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Boulanger, E.N. and Yashin, A.I.

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E.N. Boulanger
A.I. Yashin

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IIASA International Institute for Applied Systems Analysis ◻ A-2361 Laxenburg ◻ Austria
Telephone: +43 2236 715210 ◻ Telex: 079 137 iiasa a ◻ Telefax: +43 2236 71313

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Abstract

The paper gives a survey of some recent results and ideas in the area of sustained oscillations in nonlinear age-structured population equations. The application of one parameter Hopf bifurcation technique to nonlinear integral Volterra equation is demonstrated. Two parameters Lyapunov and Schmidt bifurcation method are implemented to both nonlinear integral equation and nonlinear McKendrik-von-Foerster equation. The direction of bifurcation and oscillation period is calculated for two examples.

SELF-REGULATION IN AGE-STRUCTURED POPULATIONS

E.N. Boulanger Institute for Control Sciences, Russian Academy of Sciences, Moscow
A.I. Yashin Institute for Control Sciences, Russian Academy of Sciences, Moscow and Odense University, Odense, Denmark

Introduction

The behavior of some populations reveals the signs of some unknown forces acting periodically. The theoretical explanations of the observed oscillations are discussed in the numerous literature. Traditionally most of the authors refer to either the periodic external influence like seasonable changes of the environment (see, for example, Oster and Takahashi (1974) or to the populations interaction like in predator-prey models (see, for example, Pielou (1977)).

Several recent studies are focused on the oscillations produced by the populations self-regulatory mechanisms. For the human population the nature of these mechanisms appear in the fact that the size of the cohorts influences its living standards, which in their turn, influence the cohort's future fertility rates. As a result of this cohort-controlled mechanism the women born in a large cohort tend to produce fewer children than women born in a small cohort. This idea, suggested by Easterlin (1961), was studied extensively in subsequent papers (see, for example, Lee (1974), Frauenthal (1975), Easterlin (1980), Smith (1981), Swick (1981, 1985), Alburg (1983), Frauental and Swick (1983), Wachter and Lee (1989), Feichtinger and Sorger (1990), Wachter (1991a, 1991b).

Mathematically this idea is expressed in the fact that the net maternity function in the population equation becomes density dependent, so the equation itself becomes nonlinear.

The nonlinearity of the population equations does not guarantee the existence of the periodic solutions. Sustained oscillations may occur only if some special conditions are satisfied. In particular, the presence of a delay in the response to changes in population density function is the crucial feature for the existence of sustained oscillations in populations characteristics (Cushing 1983).

It is clear that a sustained cyclic behavior is not possible if the parameters of the equation provide the existence and the uniqueness of stable steady state solution. The oscillations may occur only if the situation becomes unstable, i.e. when the parameter values cross the boundary of some set in the parameter space within which the stable stationary state is guaranteed. Perhaps the simplest way to check the existence of nonlinear cycles is to vary one parameter beyond some threshold value and to analyze the properties of the solution. The approach based on this idea is known as the Hopf bifurcation technique (see, for example, Marsden and McCraken 1976, Hale and Oliveira 1980).

The possibility of oscillations in nonlinear demographic models was discussed by Keyfitz (1968). Lee (1974) suggested several discrete time cohort controlled population models that produce oscillations in population size. Frauental (1975) suggested and analyzed a particular mathematical model of nonlinear maternity function and calculated for this example the period of oscillations and the threshold parameter value. Swick (1981), (1985) generalized this approach to broader class of maternity functions and suggested to use the one-parameter Hopf bifurcation technique to study the problem of existence of sustained cycles as the solutions of nonlinear integral Volterra equations for the numbers of births. Frauenthal and Swick (1983) calculated the parameter estimates for the cohort feedback model using U.S. data. Wachter and Lee (1989) criticized their approach and discussed the applicability of several nonlinear population models to demographic data. Wachter (1991a, 1991b) proved that strictly positive lower bound on age of procreation plays an important part in the question of existence of nonlinear cycles in population models and discussed the applicability of Lee-Easterlin models for U.S. data. The ecological aspects of self-regulation mechanisms are discussed by Oster (1976), Botsford and Wichham (1978), Roughgarden, Iwasa and Baxter (1985), Gurtin and Levine (1982), Levin and Gurtin (1981).

In most of these papers the population dynamics is described by nonlinear integral Volterra equations. The properties of their solutions depend on the values of the parameters which specify the nonlinear feedback mechanism and the vital characteristics of the population. When there is only one parameter the Hopf bifurcation technique is the appropriate tool to study the existence conditions for nonlinear oscillations. Note that the period of nonlinear oscillations is not constant: it changes when the parameter changes beyond some threshold level. A more detailed specification of the changes of the period of oscillations as a function of small parameter within the Hopf bifurcation technique requires the additional efforts. This problem can be easily solved, however, in the framework of Lyapunov and Schmidt multiparameter bifurcation analysis (see, for example, Vainberg and Trenogin 1962). The respective techniques for population equations were developed by Cushing in a series of papers (Cushing 1978, 1979, 1983). His results determine the existence of both the nonlinear cycles as a solution of population equations and the direction in the parameter space along which the period of oscillations is constant.

Using this methodology Tuljapurkar (1987), (1991) elaborated a tool whereby the direction of bifurcation can be specified in terms of characteristics of the nonlinear population model. He also obtained the stability conditions for the periodic solution of population equations. By this method the nonlinearities in the population equations can be translated explicitly into features of population dynamics. One can use this method either to test the basic assumptions by confronting theoretical results with data or to infer from data the features of the feedback mechanism.

The purpose of this paper is to give a survey of recent results in the area of periodic solutions of the nonlinear population equations with the age structure. We start with the one parameter Hopf bifurcation result implemented to population equation by Swick (1981), and demonstrate the Frauenthal's (1975) method for the calculation of the oscillation's period and the threshold parameter value. Then we discuss Cushing's (1978) two-parameters bifurcation result concerning the existence of nonlinear oscillations as the solutions of nonlinear integral Volterra equations. Such equations describe the dynamics of the number of births in the population with the density dependent vital rates. After that the Tuljapurkar (1987) result which specifies the direction of bifurcation for such equations is formulated and discussed. Two examples of typical calculations are also presented.

When nonlinear feedback mechanisms appear in both mortality and fertility coefficients, the population evolves in accordance with the nonlinear McKendrik equation with nonlinear boundary condition. Following Tuljapurkar we describe the method that allows the calculation of the direction of bifurcation and specify the stability conditions. This approach uses the result of Cushing (1983), concerning the existence of nonlinear cycles in the solutions of integro-differential equations.

