Competitive Predator-Prey Systems with Time-Dependent Coefficients: A Multistage Homotopy Perturbation Analysis

Tekmovalni sistemi plenilec-plen s časovno odvisnimi koeficienti: Večstopenjska homotopsko perturbacijska analiza

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Abstract: This paper treats competitive predator-prey systems, which growth of populations and their mutual interactions are time dependent. For solving a general Lotka-Volterra system of equations, the multistage homotopy perturbation (MH-P) method is developed to predict the time evolution of the dynamical system and its properties, such as existence of stable periodic orbits. As the newest achievement, the efficiency of MH-P method is provedintreatment of almost-periodic variations of coefficients with incommensurate excitation frequencies.The periodic variations of coefficients are analyzed as special case by assuming that excitation frequencies are commensurate. By using MH-P method, the approximate analytic solutions are obtained, which are very accurate in the long term behaviour. Although an usefull convergence test of the computed solution is provided, the accuracy of MH-P method is compared also by results of the numerical integration of Lotka-Volterra equations by using the Runge-Kutta method, where an excellent agreement is obtained.

Key words: predator-prey system; almost-periodic coefficients; MH-P method

Povzetek: Članek obravnava tekmovalne sisteme plenilcev-plen, katerih rasti populacij in njih medsebojni vplivi so časovno odvisni. Za reševanje splošnega sistema enačb tipa Lotka-Volterra je razvita večstopenjska homotopsko perturbacijska (VH-P) metoda, s katero določimo časovni razvoj dinamičnega sistema in njegove lastnosti, kot denimo obstoj stabilnih periodičnih orbit. Kot najnovejši dosežek je prikazana učinkovitost VH-P metode v obravnavi skoraj periodičnih variacij koeficientov z nekomenzurnimi vzbujevalnimi frekvencami. Periodične variacije koeficientov so analizirane kot posebni primer s komenzurnimi vzbujevalnimi frekvencami. Z uporabo VH-P metode dobimo približne analitične rešitve, ki so zelo natančne v daljšem časovnem obdobju. Čeprav metoda predvideva uporaben test konvergence izračunanih rešitev, je natančnost VH-P metode preverjena tudi s primerjavo rezultatov, dobljenih z numerično integracijo enačb Lotka-Volterra ob uporabi metode Runge-Kutta, pri čemer je ugotovljeno odlično ujemanje rezultatov.

Ključne besede: sistemi plenilci-plen; skoraj periodični koeficienti; VH-P metoda

1. Introduction

Dynamical systems of predator-prey type appear in diverse branches of science and engineering. Predator-prey systems are applied successfully in the combustion theory to model the evolution of chemical radicals formed during

H_2 and O_2 combustion [1] and are widely used in chemistry, biology, economics, medicine and ecology [2]. Due to the wide applicability such systems represent a great research challenge.The interaction mechanisms in predator-prey ecosystems are nonlinear because harvest-, birth-, death-, and migration rates depend strongly on

populations. Unfortunately, such models does not take into account the exogenous environmental factors, such as food, temperature, humidity, light, etc., which vary periodically or even almost-periodically in dependence on the season-, daily-, month- and year cycles. The objective of this paper is the inclusion of such exogenous factors into dynamical system to obtain a more realistic model of the predator-prey system.

Dynamical system describing the predator-prey ecosystem, which takes into account the time-dependent coefficients of populations growth rates as well as the time-dependent coefficients of mutual interactions between populations of species, is written in the following form of generalized Lotka-Volterra equations:

$$\begin{cases} \dot{x}_i = \varepsilon_i(t) x_i - \sum_{j=1}^{n} a_{ij}(t) x_i x_j, \\ x_{i0} = x_i(0) = c_i, \quad (i = 1, \cdots, n) \end{cases} \tag{1}$$

Functions $\varepsilon_i(t)$ represent the time-dependent coefficients of populations growth rates and functions $a_{ij}(t)$ stand for time-dependent coefficients of mutual interactions between populations of species. Because the right hand sides of ODE's are explicitly dependent on the time, the dynamical system, described by Eqs. (1) is nonautonomous. It is required, that all $\varepsilon_i(t)$ and $a_{ij}(t)$, respectively, are continuous functions of time, which for example may be polinomials, periodic or even almost-periodic functions. In this paper, almost-periodic functions will be treated in details, because they represent the most relevant basis for modelling the realistic predator-prey ecosystems. When all coefficients of mutual interactions between populations of speciesare nonnegative, $a_{ij}(t) \geq 0$ for all times and for all indexes i,j, the ecosystem is competitive and when $a_{ij}(t)|_{i \neq j} < 0$, then ecosystem iscooperative [3]. To restrict yourself in this paper, only competitive ecosystems will be treated, although the present formulation of the MH-P method is not limited on the competitive systems only. By means of equations $x_{i0} = c_i$, the corresponding initial conditions in the time $t = 0$ are prescribed.

