed. Using Lemma 1 and representation (16) for $\rho_\varepsilon(a,t)$ it is easy to get the following

$$\sup_{\substack{a \ge 0 \\ 0\le t\le T}} |\ \rho(a,t) - \rho_\varepsilon(a,t)\ | = \sup_{\substack{a \ge 0 \\ 0\le t\le T}} P(a,t)\ |\ u_\varepsilon(a,t) - v_0(\varepsilon t)\ | \le$$
$$\le \hat{P} \sup_{\substack{a \ge 0 \\ 0\le t\le T}} |\ u_\varepsilon(a,t) - \bar{u}_\varepsilon(a,t)\ | + |\ v_0(\varepsilon t) - \bar{u}_\varepsilon(a,t) |, \tag{53}$$

where $\hat{P} = \sup\limits_{\substack{a\ge0 \\ t\ge0}} P(a,t)$ and functions $u_\varepsilon(a,t)$, $\bar{u}_\varepsilon(a,t)$ satisfy the equations (28)-(30), (31)-

(33) respectively, $v_0(\varepsilon t)$ being given by (39).

According to Lemma 2 for any $\delta>0$ $\exists$ $\hat{\varepsilon}_0>0$ *such that, for any* $\varepsilon<\hat{\varepsilon}_0$ we have

$$\sup_{\substack{a \geq 0 \\ 0 \leq t \leq L/\varepsilon}} = \mid u_\varepsilon(a,t) - \bar{u}_\varepsilon(a,t) \mid \leq \delta.$$

Let us choose $\tilde{\varepsilon}_0(T)$ such that for $\varepsilon<\tilde{\varepsilon}_0(T) \wedge \hat{\varepsilon}_0$, $L/\varepsilon \geq T$. Then for such ε

$$\sup_{\substack{a \geq 0 \\ 0 \leq t \leq T}} = \mid u_\varepsilon(a,t) - \bar{u}_\varepsilon(a,t) \mid \leq \delta \tag{54}$$

and in accordance with Lemma 3:

$$\sup_{\substack{a \geq 0 \\ 0 \leq t \leq T}} \mid v_\varepsilon(a,\varepsilon t) - v_0(\varepsilon t) \mid \leq \varepsilon K_2. \tag{55}$$

Finally we obtain

$$\sup_{\substack{a \geq 0 \\ 0 \leq t \leq T}} \mid \rho(a,t) - \rho_\varepsilon(a,t) \mid \leq (\varepsilon K_2 + \delta). \tag{56}$$

It is clear that for any fixed $\gamma>0$ there is $\bar{\varepsilon}_0(T)$ such that for $\varepsilon < \tilde{\varepsilon}_0(T) \wedge \hat{\varepsilon}_0 \wedge \bar{\varepsilon}_0(T)$ the right hand side of this inequality can be chosen less then γ.

To prove Theorem 1 is enough to define $\varepsilon_0(T) = \tilde{\varepsilon}_0(T) \wedge \hat{\varepsilon}_0 \wedge \bar{\varepsilon}_0(T)$.

Proof of Theorem 2.

Notice that the coefficient f in the expression (16) has the form

$$f = \int_0^\infty F(s,t)\ P(s,t)\ ds \tag{57}$$

and does not depend on t .

Substituting the expression (16) into equation (19) and taking into account conditions (20),(21), we come to an identity. Therefore the proof of the proposition follows from the uniqueness of the solution of equation (19).

Proof of Theorem 3.