Despite the fact that all results which we discuss here have the precise mathematical formulation, we focus most of our attention on substantive issues sometimes sacrificing mathematical accuracy to the benefits of simplicity.

Nonlinear Integral Volterra Equation for the Number of Birth

Let us consider the following nonlinear Volterra integral equation for the number of births in the population

$$B(t) = \int_0^{\infty} \phi(s, B_0^{t-s})\, B(t-s)\, ds, \qquad (1)$$

here we use the notation for the birth trajectory on the interval .

One Parameter Hopf Bifurcation

Let us assume that density dependent net maternity function may be represented as follows

(2)

where nonnegative functions and .

So the equation (1) may be written as follows

$$B(t) = \int_0^{\infty} \phi(s) R_0(B(t-s)) B(t-s)\, ds. \qquad (3)$$

The Easterlin's hypothesis will be satisfied if $R_0(B)$ is a decreasing function of B. Let $B_0 > 0$ be an equilibrium birth level. It is clear that $R_0(B_0) = 1$. Expanding $R_0(B)B$ about B_0, we get

$$R_0(B)B = B_0 + (1-r)(B - B_0) + g(B - B_0),$$

where $r = -B_0 R_0'(B_0)$ and $g(0) = g'(0) = 0$.

Setting $X = B - B_0$ the equation (3) can be rewritten in the form

$$X(t) = (1-r)\int_0^\infty \phi(s) X(t-s)\, ds + \int_0^\infty \phi(s) g(X(t-s))\, ds. \qquad \textbf{(5)}$$

The following statement establishes the stability conditions of B_0.

Theorem 1 (Swick 1981). If all roots of the equation

$$\int_0^\infty \phi(s) e^{-\alpha s} ds = \frac{1}{1-r} \qquad \textbf{(6)}$$

have negative real parts, then B_0 is asymptotically stable.

If the time independent solution B_0 is unstable the following theorem gives the conditions at which B_0 bifurcates into periodic solution.

Theorem 2 (Swick 1981). Suppose that for $r=r_0$ equation (6) has the pure imaginary roots $\pm\omega_0 i = \pm\dfrac{2\pi}{p_0}$, $p_0 > 0$ and $n\omega_0 i$ is not a root of (6) for $n \neq \pm 1$ and

$$C_a(\omega_0) \triangleq \int_0^\infty s\phi(s) \cos(\omega_0 s)\, ds \neq 0.$$

Then B_0 bifurcates at $r=r_0$ to a periodic solution of (1) with period near p_0.

The proof of this theorem follows easily from the general Hopf bifurcation result for functional equations proved by Hale and Oliveira (1980). In accordance with this theorem one should check that

$$Re \frac{\partial\alpha}{\partial r}\Big|_{\alpha = i\omega_0} \neq 0,$$

where α is a root of the characteristic equation (6). Differentiating both parts of (6) with respect to r we get

$$-\int_0^\infty se^{-\alpha s}\phi s\, ds\, \frac{\partial\alpha}{\partial r} = \frac{1}{(1-r)^2}.$$

So for $\alpha = i\omega_0$

$$-(C_a(\omega_0) + iS_a(\omega_0))\frac{\partial\alpha}{\partial r}\Big|_{\alpha=i\omega_0} = \frac{1}{(1-r)_2}$$

or

$$-\left(C_a^2(\omega_0) + S_a^2(\omega_0)\right)\frac{\partial\alpha}{\partial r}\Big|_{\alpha=i\omega_0} = \frac{C_a(\omega_0) - iS_a(\omega_0)}{(1-r)^2}$$

where

$$C_a(\omega_0) = \int_0^\infty s\phi(s)\, e^{-\alpha s}\cos(\omega_0 s)\, ds, \qquad S_a(\omega_0) = \int_0^\infty s\phi(s)\, e^{-\alpha s}\sin(\omega_0 s)\, ds$$

and, hence

$$Re\frac{\partial\alpha}{\partial r}\Big|_{\alpha=i\omega_0} = -\frac{C_a(\omega_0)}{\left[C_a^2(\omega_0) + S_a^2(\omega_0)\right](1-r)^2}.$$

Thus the condition of theorem 2 is equivalent to the condition of Hopf theorem (see Hale and Oliveira 1980).

To apply theorem 2 one should find the threshold value of the parameter $r = r_0$ and frequency of oscillations ω_0 from the characteristic equation.

$$\int_0^\infty \phi(s)\, e^{-i\omega_0 s}\, ds = \frac{1}{1-r_0}. \tag{7}$$

Separating (7) into real and imaginary parts we get

$$\int_0^\infty \phi(s) \cos(\omega_0 s)\; ds = \frac{1}{1-r_0}, \tag{8}$$

$$\int_0^\infty \phi(s) \sin(\omega_0 s)\; ds = 0. \tag{9}$$

One can solve the equation (9) iteratively for ω_0 and substitute this value into (8) to find out r_0 directly.

Frauenthal (1975) suggested direct method of calculation starting from the characteristics equation (7). Using this approach let us define the mean age of childbearing τ in associated stationary population by the equality

$$\tau = \int_0^\infty s\phi(s)\; ds \tag{10}$$

Let us multiply both sides of (7) by $e^{-i\omega_0\tau}$ and expanding the exponent on the left hand side in a Taylor's series around τ. Retaining terms up to the second order in $(s-\tau)$ and separating real and imaginary parts we get

$$\omega_0 \int_0^\infty (s-\tau)\,\phi(s)\; ds \approx \frac{\sin(\omega_0\tau)}{1-r_0}, \tag{11}$$

$$\int_0^\infty \left(1 - \frac{\omega_0^2 (s-\tau)^2}{2}\right)\phi(s)\, ds \approx \frac{\cos(\omega_0\tau)}{1-r_0}. \tag{12}$$

It follows from (11), (10) and that $\sin(\omega_0\tau) = 0$. Hence, $\omega_0\tau = k\pi$, where k is an integer. Choosing $k=1$ we get

$$\omega_0 = \frac{\pi}{\tau}, \qquad or \qquad p_0 = \frac{2\pi}{\omega_0} = 2\tau. \tag{13}$$

Let us now solve (12). It follows from (13) that $\cos(\omega_0\tau) = -1$ and hence from (12)

$$r_0 = 1 + \frac{1}{[1-(\omega_0\sigma)^2/2]},$$

where σ^2 is the variance of the age of childbearing is defined as

$$\sigma^2 = \int_0^\infty (s-\tau)^2\phi(s)\, ds .$$

For U.S. 1966 fertility data it was found out that B_0 is asymptotically stable for $0<r<2.3$ and bifurcates to a periodic solution of (3) with period p_0 near 52.