Homotopy perturbation (H-P) method is videly applied in a broad range of nonlinear problems describing various physical phenomena [4].Such a phenomena are governed by systems of nonlinear ordinary or partial differential equations. The strength of the H-P method comes from the fact, that solutions can be expressed in the form of power series, where the coefficients of power series are determined in a similar manner as in perturbation methods

without the need for the introduction of a small expansion parameter [5],[6].Due to this, the H-P method is ideally suited to solve strongly nonlinear problems if the nonlinearities appear in the polinomial form. Besides this, the power series produce analytical solutions, which offer numerous advantages (the implementation of parametric studies, stability and bifurcation analysis).On the other side, there is a limiting factor in the H-P method, namely the length of the time intervalin which is desired to obtain an accurate solution. In dynamical systems exhibiting chaos, the length of the time interval as a rule must be very large in order to obtain the fully developed characteristics of chaos. The standard H-P method applied on dynamical systems in which chaos appears, fails on large time intervals.To overcome this deficiency, the multistage homotopy perturbation (MH-P) method is first proposed in [7] and then applied in predator-prey systems in [8]. The main idea behind the MH-P method is the division of the entire time interval on the finite number of subintervals with equal length and succesive application of the H-P algorithm on each subinterval. The only difficulty in such a procedure are unknown initial conditions on all subintervals except on the first. This difficulty can be easily overcomed by assuming that unknown initial conditions must be equal to the final values on the preceding interval in order to ensure the C^0 continuity.

MH-P method can be applied purely natural on Lotka-Volterra Eqs. (1), because these equations contain nonlinearities in the polinomial form. In this paper, the general form of the MH-P method is presented, which is capable to solve Lotka-Volterra equations with time-dependent coefficients. The solution obtained has an explicit form. Application of the method is shown in details for almost-periodic coefficients with incommensurate excitation frequencies including two special examples. The first special example is reduced on the standard Lotka-Volterra equations with constant coefficients giving an autonomous dynamical system. Nevertheless, interesting properties of the competitive predator-prey model are demonstrated in this case: the exinction of all populations of predators except the dominant one from ecosystem viewpoint and the absolute necessity of the multistage homotopy perturbation in the long term behaviour ensuring the desired accuracy. In the second special example, excitation frequencies are chosen commensurate, excluding the phenomenon of the extinction and leading to the stable periodic orbit in the long term behaviour.

2. Multistage Homotopy Perturbation (MH-P) Method for Predator-Prey Systems with Time-Dependent Coefficients

The multistage homotopy perturbation (MH-P) method is improvement of the standard homotopy perturbation (SH-P) method. The SH-P method is distinguished by high accuracy on short time intervals.Short time intervals represent a serious limitation in dynamical systems, exhibiting chaos. An example of such a dynamical system is the famous Lorenz system, where the chaos is fully developed on the relatively long time interval.In this paper will be shown, that short time intervals represent a serious limitation in respect of the required accuracy in the predator-prey systems, too. Fortunately, the desired high accuracyof the method can be maintained even on long time intervals, when the entire time interval is divided into finite number of subintervals with equal length and the homotopy perturbation method is applied on each subinterval.In such a way, the MH-P method is obtained. To implement MH-P method on the some subinterval, the initial values at the beginning of the subinterval must be known, however these values are actually known at the beginning of the first subinterval only. To overcome this difficulty, the final values of the preceding subintervals are computed and chosen as initial conditions on the next subinterval to ensure the C^0 continuity (an exception of this procedure represents the first subinterval, which does not have a preceding subinterval at all).

Suppose, that we are interested in the solution of Eqs. (1) on the time interval $[t_0, t)$. According to the MH-P method, the time interval $[t_0, t)$ is divided into s subintervals of equal length Δt. The solution is sought iteratively on subintervals $[t_0, t_1), [t_1, t_2), [t_2, t_3), \cdots, [t_{s-1}, t)$, where initial values on each particular subinterval are unknown except initial values on the first subinterval in the time $t^* = t_0$. The homotopy perturbation method on a particular subinterval can be formulated in the simplest way, if the folowing homotopy:

$$L(x_i) - L(v_i) + pL(v_i) + p\left[-\varepsilon_i(t)x_i + \sum_{j=1}^{n} a_{ij}(t)x_i x_j\right] = 0, \quad (i = 1, \cdots, n) \tag{2}$$

is assigned to the system of ODE's (1), where $L = \frac{\mathrm{d}}{\mathrm{d}t}$ denotes the linear operator, $p \in [0,1]$ is an embedding parameter and variables v_j denote initial approximations of the solution, which must satisfy initial conditions. Homotopy (2) is reduced on the linear system of equations, when $p = 0$ and is transformed during the so called deformation process into the original nonlinear system of equations, when embedding parameter approaches $p \to 1$. The approximate solution of Eqs. (1) is represented in the form of power series:

$$x_i(t) = x_{i0}(t) + px_{i1}(t) + p^2 x_{i2}(t) + p^3 x_{i3}(t) + \cdots = \sum_{k=0}^{\infty} p^k x_{ik}(t), \quad (i = 1, \cdots, n), \tag{3}$$

where $x_{ik}(t)$, $(k = 1, 2, \cdots)$ denote unknown functions of time, which must be determined in the following perturbation procedure.By introduction of power series (3) into equation of homotopy (2) one obtains:

$$L\left[\sum_{k=0}^{\infty} p^k x_{ik}(t)\right] - L(v_i) + pL(v_i) - \varepsilon_i(t)\sum_{k=0}^{\infty} p^{k+1} x_{ik}(t)$$
$$+ \sum_{j=1}^{n} a_{ij}(t)\sum_{k=0}^{\infty}\sum_{l=0}^{\infty} p^{k+l+1} x_{ik}(t)x_{jl}(t) = 0, \quad (i = 1, \cdots, n) \tag{4}$$