Any stationary solution $\rho(a)$ of equation (1) with boundary condition (2) must satisfy the equation

$$\frac{d\rho(a)}{da} = - \rho(a) \left(\mu_0(a) - \varepsilon + \varepsilon \int_0^\infty \bar{\beta}(a,s) \rho(s)\, ds \right), \tag{58}$$

with boundary condition

$$\rho(0) = \int_0^\infty b(s) \rho(s) ds. \tag{59}$$

We will seek for the solution of this equation in the form of a power series with respect to ε :

$$\rho(a) = \sum_{i=0}^\infty \varepsilon^i \rho_i(a). \tag{60}$$

After substituting (60) into (58),(59) we have for $\rho_0(a)$

$$\frac{d\rho_0(a)}{da} = \rho_0(a)\mu_0(a),$$
$$\rho_0(0) = \int_0^\infty b(s) \quad \rho_0(s) \quad ds, \tag{61}$$

from which results

$$\rho_0(a) = \rho_0(0) \quad l_0(a), \qquad l_0(a) = e^{-\int_0^a \mu_0(s) \, ds}. \tag{62}$$

In order to find $\rho_0(0)$ let us write the equation for $\rho_1(a)$:

$$\frac{d\rho_1(a)}{da} = -\rho_1(a) \quad \mu_0(a) + \rho_0(0) \, l_0(a) \left(1 - \rho_0(0) \int_0^\infty \bar{\beta}(a,s) \, l_0(s) \, ds \right), \tag{63}$$

with boundary condition

$$\rho_1(0) = \int_0^\infty b(s) \quad \rho_1(s) ds. \tag{64}$$

Let us introduce the new function

$$y(a) = \rho_1(a) \quad l_0^{-1}(a), \tag{65}$$

for which we have

$$\frac{dy(a)}{da} = \rho_0(0)\left(1 - \rho_0(0)\int_0^\infty \bar{\beta}(a,s)\, l_0(s)\, ds\right). \tag{66}$$

$$y(0) = \int_0^\infty b(s)\, l_0(s)\, y(s) ds. \tag{67}$$

After the integration of this equation and substituting the result in (67) we get the following expression for the constant $\rho_0(0)$

$$\rho_0(0) = \frac{\int_0^\infty a\, b(a)\, l_0(a)\, da}{\int_0^\infty b(a)\, l_0(a) \int_0^\infty\int_0^a \bar{\beta}(s,p)\, dsdpda}. \tag{68}$$

A representation for $\rho_0(a)$ then follows from (68) and (62) and coincides with the expression (25) for $\hat{\rho}(a)$.

Discussion

1.Equation (1) as a perturbed linear equation

The equation (1) with conditions (1), (3) and assumptions (A), (B) can be considered as a perturbation of the linear population equation (9) with the conditions (10), (11). It is interesting to compare the dynamics of these two equations. In order to do that let us consider the following example.

Assume that

$$\bar{\beta}(a,s) = \bar{\beta}(s) \qquad for \quad all \quad a \geq 0, \tag{69}$$

and consider the equation

$$\frac{\partial x(a,t)}{\partial a} + \frac{\partial x(a,t)}{\partial t} = -x(a,t)\ [\ \mu_0(a) - \varepsilon + \varepsilon \int_0^\infty \bar{\beta}(s)\ x(s,t)\ ds\ ],$$

$$x(0,t) = \int_0^\infty b(s) \quad x(s,t)\ ds, \tag{70}$$

$$x(a,0) = \phi(a).$$

The solution of this equation has the form [Bulanzhe, 1988]

$$x(a,t) = P(a,t) \quad u_\varepsilon(t), \tag{71}$$

where $P(a,t)$ is the solution of (9),(11),(13) and $u_\varepsilon(t)$ satisfy the following equation

$$\frac{du_\varepsilon(t)}{dt} = \varepsilon u_\varepsilon(t)\ \left[1 - f(t) u_\varepsilon(t)\right], \quad u_\varepsilon(0) = 1,$$

$$where \qquad f(t) = \int_0^\infty \bar{\beta}(s)\ P(s,t)\ ds. \tag{72}$$

The solution of equation (72) is the following

$$u_\varepsilon(t) = \left(e^{-\varepsilon t} + \varepsilon \int_0^t f(s)\, e^{\varepsilon(s-t)} ds \right)^{-1} \tag{73}$$

with the property

$$\lim_{t\to\infty} u_\varepsilon(t) = \left(p_0 \int_0^\infty \bar{\beta}(s)\, l_0(s)\, ds \right)^{-1} . \tag{74}$$

Finally from (71) we have

$$\lim_{t\to\infty} x(a,t) = \frac{l_0(a)}{\int_0^\infty \bar{\beta}(s)\, l_0(s)\, ds}, \tag{75}$$

where p_0 *and* $l_0(a)$ are given by (15).