Two parameters Bifurcation

In the case when the solution of the population equation depends on more then one parameters more general multiparameter bifurcation methods are needed. We will demonstrate the implementation of two parameters bifurcation technique to the population equation (1).

Assume that a time-independent solution of (1) to be written as $B_0(\mu)$, where μ is a parameter vector. The conditions of stability of this steady-state solution (see, for example Pruss 1981) define some area in the parameter space for which $B_0(\mu)$ is locally stable.

Let us write the equation for the deviation of $B(t,\mu)$ from the steady state solution of (1) $B_0(\mu)$ in the following form

$$X - M(X,\mu) = N(X,\mu)\,, \tag{14}$$

where $X(t,\mu = B(t,\mu) - B_0(\mu)$, M is linear operator and N is nonlinear operator. Note that the transition from (1) to (14) may require the Taylor expansion, thus we assume the appropriate smoothness of Φ.

Following Tuljapurkar (1987) let us assume that there are also threshold parameter values denoted by μ^* at which $B_0(\mu^*)$ looses stability. These values are characterized by the fact that the linearized equation for deviation $X(t,\mu^*)=B(t)-B_0(\mu^*)$ has a pair of periodic solutions. The main problem of interest is whether the nonlinear equation (1) has periodic solutions in the vicinity of μ^*. Let us select two parameters b_1 and b_2 from the parameter vector μ and introduce two values λ_1 and λ_2 by the equalities

$$\lambda_1=b_1-b_1^*; \qquad \lambda_2=b_2-b_2^*$$

here b_1^*, b_2^* corresponds the threshold values of b_1 and b_2.

Let us linearize the equation (14) with respect to λ_1, λ_2. As a result we have

$$X(t,\lambda)-L(X)=\lambda_1K_1(X)+\lambda_2K_2(X)+T(X,\lambda) \tag{15}$$

Here L, K_1, K_2, are linear operators which do not explicitly depend on λ, while T is a nonlinear operator which does. The following assumptions will be used in formulation of main result of this section.

Assumption H1. The linearized version of (15) around $B_0(\mu^*)$, is of the Volterra form

$$X(t)-L(X)=0 \tag{16}$$

with

$$L(X)(t)=\int_0^\infty k(s)X(t-s)\,ds. \tag{17}$$

where *k(s)* is some bounded function.

Assumption H2. Equation (16) has one pair of linearly independent periodic solutions of period $p_0=(2\pi/\omega_0)$ which may be chosen to be

$$Y_0(t)=\exp(i\omega_0 t), \quad i=\sqrt{-1}, \tag{18}$$

and a complex conjugate $\overline{Y}_0(t)$. It follows from (16) and (17) that ω_0 satisfies the characteristics equation

$$1=\int_0^\infty k(s)\exp(-i\omega_0 s). \tag{19}$$

Let B_{p_0} be a space of periodic functions $u(t)=u(t+p_0)$ with the norm

$$\|u\|=\sup_{0<t<p_0}|u(t)|. \tag{20}$$

Assumption H3. The operators $L,\ K_i,\ i=1,2,$ are bounded linear operators from B_{p_0} to B_{p_0}. $i=1,2.$

Assumption H4. Nonlinear operator $T(x,\lambda)$ is sufficiently Frechet differentiable in some open neighborhood of $x=\lambda=0$ to allow an expansion in the form

$$T(x,\lambda)=g_2(x,x)+\lambda_1 g_{21}(x,x)+\lambda_2 g_{22}(x,x)+g_3(x,x,x)+g_4(x,\lambda) \quad (21)$$

where the vector functions $g_2(X,Y)$, $g_{21}(X,Y)$, $g_{22}(X,Y)$, $g_3(X,Y,Z)$, are linear functions of each argument and also symmetric in these vectors, and $\|g_4\|$ being $O(|\lambda|^2\|x\|+|\lambda|\|x\|^2)$.

Define the Fourier coefficients of any function $u(t)\in B_{p_0}$ as

$$\hat{u}_j=(1/p_0)\int_0^{p_0} u(s)\exp(-ij\omega_0 s) \quad (22)$$

for all integers j. Two functions $r(t)$ and $s(t)$ in B_{p_0} will be called ortogonal if

$$(r(t)\,s(t))=\frac{1}{p_0}\int_0^{p_0} r(v)\,s(v)\,dv=0. \quad (23)$$

Define the Fourier coefficients

$$W_m=[\hat{K}_m(Y(t))]_1=P_m+iQ_m,\quad m=1,2 \quad (24)$$

where

$$Y(t)=Y_0(t)+\overline{Y}_0(t)$$

and K_m, $m=1,2$ are the linear operators on the right of (15).

The following statement addresses the existence of periodic solutions in (15) and , hence, in (1).

Theorem 3. (Cushing 1978). Assume *H1-H4* and also that

$$\delta = Im(\overline{W}_1, W_2) \neq 0 . \tag{26}$$

Then there is $\varepsilon_0 > 0$ such that for $|\varepsilon| < |\varepsilon_0|$ equation (15) has p_0-periodic solution of the form

$$X(t) = \varepsilon(Y(t) + Z(t))$$

with $\lambda = \lambda(\varepsilon)$, $\|Z\| = O(|\varepsilon|)$ as $\varepsilon \to 0$, and $Z(t)$ ortogonal to $Y(t)$.

The proof of this statement follows from the implicit function theorem that uses the condition (26).

Let us assume now that the conditions of the above theorem apply so the nonlinear model does have p_0-periodic solutions. Note that according to theorem 3 these solutions of amplitude ε exist near threshold at parameter values $b^* + \lambda_1(\varepsilon)$, $b^* + \lambda_2(\varepsilon)$ and have the same period as the linear model at the threshold. The differentiability assumed in assumption *H4* yields the possibility for nonlinear term *Z(t)* to be expanded, along with $\lambda(\varepsilon)$, as a series

$$\begin{aligned} Z(t) &= \varepsilon Z_1(t) + \varepsilon^2 Z_2(t) + o(\varepsilon^2) \\ \lambda_j(\varepsilon) &= \varepsilon\lambda_{j1} + \varepsilon^2\lambda_{j2} + o(\varepsilon), \quad j=1,2. \end{aligned} \tag{28}$$

The combination of the decomposition (28) and theorem 3 leads to the following statement.