By collecting coefficients at like powers of the embedding parameter p one obtain the following equations for p^0 and p^1, respectively:

$$p^0: \quad L(x_{i0}) - L(v_i) = 0, \quad \Rightarrow \quad x_{i0} = v_i, \tag{5}$$

$$p^1: \quad L\big[x_{i1}(t)\big] + L(v_i) - \varepsilon_i(t)x_{i0}(t) + \sum_{j=1}^{n} a_{ij}(t)x_{i0}(t)x_{j0}(t) = 0, \tag{6}$$

and for each p^r, $(r > 1)$ the equation:

$$p^r: \quad L\big[x_{ir}(t)\big] - \varepsilon_i(t)x_{i,r-1}(t) + \sum_{j=1}^{n} a_{ij}(t)\sum_{k=0}^{r-1} x_{ik}(t)x_{j,r-k-1}(t) = 0. \tag{7}$$

The system of equations (5-7) is obtained in an explicit form and can be solved by successive integrations of linear operators $L\big[x_{ir}(t)\big]$, $(r = 1, 2, \cdots, m)$. Although Eqs. (5-7) are developed by the perturbation procedure, the small perturbation parameter, which is present in all standard perturbation methods, is not required here at all. In other words, functions $\varepsilon_i(t)$ and $a_{ij}(t)$, respectively, do not contain such a small perturbation parameter. Consequently, the MH-P method can be applied in the analysis of the predator-prey ecosystems, which contain high polynomial nonlinearities and time-dependent coefficients. In the rest of the paper, we will apply the following explicit form of functions $\varepsilon_i(t)$ and $a_{ij}(t)$:

$$\varepsilon_i(t) = \phi_{i0} + \sum_{q=1}^{M_t} \big(\phi_{iq}\cos\omega_{iq}t + \varphi_{iq}\sin\omega_{iq}t\big),$$

$$a_{ij}(t) = \alpha_{ij,0} + \sum_{q=1}^{M_t} \big(\alpha_{ij,q}\cos\omega_{ij,q}t + \beta_{ij,q}\sin\omega_{ij,q}t\big), \quad (i, j = 1, 2, \cdots, n) \tag{8}$$

where ϕ_{i0}, $\alpha_{ij,0}$, ϕ_{iq}, φ_{iq}, $\alpha_{ij,q}$, $\beta_{ij,q}$ areexcitation amplitudes and ω_{iq}, $\omega_{ij,q}$; $(q = 1, 2, \cdots, M_t)$ are $2M_t$ excitation frequencies. If all pairs of frequencies ω_{iq}, $\omega_{ij,q}$ have an integer ratio, then frequencies ω_{iq}, $\omega_{ij,q}$; $(q = 1, 2, \cdots, M_t)$ are commensurate and all excitations are periodic. If all pairs of frequencies ω_{iq}, $\omega_{ij,q}$ have an irational ratio, then frequenciesare incommensurate and functions $\varepsilon_i(t)$ and $a_{ij}(t)$ are almost-periodic. A special example of Eqs. (8) occurs, when there are $M_t = 0$ tones. In such a case, the predator-prey ecosystem is autonomous and contains the constant coefficients.

When functions $\varepsilon_i(t)$ and $a_{ij}(t)$ are given in the form (8), then Eqs. (5-7) can be integrated analytically. Therefore, it is evident, that a very large class of predator-prey ecosystems can be analytically solved by means of the presented MH-P method. Now look for the implementation of the MH-P method on each subinterval.

Denote the starting time on an arbitrary subinterval by t^* and the corresponding final time of the subinterval by t. Then the entire time interval in SH-P method as well as the first subinterval in the MH-P method can be denoted by $[t^* = t_0, t)$, the second subinterval of the MH-P method by $[t^* = t_1, t)$ and the last subinterval by $[t^* = t_{s-1}, t)$, respectively. By using this convention, the entire time interval as well as all subintervals can be computed in the same way. As initial solutions on an arbitrary subinterval we choose initial conditions of that subinterval. Because initial conditions differ on subequent intervals, we use the same convention as above and write:

$$v_i(t) = x_{i0}\big(t^*\big) = x_i\big(t^*\big) = c_i^*, \quad (i = 1, \cdots, n), \tag{9}$$