The same result can be obtained by solving the corresponding stationary equation for $x(a)$.

Thus the stationary solution $x(a)$ does not depend on the initial condition $\phi(a)$. This result is quite different from the stationary solution in the linear case which depends on the initial distribution $\phi(a)$. This example shows how sensitive is the solution of this equation to small perturbations of parameters in the neighborhood of the bifurcation point $R=1$.

2. The weakness of the direct power series expansion

At first glance it would be natural to construct the solution of the equation (1) directly in a form of power series with respect to ε:

$$\rho(a,t) = \sum_{i=0}^{\infty} \varepsilon^i \rho_i(a,t).$$

In this case the zero order approximation coincides with the solution of the linear equation (9)-(11):

$$\rho_0(a,t) \equiv P(a,t) \tag{77}$$

with the asymptotic property (23).

However, in accordance with theorem 3 the zero order approximation of the stationary solution of the equation (1) does not depend on $\phi(a)$. Thus this zero order approximation is close to the solution of equation (1) only on a finite time interval [0,T].

3. The idea of averaging and slow time

It would be nice to find an approximate solution of equation (1), which remains close to the solution of this equation for $t \to \infty$ as well. The idea of constructing such an approximation may be illustrated by analyzing the property (71) of the solution of a more simple equation (70). It turns out that the function $u_\varepsilon(t)$ in the representation (71) is a slowly changing function of time. This property easily follows from the structure of equation (72) for $u_\varepsilon(t)$ which allows the transformation of time $\xi = \varepsilon t$ and allows to establish that $u_\varepsilon(t) = v_\varepsilon(\xi)$. The representation (71) shows that the vital characteristics of the population, such as mortality rate $\mu_0(s)$ and birth rate $b(s)$ are responsible for the changes of the "fast" component - $P(a,t)$ (which coincides with the non-perturbed system) to $P(a,\infty)$ defined by (23). However, the interaction term $\bar{\beta}(s)$ determines the "slow" evolution of $V_\varepsilon(\xi)$ and of the population as a whole to the new stationary state $\rho(a,\infty)$. This last property generates the hope that if the interaction term $\bar{\beta}(a,s)$ will be presented in the approximate solution, then "good" asymptotic properties will be guaranteed.

Note also that the structure of the equation (72) for $u_\varepsilon(t)$ allows us to use the averaging method to get the averaged equation for the approximate solution $\bar{u}_\varepsilon(t)$. There is no need to implement this approach to the one-dimensional case of the equation (68), where the explicit solution can be easily found (formula (73)). It makes sense to do, however, in the multi-dimensional case since the resulting averaged equation is simpler: its coefficients do not depend on time.

It turns out that the averaging procedure plays the crucial part in the construction of an approximate solution in the case of the general equation (1). To understand this better let us note that in accordance with lemma 1 the solution of the equation (1) has the same structure (27) as the solution of the equation (70). The function $P(a,t)$ is also the same as in (71). However, $u_\varepsilon(a,t)$ satisfies not an ordinary but the partial differential equation (28) whose coefficients depend on $P(a,t)$. Since the solution of this equation is unknown, one would like to find an approximation for it. It would be nice to find an approximation $\hat{u}_\varepsilon(a,t)$ which "captures" the important property of the solution, which we mentioned in the case of the simpler equation (70): the evolution of the "slowly" changing component $\hat{u}_\varepsilon(a,t)$ should be determined by the interaction term $\bar{\beta}(a,s)$. In this case there is hope that the respective approximate solution $\rho_\varepsilon(a,t) = P(a,t)\ \hat{u}_\varepsilon(a,t)$ of the equation (1) will remain close to its exact solution when $t \to \infty$.

So what kind of procedure should we follow in order to construct the approximate solution of the equation (28)?