Theorem 4. (Tuljapurkar 1987) Under the assumptions stated above

(a)

$$\lambda_{j1}=0, \quad j=1,2; \tag{29}$$

(*b*) The function $Z_1(t)$ in (28) satisfies the equation

$$Z_1(t)-L(Z_1)=g_2(Y,Y) \tag{30}$$

with g_2 as in (21).

(*c*) Defining the object

$$R(t)=2g_2(Y,Z_1)+g_3(Y,Y,Y), \tag{31}$$

the Fourier coefficient

$$\hat{R}(t)_1=A(t)+iB(t)$$

and the matrix

$$N=\begin{pmatrix} Q_2 & -Q_1 \\ -P_2 & P_1 \end{pmatrix} \tag{33}$$

the vector $(\lambda_{12},\lambda_{22})$ is given by the formula

$$(\lambda_{12},\lambda_{22})=-\left(\frac{1}{\delta}\right)(A,B)N \tag{34}$$

The proof of this theorem based on method of Lyapunov and Schmidt is given by Tuljapurkar (1987).

Let us demonstrate the applications of these results to some particular population models.

Self-Regulation of Fertility: Two Parameters Bifurcation

Let us consider the integral Volterra equation (1) with the density dependent maternity function in the form

$$\Phi(a, B_0^a) = R\psi(a)\, e^{-\mu a}\left(1-\int_0^\infty \psi(s)\, e^{-\mu s}\, B(t-s)\; ds\right) \tag{35}$$

Here $\psi(a)$ is a bounded function such that $\psi(a) > 0$ on age interval (a_1, a_2) and $\psi(a) \equiv 0$ if $a \notin (a_1, a_2)$.

Using (1) and (35) it is easy to find out the steady state solution

$$B_0 = \frac{R\psi_\mu - 1}{R\psi_\mu^2}, \tag{36}$$

where we use the notation

$$\psi_\mu = \int_0^\infty \psi(a)\, e^{-\mu a}\, da. \tag{37}$$

The deviation from the steady state solution of (1)

$$X(t) = B(t) - B_0 \tag{38}$$

satisfies the equation

Using (36) one can transform (39) to the

$$X(t) = R\int_0^\infty \psi(a)e^{-\mu a}X(t-a)\,da - 2R\psi_\mu B_0\int_0^\infty \psi(a)e^{-\mu a}X(t-a)\,da$$

$$-R\left(\int_0^\infty \psi(a)e^{-\mu a}X(t-a)\,da\right)^2 \tag{39}$$

$$X(t) - \left(\frac{2}{\psi_\mu} - R\right)\int_0^\infty \psi(a)e^{-\mu a}X(t-a)\,da = -R\left(\int_0^\infty \psi(a)e^{-\mu a}X(t-a)\,da\right)^2 \tag{40}$$

Following theorem 3 we should check the existence of only a pair of periodic solutions in the linear equation

$$X(t) - \left(\frac{2}{\psi_\mu} - R\right)\int_0^\infty \psi(a)e^{-\mu a}X(t-a)\,da = 0, \tag{41}$$

for some parameters values. After substitution

$$Y_0(t) = e^{i\omega_0 t}, \quad and \quad \overline{Y}_0(t) = e^{-i\omega_0 t}.$$

with arbitrary ω_0 in (41) we get the following equation for ω_0:

$$1 = \left(\frac{2}{\psi_0} - R_0\right)\int_0^\infty \psi(a)e^{-\mu_0 a}\,e^{-i\omega_0 a}da, \tag{42}$$

which is equivalent to the pair of algebraic equations

$$C(\omega_0) = \frac{\psi_0}{2-R_0\psi_0}, \quad S(\omega_0) = 0, \tag{43}$$

where

$$C(\omega_0) = \int_0^\infty \psi(a)\, e^{-\mu_0 a} \cos(\omega_0 a)\; da,$$
$$S(\omega_0) = \int_0^\infty \psi(a)\, e^{-\mu_0 a} \sin(\omega_0 a)\; da. \tag{44}$$

It is obviously from (42) that

$$2 - R_0\, \psi_0 \neq 0. \tag{45}$$

Note that the equations (43) define the values of μ_0, R_0 as functions of ω_0, i.e. the threshold values.

Let the parameters near threshold be

$$\mu = \mu_0 + \lambda_1, \qquad R = R_0 + \lambda_2, \tag{46}$$

then after substitution (46) in (40) we have the equation (15) with

$$L(X) = \left(\frac{2}{\psi_0} - R_0\right) L_0(X), \qquad L_0(X) = \int_0^\infty \psi(a)\, e^{-\mu_0 a} X(t-a)\; da, \tag{47}$$

$$K_1(X) = -\left(\frac{2}{\psi_0} - R_0\right) L_a(X) - \frac{2\psi_1}{\psi_0^2} L_0(X),$$
$$L_a(X) = \int_0^\infty a\psi(a)\, e^{-\mu_0 a} X(t-a)\; da, \tag{48}$$

$$K_2(X) = -L_0(X), \tag{49}$$

$$T(X,\lambda) = g_2(X,X) + \lambda_2 g_{22}(X,X) + g_4(X,\lambda) \tag{50}$$

$$g_2(X,X) = R_0\,(L_0(X))^2, \quad g_{22}(X,X) = -(L_0(X))^2 \tag{51}$$

Here

$$\psi_0 = \int_0^\infty \psi(a)\, e^{-\mu_0 a}\, da, \quad \psi_1 = \int_0^\infty a\psi(a)\, e^{-\mu_0 a}\, da, \tag{52}$$

In order to check the Cushing's nondegeneracy condition ($\delta(\overline{W}_1 W_2) \neq 0$) we need to calculate the real and imaginary parts of Fourier coefficients of $K_1(Y(t))$ and $K_2(Y(t))$:

$$W_m = \left[\hat{K}_m(Y)\right]_1 = P_m + i\,Q_m, \quad m=1,2. \tag{53}$$

Taking into account (48) and (49) we get:

$$P_1 = -\left(\frac{2}{\psi_0} - R_0\right) C_a(\omega_0) - \frac{2\psi_1}{\psi_0^2}\, C(\omega_0)\,,$$
$$Q_1 = \left(\frac{2}{\psi_0} - R_0\right) S_a(\omega_0)\,, \tag{54}$$

$$P_2 = C(\omega_0)\,, \quad Q_2 = 0, \tag{55}$$

where

$$S_a(\omega_0) = \int_0^\infty a\,\psi(a)\,e^{-\mu_0 a}\sin(\omega_0 a)\,da,$$

$$C_a(\omega_0) = \int_0^\infty a\,\psi(a)\,e^{-\mu_0 a}\cos(\omega_0 a)\,da \tag{56}$$