where c_i^* denote initial conditions on an arbitrary subinterval, which are equal to the computed values $x_i(t)$ on the end of the preceding subinterval. From Eq. (9) it follows:

$$L(v_i) = 0, \tag{10}$$

which in turn simplifies Eq. (6). As already mentioned, the system of Eqs. (5-7) is solved successively by using the inverse linear operator:

$$L^{-1}(\cdot) = \int_{t^*}^{t} (\cdot)\,\mathrm{d}t. \tag{11}$$

Actually, integration (11) is first applied on Eq. (6), because Eq. (5) is fullfilled trivially. After this, the integration is continued on subsequent equations. Approximate solutions of the original Lotka-Volterra

equations (1) are obtained by execution ofthe limit process $p \rightarrow 1$ on the power series (3), where only the first m terms are retained from the practical reasons:

$$\Phi_{i,m}(t) = \lim_{p \to 1} x_i(t) = \sum_{k=0}^{m-1} x_{ik}(t) \tag{12}$$

The algorithm of the MH-P method for predator-prey ecosystems with time-dependent coefficients is now completed. The algorithm is ideally suited for implementation in the programming environment Mathematica®.

3. Results and discussion

In this paper, three different competitive predator-prey ecosystems are analyzed by using the MH-P method. In the first example, the predator-prey system with three species is analyzed, where population growth rates and coefficients of mutual interactions between populationsare prescribed in the form of almost-periodic functions. The predator-prey system, which is studied in this example, is competitive, because in addition, coefficients of mutual interactions fullfill conditions $a_{ij}(t) \geq 0$.The governing Lotka-Volterra equations have the following form:

$$\begin{cases} \dot{x}_1(t) = x_1(t)\left[5 + 4\cos\omega_1 t - (3 + \cos\omega_1 t)x_1(t) - x_2(t) - x_3(t)\right] \\ \dot{x}_2(t) = x_2(t)\left[4 + 3\sin\omega_2 t - x_1(t) - (3 + \sin\omega_2 t)x_2(t) - x_3(t)\right] \\ \dot{x}_3(t) = x_3(t)\left[3 + 2\cos(2\omega_3 t) - x_1(t) - \frac{1}{5}x_2(t) - (4 + \cos(2\omega_3 t))x_3(t)\right] \end{cases} \tag{13}$$

where excitation frequencies are incommensurate having values $\omega_1 = 1$, $\omega_2 = \frac{1}{\sqrt{3}}\omega_1$, $\omega_3 = \sqrt{2}\omega_1$ and where theinitial conditions

$$x_{10} = x_1(0) = c_1 = 0.4, \quad x_{20} = x_2(0) = c_2 = 0.4, \quad x_{30} = x_3(0) = c_3 = 0.4 \tag{14}$$

are prescribed. The first equation of (13) belongs to the prey population, the second equation belongs to the superpredator population and the third belongs to the population of predators. The meaning of incommensurate frequenciesisthat grow rate cycles and cycles of mutual interactions between population of species are completely independent of each other. Because Eq. (5) is trivial, it can be omitted and only Eqs. (6,7) are written down:

$$p^1 : \begin{cases} L\left[x_{11}(t)\right] + L(v_1) - (5 + 4\cos\omega_1 t)x_{10}(t) \\ + (3 + \cos\omega_1 t)x_{10}^2(t) + x_{10}(t)x_{20}(t) + x_{10}(t)x_{30}(t) = 0, \quad (L(v_1) = 0) \\ L\left[x_{21}(t)\right] + L(v_2) - (4 + 3\sin\omega_2 t)x_{20}(t) + x_{20}(t)x_{10}(t) + (3 + \sin\omega_2 t)x_{20}^2(t) \\ + x_{20}(t)x_{30}(t) = 0, \quad (L(v_2) = 0) \\ L\left[x_{31}(t)\right] + L(v_3) - (3 + 2\cos(2\omega_3 t))x_{30}(t) \\ + x_{30}(t)x_{10}(t) + \frac{1}{5}x_{30}(t)x_{20}(t) + (4 + \cos(2\omega_3 t))x_{30}^2(t) = 0, \quad (L(v_3) = 0) \end{cases} \tag{15}$$

$$p^r : \begin{cases} L\left[x_{1r}(t)\right] - (5 + 4\cos\omega_1 t)x_{1,r-1}(t) + (3 + \cos\omega_1 t)\sum_{k=0}^{r-1} x_{1k}(t)x_{1,r-k-1}(t) \\ + \sum_{k=0}^{r-1} x_{1k}(t)x_{2,r-k-1}(t) + \sum_{k=0}^{r-1} x_{1k}(t)x_{3,r-k-1}(t) = 0 \\ L\left[x_{2r}(t)\right] - (4 + 3\sin\omega_2 t)x_{2,r-1}(t) + \sum_{k=0}^{r-1} x_{2k}(t)x_{1,r-k-1}(t) \\ + (3 + \sin\omega_2 t)\sum_{k=0}^{r-1} x_{2k}(t)x_{2,r-k-1}(t) + \sum_{k=0}^{r-1} x_{2k}(t)x_{3,r-k-1}(t) = 0 \\ L\left[x_{3r}(t)\right] - (3 + 2\cos(2\omega_3 t))x_{3,r-1}(t) + \sum_{k=0}^{r-1} x_{3k}(t)x_{1,r-k-1}(t) \\ + \frac{1}{5}\sum_{k=0}^{r-1} x_{3k}(t)x_{2,r-k-1}(t) + (4 + \cos(2\omega_3 t))\sum_{k=0}^{r-1} x_{3k}(t)x_{3,r-k-1}(t) = 0 \end{cases} \tag{16}$$