The idea to seek the solution of this equation in power series form with respect to ε does not lead to the expected result since in this case the zero order approximation of $u_\varepsilon(a,t)$ is constant, and the asymptotic properties of the approximate solution of the equation (1) will coincide with the asymptotic properties of $P(a,t)$.

The idea to introduce the "slow time" transformation $\xi=\varepsilon t$ in the equation (28) and then to seek its solution in the power series form with respect to ε fails as well, since the coefficients of the equation (28) become the unknown functions of ε (through $P(a,\xi/\varepsilon)$).

If, however, we implement the averaging procedure to the equation (28) and then use the power series expansion of the solution of the averaged equation (35) with "slow time" ξ then the zero order approximation of the solution of this equation "captures" the interaction term $\bar{\beta}(a,s)$ (see (39)), which is crucial for the asymptotic properties of the approximate solution $\rho_\varepsilon(a,t)$ formulated in the theorem 3. This construction procedure for the approximate solution allows also to avoid its dependency on the initial distribution $\phi(a)$.

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REFERENCES

Andreason V.(1989) Disease regulation of age-structured host populations. Theoretic.Popul.Biology,36,pp.214-239.

Boulanger E.N. and A.I.Yashin (1991). Non-linear effects in population dynamics: Interaction of generations. WP-CPOP. University of Minnesota.

Boulanger E.N.(1984).Investigation of the forest-pest dynamics development model.Vestnik Moscovskogo Universiteta,Vol.15,No.4.pp.34-46.(In Russian).

Bulanzhe E.N.(1988). Qualitative analysis of a dynamic model of a resource-limited age distribution. U.S.S.R. Comput. Maths. Math. Phys., Vol.28,No.4,pp.151-158.

Busenberg S.N., Iannelli M. and Thieme H.R.(1991).Global behavior of an age-structured epidemic model.SIAM J.Math.Anal.,Vol.4,pp.1065-1080.

Cole J.D. and Kevorian J.(1981)Perturbation methods in applied Mathematics. Springer-Verlag.N.Y.

Frauenthal J.C.(1975). A dynamic model for human population growth.Theoretic Population Biology,8,pp.64-74.

Frauenthal J.C. and Swick K.E.(1983). Limit cycle oscillations of the human Population. Demography,Vol.20,N.3.pp.285-298.

Gurtin M.E. and Levine D.S.(1982). On populations that cannibalize their young. SIAM J.Appl.Math.,Vol.42,No.1,pp.94-108.

Gurtin,M.E.,MacCamy R.C.(1974). Nonlinear age-dependent population dynamics. Arch.Rat.Mech.Anal.54,pp.281-300.

Hoppenstead F.(1974).An age-dependent epidemic model.J.Franklin Inst.197,pp.325-333.

Keyfitz N.(1977) Applied mathematical demography.N.Y.,Springer.

Mitropolski Yu.A.(1971) Averaging method in nonlinear mechanics, Kiev, Naukova Dumka,(in Russian)

Murray J.D. (1989) Mathematical biology.London, Springer-Verlag.

Prüss J.(1981) Equilibrium solutions of age-specific population dynamics of several species. J.Math.Biol.11,pp.65-84.

Prüss J.(1983).On the qualitative behavior of populations with age-spesific interaction.Internat.J.Comput.Math. Appl.9.,No.3,pp.327-339.

Sharpe F.R. and Lotka A.J.(1911) A problem in age distribution. Phil.Mag.21,pp.435-438.

Swick K.E.(1981). A nonlinear model for human population dynamics.SIAM J.Appl.Math.,Vol.40, No2,pp.266-278.

Samuelson P.A.(1976).Resolving a historical confusion in population analisis. Human Biol.48,pp.559-580.

Von Foerster H.(1959). Some remark on changing populations,The Kinetics of Cellure Proliferations, Grune and Stratton.

Webb, G.F.(1984) A semigroup proof of the Sharp-Lotka theorem. Lecture Notes in Mathematics.1076,pp.254-268.

Webb, G.F.(1985) Theory of Nonlinear Age-Dependent Population Dynamics. N.Y.Marcel Dekker, Inc.