So $\delta = P_2 Q_1 = S_a(\omega_0)$. Thus the conditions of theorem 3 can be rewritten in the following form:

$$S_a(\omega_0) \neq 0, \quad C(\omega_0) = \frac{\psi_0}{2-R_0\psi_0}, \quad S(\omega_0) = 0$$

$$2 \neq R_0\,\psi_0, \qquad R_0\,\psi_0 > 1 \tag{57}$$

(see (43), (45)). The last inequality follows from the positiveness of the stationary state (see (36) with $\mu = \mu_0$, $R = R_0$).

According to theorem 3 for all such values μ_0, R_0 satisfying (57) the linearized equation (15) has a pair of p_0-periodic solutions and for some $\varepsilon>0$ small enough there exists $\lambda(\varepsilon)$ (the direction of the bifurcation) such that for $\mu=\mu_0+\lambda_1$ *and* $R=R_0+\lambda_2$ the nonlinear equation (42) also has p_0-periodic solution (with the same period p_0) of the form

$$X(t)=\varepsilon(Y(t)+Z(t)), \quad |Z|=o(\varepsilon) \quad as \quad \varepsilon\to 0. \tag{58}$$

Note that theorem 3 guarantees only the existence of the direction $\lambda(\varepsilon)$ in parameter space, which "saves" the period p_0 of the solution.

Using theorem 4 we can evaluate the nonlinear contribution on the bifurcation cycle

$$Z(t) = \varepsilon Z_1 + o(\varepsilon).$$

and calculate the direction $\lambda(\varepsilon)$ of parameters changes in the parameter space beyond the threshold level that guarantees the nonlinear oscillations with the same period.

Let us define

$$Y(t) = Y_0(t) + \overline{Y}_0(t), \tag{60}$$

i.e. $Y(t)$ is the solution of equation (41) with μ_0, R_0 and ω_0.

Taking into account that according to (47) and (51).

$$g_2(Y,Y) = -R_0\left[\int_0^\infty \psi(a)\,e^{-\mu_0 a}\,Y(t-a)\,da\right]^2 \tag{61}$$

the equation (29) for Z_1 is:

$$Z_1(t) - \left(\frac{2}{\psi_0}-R_0\right)\int_0^\infty \psi(a)\,e^{-\mu_0 a}\,Z_1(t-a)\,da = -R_0\left(\frac{\psi_0}{2-R_0\psi_0}\right)^2 Y^2(t), \tag{62}$$

where $Y(t)$ is from (60).

Let us solve this equation by using Fourier decomposition. As a result the solution of (62) has the form

$$Z_1(t) = \hat{Z}_{-2}\,e^{-2i\omega_0 t} + \hat{Z}_0 + \hat{Z}_2 e^{2i\omega_0 t} \tag{63}$$

with

$$\hat{Z}_0 = -\frac{2R_0\psi_0^2}{(R_0\psi_0-1)(2-R_0\psi_0)^2}; \qquad \hat{Z}_2 = -\frac{R_0\psi_0^2}{(2-R_0\psi_0)^2}D; \qquad \hat{Z}_{-2} = -\frac{R_0\psi_0^2}{(2-R_0\psi} \tag{64}$$

where

$$D^{-1} = 1 - \left(\frac{2}{\psi_0} - R_0\right)[C(2\omega_0) - iS(2\omega_0)]. \quad \textbf{(65)}$$

Now let us calculate the direction of bifurcation. In accordance with (31) we should calculate the Fourier coefficients of the function

$$R(t) = 2\, g_2(Y, Z_1) \quad \textbf{(66)}$$

Using (55), (61) and (63) we get

$$[\hat{R}(t)]_1 = A + i\, B \quad \textbf{(67)}$$

where

$$A = 2\frac{R_0^2 \psi_0^3}{(2-\psi_0 R_0)^3}\left(\frac{2\psi_0}{R_0\psi_0 - 1} + ReD\, C(2\omega_0) + ImD\, S(2\omega_0)\right)$$

$$B = 2\frac{R_0^2 \psi_0^3}{(2-R_0\psi_0)^3}\left(ImD\, C(\omega_0) - ReD\, S(2\omega_0)\right).$$

Thus from (34) we have

$$\lambda_{12} = \frac{1}{S_a(\omega_0)} BP_2, \quad \lambda_{22} = -\frac{1}{S_a(\omega_0)}(-AQ_1 + BP_1)$$

or

$$\lambda_{12} = \frac{C(\omega_0)}{S_a(\omega_0)} B; \quad \lambda_{22} = \frac{2-\psi_0 R_0}{\psi_0} A + B\left(\frac{C_a(\omega_0)}{S_a(\omega_0)}\frac{2-\psi_0 R_0}{\psi_0} + \frac{2\psi_1}{\psi_0(2-R_0\psi_0)}\frac{\vdots}{S_a(}\right.$$

(69)

One parameter Hopf bifurcation technique allows us to establish the existence conditions for sustained oscillations in nonlinear population equations. However, when the parameter varies beyond the threshold level the period of oscillations also changes. The calculations of these changes within Hopf bifurcation approach requires additional efforts. It turns out that one can solve this problem also using two parameters Lyapunov-Shmidt bifurcation technique (see, for example, Marsden and McCraken 1976). We will illustrate this idea using the same example of self-regulation in fertility function.