System of equations (15,16) is complete, because equation of an arbitrary order can be constructed in the explicit form. By successive integration of equations, analytical solutions $x_{i1}(t), x_{ir}(t); (i=1,2,3), (r=2,\cdots,m)$ are

obtained, which are then used in Eq. (12) to construct approximate analytical solutions $\Phi_{i,m}(t)$ of the *m*-th order. As an example, the integration of Eq. (15) is shown, which leads on the result:

$$
\left\{
\begin{array}{l}
x_{11}(t) = x_{11}\left(t^*\right) + \int_{t^*}^{t}\left[\left(5+4\cos\omega_1\tau\right)c_1^* - \left(3+\cos\omega_1\tau\right)\left(c_1^*\right)^2 - c_1^* c_2^* - c_1^* c_3^*\right]d\tau \\[2mm]
\quad = c_1^*\left[\frac{1}{\omega_1}\left(4-c_1^*\right)\left(\sin\omega_1 t - \sin\omega_1 t^*\right) + \left(5-3c_1^* - c_2^* - c_3^*\right)\left(t-t^*\right)\right], \\[2mm]
x_{21}(t) = x_{21}\left(t^*\right) + \int_{t^*}^{t}\left[\left(4+3\sin\omega_2\tau\right)c_2^* - c_2^* c_1^* - \left(3+\sin\omega_2\tau\right)\left(c_2^*\right)^2 - c_2^* c_3^*\right]d\tau \\[2mm]
\quad = c_2^*\left[-\frac{1}{\omega_2}\left(3-c_2^*\right)\left(\cos\omega_2 t - \cos\omega_2 t^*\right) + \left(4-c_1^* - 3c_2^* - c_3^*\right)\left(t-t^*\right)\right], \\[2mm]
x_{31}(t) = x_{31}\left(t^*\right) + \int_{t^*}^{t}\left[\left(3+2\cos(2\omega_3\tau)\right)c_3^* - c_3^* c_1^* - \frac{1}{5}c_3^* c_2^* - \left(4+\cos(2\omega_3\tau)\right)\left(c_3^*\right)^2\right]d\tau \\[2mm]
\quad = c_3^*\left[\frac{1}{\omega_3}\left(1-\frac{1}{2}c_3^*\right)\left(\sin(2\omega_3 t) - \sin(2\omega_3 t^*)\right) + \left(3-c_1^* - \frac{1}{5}c_2^* - 4c_3^*\right)\left(t-t^*\right)\right]
\end{array}
\right.
\tag{17}
$$

where is considered, that relations $x_{11}\left(t^*\right) = x_{21}\left(t^*\right) = x_{31}\left(t^*\right) = 0$ always hold, because initial conditions are fulfilled already by values $x_{10}\left(t^*\right)=x_1\left(t^*\right)=c_1^*$, $x_{20}\left(t^*\right)=x_2\left(t^*\right)=c_2^*$, $x_{30}\left(t^*\right)=x_3\left(t^*\right)=c_3^*$.
On the same way, the integration of subsequent equations of higher order is carried out. Results of computation of populations evolution by using the MH-P method and comparison with Runge-Kutta method are shown on Figures 1, 2 and 3, respectively, where an excellent agreement is established. The high accuracy of the MH-P method in the entire observation range is achieved with relatively small number (*m*=4) of terms in power series (12), but using a great number of subintervals *s*=500. To evaluate the accuracy of results, one computes the integral of the absolute error between two subequent solutions $x_i^{(s-1)}(t)$ and $x_i^{(s)}(t), (i=1,\cdots,n=3)$ over the entire time interval $[t_0,t]$, where the first solution contains *s*-1 subintervals and the next solution has s subintervals,

respectively and check, if the values of the computed integral are less than the prescribed tolerance *tol*:

$$
J_i = \int_{t_0}^{t}\left|x_i^{(s)}(t) - x_i^{(s-1)}(t)\right|dt < tol, \quad (i=1,2,3)
\tag{18}
$$