Self-Regulation Fertility: Relation to Hopf Bifurcation

Let us consider the equation (1) with the maternity function (35) and chose R and p as two varying parameters; here p is the unknown period of nonlinear cycles. After rescaling the time variable from t to t/p the equation for the deviation becomes

$$X(t) - p\left(\frac{2}{\psi_\mu}-R\right)\int_0^\infty \varphi(pa)\, X(t-a)\, da = -R\left(p_0 \int_0^\infty \varphi(pa) X(t-a)\, da\right)^2 \quad (70)$$

where

$$\varphi(a) = \psi(a)\, e^{-\mu a}. \quad (71)$$

Note that at the threshold (R_0, p_0) the equation

$$X(t) - p_0\left(\frac{2}{\psi_\mu}-R_0\right)\int_0^\infty \varphi(p_0 a)\, X(t-a)\, da = 0 \quad (72)$$

should have a pair of periodic solutions with the unit period, i.e. functions $Y(t) = e^{2i\pi t}$, $\bar{Y}(t) = e^{-2i\pi t}$ ($\omega = 2\pi$) satisfy the equation (72). Thus the threshold values R_0 , p_0 are defined from two algebraic equations

$$\tilde{S}(\omega_0) = 0, \quad where \quad \tilde{S}(\omega_0) = \int_0^\infty \varphi(a)\sin(\omega_0 a)\, da,$$

$$\tilde{C}(\omega_0) = \frac{\psi_\mu}{(2-R_0\psi_\mu)}, \quad where \quad \tilde{C}(\omega_0) = \int_0^\infty \varphi(\omega_0 a)\cos(\omega_0 a)\, da. \quad (73)$$

It is obviously from (73) that

$$R_0\psi_\mu \neq 2. \tag{74}$$

Now we set

$$R = R_0 + \lambda_1, \qquad p = p_0 + \lambda_2 \tag{75}$$

and use the first order Taylor expansions in the parameters (λ_1, λ_2) for the equation (70). So for the deviation $X(t,\lambda)$ we get

$$X(t,\lambda) - L(X) = \lambda_1 K_1(X) + \lambda_2 K_2(X) + g_2(X,X) \tag{76}$$

with

$$L(X) = p_0\left(\frac{2}{\psi_\mu} - R_0\right)\int_0^\infty \varphi(p_0 s)\,X(t-a)\,da \tag{77}$$

$$K_1(X) = -\,p_0 \int_0^\infty \varphi(p_0 s)\,X(t-a)\,da, \tag{78}$$

$$K_2(X) = \left(\frac{2}{\psi_0} - R_0\right)\int_0^\infty \left[\varphi(p_0 a) + p_0 a\varphi'(p_0 a)\right] X(t-a)\,da, \tag{79}$$

$$g_2(X,X) = R_0\,p_0^2\left(\int_0^\infty \varphi(p_0 s)\,X(t-a)\,da\right)^2. \tag{80}$$

Fourier coefficients for the functions $K_m(Y)$, $m=1,2$

$$[\hat{K}_1]_1 = P_1 + iQ_1, \quad [\hat{K}_2]_1 = P_2 + iQ_2, \tag{81}$$

where

$$P_1 = -\tilde{C}(\omega_0), \quad Q_1 = 0,$$

$$P_2 = \frac{1}{p_0}\left(\frac{2}{\psi_\mu} - R_0\right)\left[\tilde{C}(\omega_0) + \omega_0 \tilde{S}_a(\omega_0)\right]; \quad Q_2 = \frac{\omega_0}{p_0}\left(\frac{2}{\psi_\mu} - R_0\right)\tilde{C}_a(\omega_0), \tag{82}$$

with

$$\tilde{S}_a(\omega_0) = \int_0^\infty s\varphi(s)\sin(\omega_0 s)\, ds,$$

$$\tilde{C}_a(\omega_0) = \int_0^\infty s\varphi(s)\cos(\omega_0 s)\, ds.$$

Since in our case the nondegeneracy condition (25) has the form $\delta = P_1 Q_2$ or $\delta = \frac{\omega_0}{2\pi} C_a(\omega_0) \neq 0$ which is equivalent to

$$C_a(\omega_0) \neq 0.$$

Next we need to calculate $z_1(t)$ (see (28)), which satisfies the equation (see (30))

$$Z_1(t) - p_0\left(\frac{2}{\psi_\mu} - R_0\right)\int_0^\infty \varphi(p_0 s) Z_1(t-s)\, ds = R_0 (Y(t))^2 C^2(\omega_0), \qquad (84)$$

where we took into account (73) and the fact that

$$g_2(Y,Y) = R_0\left(\frac{2}{\psi_\mu} - R_0\right)^{-2} (Y(t))^2 ..$$

Using Fourier decomposition from (84) we have

$$Z_1(t) = \hat{Z}_2 e^{4\pi i t} + \hat{Z}_0 + \hat{Z}_{-2} e^{-4\pi i t}$$

$$with$$

$$\hat{Z}_0 = 2 R_0 C^2(\omega_0) ; \quad \hat{Z}_2 = R_0 C^2(\omega_0) .$$

In order to find the direction of bifurcation we need to calculate the Fourier coefficients for the function $R(t)$ (see (31)) , which in our case has the form

$$R(t) = g_2(Y, Z_1) .$$

Thus

$$\hat{R}_1 = A + iB,$$

where

$$A = 2 R_0^2 C^3(\omega_0)\left(\frac{2\psi_\mu}{R_0\psi_\mu - 1} + ReW\right),$$

$$B = 2 R_0^2 C^3(\omega_0)\, ImW, \qquad (85)$$

$$W = \frac{C(2\omega_0) - iS(2\omega_0)}{1 - \left(\frac{2}{\psi_\mu} - R_0\right)(C(2\omega_0) - iS(2\omega_0))} .$$

In accordance with (34)

$$\lambda_{12} = -\frac{1}{\delta}(AQ_2 - BP_2); \qquad \lambda_{22} = -\frac{1}{\delta}BP_1.$$

Using (82) finally we get

$$\lambda_{12} = 2R_0^2 C^2(\omega_0)\left(\frac{2\psi_\mu}{R_0\psi_\mu - 1} - ReW + ImW\frac{1}{C_a(\omega_0)}\left(\frac{C(\omega_0)}{\omega_0} + S_a(\omega_0)\right)\right);$$

$$\lambda_{22} = \frac{4\pi}{\omega_0^2}R_0^2\frac{C^4(\omega_0)}{C_a(\omega_0)}ImW.$$

Thus formula for λ_{22} describes the changes of the oscillation period as a function of ε.

The multiparameter bifurcation technique can be also implemented to the nonlinear McKendrik-von-Foerster equation. The approach is very similar to the previous one. It should, however, take into account the specific features of this equation. Following Tuljapurcar (1991)here we illustrate the main ideas of this approach using two parameters bifurcation.