If this check fails, then the number of subintervals is too small. In the predator-prey system (13), the tolerance *tol* is prescribed to be equal $tol = 10^{-4}$. The number of subintervals *s*=500 is then sufficient to fulfill the criterion (18) on the entire time interval $[t_0 = 0, t = 50]$ with computed values of integrals: $J_1 = 4.72776\times10^{-5}, J_2 = 1.53379\times10^{-5}$ and $J_3 = 8.23404\times10^{-5}$. On the Figure 4, the parametric dependencies of evolutions of populations $x_1(t), x_2(t)$ and $x_3(t)$, which are computed by MH-P method and comparison of results with Runge-Kutta method are plotted, where again the excellent agreement is shown.
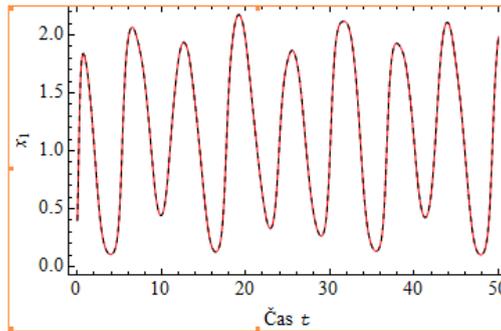
Figure 1. Evolution of population $x_1(t)$ in the almost-periodic case. ⸻Solution, computed by MH-P method, - - - Solution, computed by numerical integration using Runge-Kutta method.
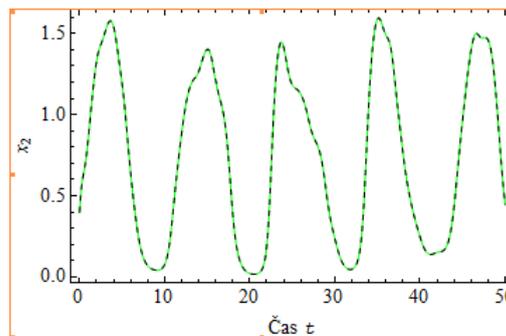
Figure 2. Evolution of population $x_2(t)$ in the almost-periodic case. ⸺ Solution, computed by MH-P method, - - - Solution, computed by numerical integration using Runge-Kutta method.
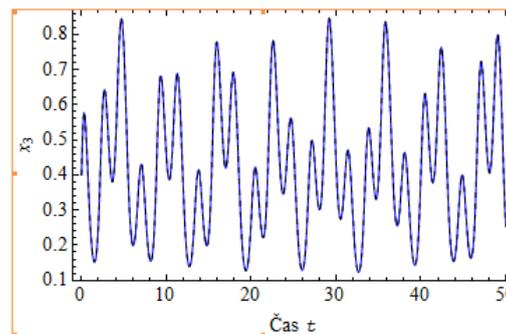
Figure 3. Evolution of population $x_3(t)$ in the almost-periodic case. ⸺ Solution, computed by MH-P method,- - -Solution,computed by numerical integration using Runge-Kutta method.
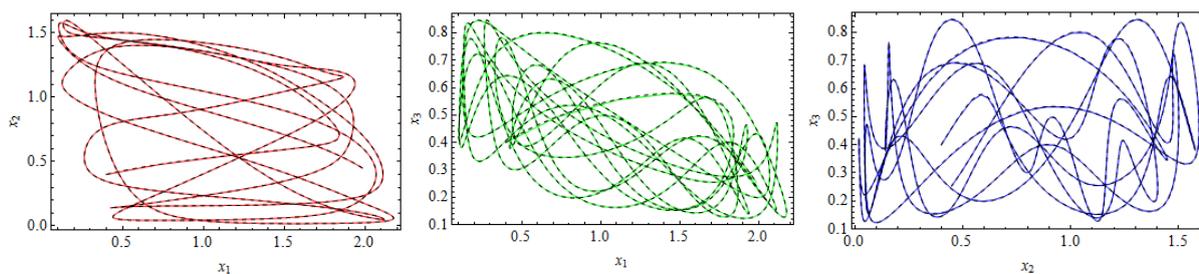
Figure 4. Parametric dependencies of populations $x_1(t)$, $x_2(t)$ in $x_3(t)$ in the almost-periodic case. ⸺ Solution, computed by MH-P method, - - - Solution, computed by numerical integration using Runge Kutta method.

Time histories on Figures 1-3, as well as orbits on the Figure 4 reveal the essential nature of almost-periodic oscillations. Time histories consist from series of cycles, which do not repeat. This property is a direct consequence

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of incommensurate frequencies involved. On the other side, it can be recognized, that the time histories are not random or even chaotic. This property is evident also from the parametric plots, where numerous loops can be seen, but no random behaviour.

Now look on the periodic counterpart of the predator-prey ecosystem (13). To obtain periodicity, the general form of Eqs. (13) and corresponding values of initial conditions are retained, but excitation frequencies are now required to be commensurate. To obtain the commensurability of frequencies, we prescribe an additional condition in the form $\omega_1 = \omega_2 = \omega_3 = 1$, which of course is restrictive and therefore it must be justified in reality. The results of computation by application of the MH-P method and comparison with results of numerical integration using Runge-Kutta method are plotted on

Figures 5, 6 and 7, where again an excellent agreement can be found. The convergence test with prescribed tolerance $tol = 10^{-4}$ results in values of integrals: $J_1 = 3.05072 \times 10^{-5}, J_2 = 8.46863 \times 10^{-5}$ and $J_3 = 5.82898 \times 10^{-5}$. The parametric dependencies of evolutions of populations $x_1(t), x_2(t)$ and $x_3(t)$, which are computed by MH-P method and comparison of results with Runge-Kutta method are shown on Figure 8, where again an excellent agreement is obtained.