Two Parameters Bifurcation Method for Nonlinear MacKendrik Equation

Let us consider the general demographic model given by McKendric-von-Foerster equation (McKendrik 1926, von Foerster 1959)

$$\frac{\partial P(t,a)}{\partial t} + \frac{\partial P(t,a)}{\partial a} + D(P)\;P(t,a) = 0, \qquad \textbf{(87)}$$

$$P(t,0) = B(P).$$

Here $D(P)$ and $B(P)$ are density dependent death rate and the number of birth at time

t..

Let μ be the parameters vector which affected the solutions of (87). Under some conditions (see, for example, Pruss, 1981) the equation (87) has nonzero time independent solution $P^*(a,\mu)$.

Let

$$\tilde{X}(t,a,\mu) = P(t,a,\mu) - P^*(a,\mu) \qquad \textbf{(88)}$$

be the deviation from the steady state solution of (87). It is convenient henceforth to change variables from t,a to u,a with $u=t-a$ and function from $\tilde{X}(u+a,a)$ to $X(u,a)$. Using these new variables one can easily write down the equation for the deviation in the form

$$\begin{aligned} \frac{\partial X(u,a,\mu)}{\partial a} - M_1(X,\mu) &= N_1(X,\mu), \\ X(u,0,\mu) - M_2(X,\mu) &= N_2(X,\mu). \end{aligned} \qquad \textbf{(89)}$$

Here M_1, M_2 are linear operators and N_1, N_2 are nonlinear operators. Note that transformation of (87) into (89) may require a Taylor expansion and thus appropriate smoothness of linear functions D *and* B in (87).

The starting point for the bifurcation analysis here is the assumption that for some threshold parameters values $\mu = \mu^*$ the linear version of (89) (with $N_1 = N_2 = 0$) has a pair of periodic solutions.

Then we chose two parameters $b=(b_1,b_2)$ from μ with the corresponding threshold values $b^*=(b_1^*,b_2^*)$. For the values near threshold $b=B^*+\lambda$ *with* $\lambda=(\lambda_1,\lambda_2)$. Assuming the appropriate smoothness in (x,λ) we transform (89) to the form

$$\partial X(u,a)/\partial a - H_1(X) = \lambda_1 L_1(X) + \lambda_2 L_2(X) + g(X,\lambda) \equiv T_1(X,\lambda), \tag{90}$$
$$X(u,0) - H_2(X) + \lambda_1 K_1(X) + \lambda_2 K_2(X) + h(X,\lambda) \equiv T_2(X,\lambda).$$

Here $H_1(X) \equiv M_1(X,\mu^*)$; $H_2(X) \equiv M_2(X,\mu^*)$; L_i, K_i are linear operators and g, h, T_i are nonlinear operators, $i=1,2$.

Assumption H1. For equation (90):

$$-H_1(X)(u,a) = c_1(a)X(u,a) + c_2(a)\int_0^\infty k_1(s)X(u+a-s,s)\,ds,$$
$$H_2(X)(u) = \int_0^\infty k_2(v)X(u-v,v)\,dv. \tag{91}$$

At the threshold the local linear equations are

$$\partial X(u,a)/\partial a - H_1(X) = 0, \qquad X(u,0) - H_2(X) = 0. \tag{92}$$

Assumption H2. Linear equations (92) have only one pair of periodic solutions $Y_1(u,a) = Y_1(a)\exp(i\omega u)$ *and* $\overline{Y_1}(u,a)$ (bar indicates a complex conjugate).

Fourier coefficients of a periodic function $g(u,a)$ are as

$$\hat{g}_j(a) = \frac{1}{p}\int_{-p/2}^{p/2} g(u,a)\,\exp(-ij\omega u)\,du, \tag{93}$$

for $j=0,\pm1,\pm2,\ldots,$ *with* $p=2\pi/\omega$ *and* $g(u,a)=g(u+p,a)$. The solvability of a system like (90) is to be expressed via Fredholm conditions and these require a

$$\Omega[g,h] = \int_0^\infty k_2(v)\ \exp[-i\omega(v)]\ x_2(v)\ dv + \hat{h}_1. \tag{94}$$

particular functional:

for a pair of functions $(g(u,a), h(u))$, both p-periodic in u,

Here $\hat{h}_1$ is a Fourier component as in (93) and x_2 depends on Fourier component $\hat{g}_1(a)$ as follows: write

$$l(a) = \exp[-\int_0^a c_1(v)\ dv],$$
$$m(a) = \frac{1}{l(a)}; \tag{95}$$

then set

$$x_2(a) = l(a)\int_0^a [\ \hat{g}_1(s) - Wc_2(s)\exp(i\omega s)\ ]\, m(s)\ ds, \tag{96}$$

with

$$W_1 W = \int_0^\infty k_1(s)\, l(s)\exp(-i\omega s)\int_0^s \hat{g}_1(v)\, m(v)\ dv\ ds, \tag{97}$$

$$W_1 = 1 + \int_0^{\infty} k_1(s)\, l(s) \exp(-i\omega s) \int_0^{s} c_2(v)\, m(v) \exp(i\omega v)\; dv\, ds. \quad \textbf{(98)}$$

Assumption H3.

$$W_1 \neq 0.$$

Assumption H4. $L_i,\ K_i$ for $i=1,2$ are bounded linear operators.

Assumption H5. For periodic functions X and real parameters λ in open neighborhood of $X=0,\ \lambda=0$, the nonlinear functions in (90) satisfy $(g(\varepsilon X, \lambda),\ h(\varepsilon X, \lambda)) = \varepsilon(\tilde{g}(X, \lambda, \varepsilon), \tilde{h}(X, \lambda, \varepsilon))$. Here $\tilde{g}, \tilde{h}$ are at least once continuously Frechet differentiable and $0 = \tilde{g}(X,0,0) = \tilde{g}_x(X,0,0) = \tilde{h}(X,0,0) = \tilde{h}_x(X,0,0)$ where subscript x denotes the derivative with respect to x.

Theorem 5 (Cushing 1983). Assume H1 to H5 and further that

$$\delta = Im(\Omega[L_1(Y_1),\ K_1(Y_1)]\ \Omega[L_2(y_1), K_2(y_1)]) \neq 0, \quad \textbf{(99)}$$

with Y_1 being the solution of (92). Than for all ε satisfying $|\varepsilon| < \varepsilon_1\ (0 < \varepsilon_1 \leq \varepsilon_0)$ equation (90) has a p-periodic solution of the form

$$X(u,a) = \varepsilon Y_1(u,a) + \varepsilon z(u,a,\varepsilon), \qquad \lambda = \lambda(\varepsilon), \quad \textbf{(100)}$$

and $\|z\| = O(|\varepsilon|)$ as $\varepsilon \to \infty$.