Unlike time histories of populations in almost-periodic case, oscillations on Figures 5-7 after the transient phase now consist from repeating cycles, which confirm the periodicity. The same conclusion follows also from the Figure 8, where trajectories approaches the periodic orbits after the transient phenomenon dies.
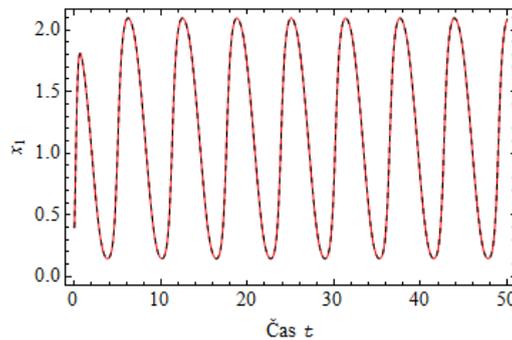
Figure 5. The evolution of population$x_1(t)$ in the periodic case. —— Solution, computed by MH-P method, - - - Solution, computed by numerical integration using Runge-Kutta method.
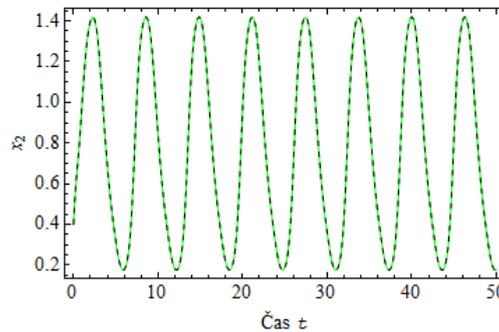
Figure 6. The evolution of population$x_2(t)$ in the periodic case. —— Solution, computed by MH-P method, - - - Solution, computed by numerical integration using Runge-Kutta method.
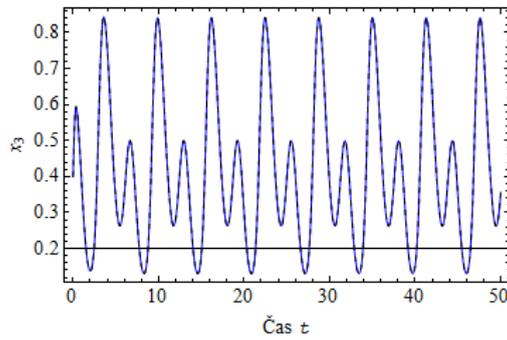
Figure 7. The evolution of population $x_3(t)$ in the periodic case. _____ Solution, computed by MH-P method, - - - Solution,computed by numerical integration using Runge-Kutta method.
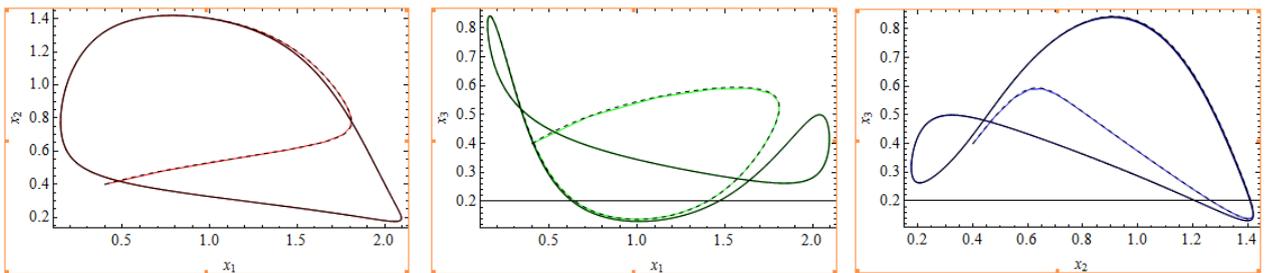
Figure 8. Parametric dependencies of populations $x_1(t)$, $x_2(t)$ in $x_3(t)$ in the periodic case. —— Solution, computed by MH-P method, - - - Solution, computed by numerical integration using Runge-Kutta method

As third example, the competitive predator-prey ecosystem (13) is analyzed, which has constant coefficients only. Therefore, all time-dependent terms in Eqs. (13) are omitted and corresponding Lotka-Volterra equations are reduced on the form:

$$\begin{cases} \dot{x}_1(t) = x_1(t)\left[5 - 3x_1(t) - x_2(t) - x_3(t)\right] \\ \dot{x}_2(t) = x_2(t)\left[4 - x_1(t) - 3x_2(t) - x_3(t)\right] \\ \dot{x}_3(t) = x_3(t)\left[3 - x_1(t) - \frac{1}{5}x_2(t) - 4x_3(t)\right] \end{cases} \quad (19)$$

The computation by MH-P method is performed with the same initial conditions as in first two examples. The results of computation by application of the MH-P method are plotted on the Figure 9. The comparison with results of numerical integration using Runge-Kutta method is shown and an excellent agreement is obtaned again. The convergence test with prescribed tolerance $tol = 10^{-4}$ results in values of integrals: $J_1 = 8.35791 \times 10^{-5}, J_2 = 3.40169 \times 10^{-5}$ and $J_3 = 2.45845 \times 10^{-6}$.
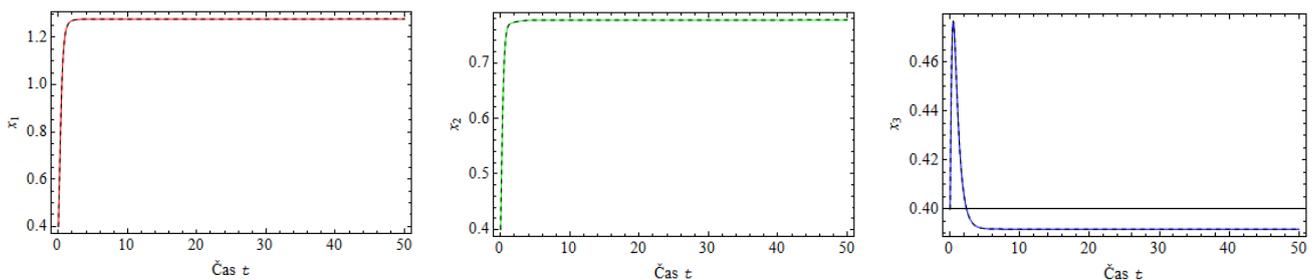
Figure 9. The evolution of population $x_3(t)$ in the periodic case. —— Solution, computed by MH-P method, - - - Solution,computed by numerical integration using Runge-Kutta method.

Time histories on the Figure 9 reveal, that first two species, which belong to the prey and predator, respectively, survive. Their populations grow according to the logistic curve, approaching the corresponding carrying capacities. On the contrary, the third species of superpredator is after some growth in a short initial phase driven to the extinction.

4. Conclusions

In this paper, a generalized predator-prey model with time-dependent coefficients of populations growth rates and time-dependent coefficients of mutual interactions between populations of speciesis treated, where competitive ecosystems with almost-periodic, periodic and constant coefficients are analyzed in details. To obtain approximate analytical solutions of generalized Lotka-Volterra equations for almost-periodic, periodic and constant coefficients, respectively, the MH-P metod is developed in an explicit form, which is appropriate for analysis on long time intervals. To ensure the desired accuracy of the MH-P method on the entire time interval, the useful convergence test of the subsequent solutions is provided.Nevertheless, the results computed by MH-P method are in all examples compared with results of the numerical integration using Runge-Kutta method, where an excellent agreement is always obtained. The analytical form of solutions has many advantages, which allow analysis of stability, parametric studies and bifurcations. Such possibilities as well as the study of the chaotic behaviour in predator-prey ecosystems [9] are challenging for the future research work. Besides this, the MH-P method is well suited for computation of highly nonlinear ecosystems.

References

1. Hoppensteadt, F.Predator-prey model. *Scholarpedia*1, **2006**, pp.1563.

2. Hoppensteadt, F. C.Mathematical methods of population biology. *Courant Institute of Mathematical Sciences New York University*, New York, 1977.

3. Smith, H. L.Periodic orbits of competitive and cooperative systems.*Journal of Differential Equations***65**, **1986**, pp. 361-373.

4. He, J. H. A coupling method of homotopy technique and perturbation technique for nonlinear problems,*Int. J. Non-Linear Mech.***35**(1),**2000**, pp. 37-43.

5. Pušenjak, R. R., Oblak, M. M., Tičar, I. Nonstationary Vibration and Transition through Fundamental Resonance of Electromechanical Systems Forced by a Nonideal Energy Source. *International Journal for Nonlinear Sciences and Numerical Simulation*, vol. **10**, no. 5, May **2009**, pp. 637-660.

6. Pušenjak, R. R., Oblak, M. M., Tičar, I. Modified Lindstedt-Poincare method with multiple time scales for combination resonance of damped dynamical systems with strong non-linearities. *Int. j. of nonlinear sci. & numer. simul.*, vol. **11**, no. 3,**2010**, pp. 173-201.

7. Chowdhury, M. S. H.,Hashim, I., Momani, S. The multistage homotopy-perturbation method: A powerful scheme for handling the Lorenz system. *Chaos, Solitons and Fractals* **40**,**2009**, pp. 1929-1937.

8. Pušenjak, R., Oblak, M., Lipičnik, M.Evolution of a Predator-Prey System with Periodic Excitation by Using Multistage Homotopy Perturbation Method.*Kuhljevi dnevi*, 26-27. September 2012, Rogaška Slatina.(accepted for publication).

9. Vano,J. A., Wildenberg, J. C., Anderson,M. B., Noel,J. K. and Sprott, J. C.Chaos in low-dimensional Lotka-Volterra models of competition.*Nonlinearity***19**, **2006**, pp. 2391-2404.