Nonlinear Terms

Assume that the birth and death rates in the model are sufficiently many times continuously differentiable functions in some open neighborhood of $x=0$, $\lambda=0$ so that one can make the expansion

$$g(x,\lambda)=g_2(x,x)+\lambda_1 g_{21}(x,x)+\lambda_2 g_{22}(x,x)+g_3(x,x,x)+g_4(x,\lambda),$$
$$h(x,\lambda)=h_2(x,x)+\lambda_1 h_{21}(x,x)+\lambda_2 h_{22}(x,x)+h_3(x,x,x)+h_4(x,\lambda). \tag{101}$$

Here g_p, g_{pq}, h_p, h_{pq} are p-linear symmetric in x for $p\le 3$. The terms g_4, h_4, are $O(\|x\|^4+|\lambda|\|x\|^3+|\lambda|^2\|x\|)$.

A Lyapunov-Schmidt expansion (Poore 1976) yields the following results.

Theorem 6 (Tuljapurcar (1991)). Assume the conditions of Cushing's theorem, the representation (101), and consider the expansions

$$\lambda_j(\varepsilon)=\lambda_{j1}\varepsilon+\lambda_{j2}\varepsilon^2+0(\varepsilon^2), \quad j=1,2,$$
$$X(u,a)=\varepsilon Y(u,a)+\varepsilon^2 Z_1(u,a)+o(\varepsilon^2), \tag{102}$$

where Y is a real periodic solution of (92).

Then

(a) $\lambda_{j1}=0$, $j=1,2$.

(b) $Z_1(u,a)$ is the solution of the inhomogeneous equations

$$\partial Z_1/\partial a-H_1(Z_1)=g_2(Y,Y),$$
$$Z_1(u,0)-H_2(Z_1)=h_2(Y,Y). \tag{103}$$

(c) defining the matrix

$$N = \begin{pmatrix} Re\Omega[L_1(Y), K_1(Y)] & Im\Omega[L_1(Y), K_1(Y)] \\ Re\Omega[L_2(Y), K_2(Y)] & Im\Omega[L_2(Y), K_2(Y)] \end{pmatrix} \qquad \textbf{(104)}$$

and letting A, B be the real and imaginary parts respectively of the function $\Omega[2g_2(Y, Z_1) + g_3(Y, Y, Y),\ 2h_2(Y, Z_1) + h_3(Y, Y, Y)]$, one has

$$(\lambda_{12}, \lambda_{22}) = (A, B)N^{-1}. \qquad \textbf{(105)}$$

The proof of this result is based on the Fredholm alternative for the solution of the integrodifferential equations.

Discussion

The interaction of generations in age-structured populations is responsible for nonlinear self-regulatory feedback mechanisms of population evolution. The properties of the feedback mechanism depend on the parameters values and type of nonlinearities that specify the mutual influence of different cohorts and determine the population vital rates. The stable stationary state which may exist for some parameter values is one possible result of self-regulation. When the parameters of equations reach some threshold values the steady state solution becomes unstable. The sustained nonlinear oscillations are the most interesting results of this instability. Some special conditions must be specified in order to guarantee the unstable solution to be the sustained nonlinear oscillations.

The important practical problem is: how our knowledge of the interaction mechanisms (nonlinear feedback) can help in understanding the dynamic properties of the population, i.e. when the nonlinear oscillations occur, what is their period and shape, what is the direction in the parameters space along which the period of oscillations is constant, whether the revealed oscillations are stable.

The machinery that helps to answer all these questions is readily available: one should write down the nonlinear equation for population evolution, find its steady-state solution and write down the equation for deviation from this steady state solution. The linear part of this equation is used for finding the threshold parameter values, i.e. the values for which the linear version of this equation has a pair of periodic solutions. In order to check whether the nonlinear equation has a periodic solution let us choose two parameters (that will be varied near the threshold level) from the parameter set and keep the other on the threshold. Linearize the equation for deviation with respect to increments of these two parameters. Note that zero deviation is usually a solution of this nonlinear equation since the (unstable) steady state solution exists. However, if the situation is unstable this solution may be not unique. It turns out that other solutions exist in the vicinity of zero solution. The Cushing's "nondegeneracy" condition guarantees the existence of periodic solutions as well as the existence of some special direction in the parameter space. Changing two selected parameters in this direction will not change the period of nonlinear oscillations. Power series expansion of the solution of the nonlinear population equation with respect to small parameter - the amplitude of nonlinear oscillations, allows to identify this direction. Special efforts needed to analyze the stability property of the periodic solutions.

Conclusion

Real problems of population dynamics can motivate the variety of research activities from building large simulation models till development the abstract mathematical constructions. The idea of this paper is to elucidate approaches that allow us to better understand the mechanism of sustained oscillations in population size and structure.

The nature of these oscillations appears in nonlinear feedback which generates the delay of response of the population vital rates to the changes in population structure. The effects appear automatically when the parameters of equations cross some threshold levels. This feature of nonlinear population equation is extremely important for applications: human as well as other biological populations evolve in the changing environment that influences the parameters of their vital rates. To predict or to avoid the surprises in population behavior one should know the nature of the bifurcation mechanisms and the regularities in the parameters changes that might lead to the bifurcation phenomena.

The reasons for these changes in real systems may be numerous. For human populations they are associated with the industrial development, changes of living standards, or cultural evolution. Biological species demonstrate the sensitivity to the changes of the environmental conditions induced by natural evolution or human activity.

Note that the sustained oscillations as a bifurcation phenomena is by no means a unique event. According to Prigogine and Nicolis (1985) rather, it is the beginning of a complex systems transitions. The cascades of new properties of the solution may be revealed. The systematic studies of these phenomena that include the bifurcation analysis as well as the identification of nonlinear feedback mechanisms from real data are needed.

The nonlinear population models with self-exciting oscillations are very often the mathematical abstractions. In many situations they arise as an attempt to exclude some intermediate variables and to reduce the dimension of the problem. The explanation of the Easterlin cycles, for instance, involves such economical categories as level of well-being or standards of living. The approach that allows to combine the evolution of population age structure with changing environmental indices still need to be developed. This variety of exiting and still unsolved problems only supports the idea that the world of dynamical systems is fascinating and still largely unexplored.

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