Numerical Research of the Chemostat Model for the Single-Nutrient Competition

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Abstract. *The continuous culture of micro-organisms using the chemostat is an important research technique in microbiology and population biology. We consider here chemostat model for the single-nutrient competition. For the model we find the solution when the parametric relation $a_1 = a_2$ is observed. It is to be proved that integration of the original system of the differential equations of the third order is reduced to integration of the differential equation of the first order. By performing a numeric integration we can find the solution to the model considered. The program module is built which allows visualizing the solutions for the concrete values of parameters changing in the set intervals.*

1 Introduction. Setting the problem

Competition modeling is one of the more challenging aspects of mathematical biology. The one of the simplest form of competition, when two or more populations compete for the same resource such as a common food supply. This is called exploitative competition. A simple example of this type of competition occurs in a laboratory device, called a *chemostat*. The chemostat models an open system, and although the exact assumptions of the model may be limited to laboratory environments, it can serve as a paradigm for more complicated naturally occurring open systems. The input and removal of nutrients to and from the chemostat represent the continuous turnover of nutrients in nature. The outflow of organisms is formally equivalent to nonspecific death, predation, or emigration, which always occur in nature.

An important advance of this model over classical Lotka-Volterra formulations of competition is that the limiting resource for which competition is being expressed is represented explicitly by an equation in the system. In the Lotka-Volterra model, only the numbers of competing organisms are represented. The result of leaving out an equation for the resource is that the outcome of competition cannot be predicted before the organisms are actually grown together. In the present formulation, the outcome of competition can be predicted before the organisms compete, from measurements of growth parameters of the organisms when grown alone on the resource.

The present analysis concerns the behavior of a predator-prey system consisting of two predator species, x_1 and x_2, and a single prey species, S. We assume that the predator species compete purely exploitatively, with no interference between rivals. Both species have access to the prey and compete only by lowering the population of shared prey. The model is given by the system of the differential equation. The model is given by the system of the differential equations

$$\begin{cases} s'(t) = D - s(t) - \dfrac{m_1 x_1(t) s(t)}{a_1 + s(t)} - \dfrac{m_2 x_2(t) s(t)}{a_2 + s(t)}, \\ x_1'(t) = \left(\dfrac{m_1 s(t)}{a_1 + s(t)} - D \right) x_1(t), \\ x_2'(t) = \left(\dfrac{m_2 s(t)}{a_2 + s(t)} - D \right) x_2(t), \end{cases} \tag{1}$$

where $x_i(t)$ (i=1 or 2) is the number of the i^{th} predator at time t, $s(t)$ is the number of the prey at time t, m_i is the maximum growth rate of the i^{th} predator, D is the death rate for the i^{th} predator, a_i is the half-saturation constant for the i^{th} predator, which is the prey density at which the functional response of the predator is half maximal. We analyze the behavior of solutions of this system of ordinary differential equations in order to answer the biological question: under what conditions will neither, one, or both species of predator survive? If only one predator survives, we also seek to determine the limiting behavior of the surviving predator and its prey. The mathematical results, the biological background, etc. for our system (1), may be found in Smith, Waltman [1] and Hsu, Waltman [2].

2 Statement of results

A qualitative theory and numerical methods for solving differential equations were used to study the properties of solutions of differential equations (1) in [1]. Let us consider the principal results obtained for the system (1) in [1], [3].

Definition. For $m > 1$, $\lambda = \frac{a}{m-1}$; λ is called the *break-even concentration.*

THEOREM 1[1]. Suppose that $m_i > 1$, $(i = 1,\ 2)$ and that $0 < \lambda_1 < \lambda_2 < 1$.
Then any solution of the system (1) with $x_i(0) > 0$ satisfies

$$\lim_{t\to\infty} S(t) = \lambda_1, \quad \lim_{t\to\infty} x_1(t) = 1 - \lambda_1, \quad \lim_{t\to\infty} x_2(t) = 0.$$

Thus the Theorem 1 is an example of the principle of competitive exclusion: only one competitor can survive on a single resource while it survives competitor whose break-even concentration is lower. If $\lambda_1 = \lambda_2$ then coexistence is possible [1]. This exactly balanced parameters - and cannot be expected to be found in nature.

Problem: To find a solution of the system (1) by interpolating functions for $a_2 = a_1$ using a numerical integration.

Solving of the problem. Using the *Mathematica* system we obtain two functions s, x_1 in the analytical form as a functions of variables t and x_2. After this we find the function x_2 in the form of the interpolating function.

Without loss generality we set [1] $D = 1$. We also set $a_2 = a_1,\ m_2 = \mu\ m_1$, where μ is a constant. Then system (1) may be rewritten in the form

$$\begin{cases} s'(t) = \dfrac{a_1 - s(t)\left(a_1 + m_1\left(\mu x_2(t) + x_1(t)\right) - 1\right) - s(t)^2}{a_1 + s(t)}, \\ x_1'(t) = x_1(t)\left(\dfrac{m_1 s(t)}{a_1 + s(t)} - 1\right), \\ x_2'(t) = x_2(t)\left(\dfrac{\mu m_1 s(t)}{a_1 + s(t)} - 1\right). \end{cases} \tag{2}$$

We write system (2) in the codes the *Mathematica* system as

$f[u\_\,, i\_\,] := \dfrac{m_i u}{a_i + u};$

$ex1 = 1 - s[t] - f[s[t], 1]x_1[t] - f[s[t], 2]x_2[t];$

$ex2 = x_1[t](f[s[t], 1] - 1);$

$ex3 = x_2[t](f[s[t], 2] - 1);$

$\rho 1 = \{a_2 \to a_1,\ m_2 \to \mu\ m_1\};$

$sys = \{s'[t] == ex1,\ x_1'[t] == ex2,\ x_2'[t] == ex3\}/.\rho 1//Simplify;$

We eliminate function $s(t)$ from the second and the third equations of the system *sys*

$eq0 = Eliminate[\{sys[[2]], sys[[3]]\}, s[t]]//FullSimplify$

$$x_1(t)\left(x_2'(t) - (\mu - 1)x_2(t)\right) = \mu x_2(t)x_1'(t). \quad (3)$$

We integrate the equation (3) and obtain function $x_2(t)$ in the form (4)

$sol1 = Simplify[Solve[\int \frac{eq0[[1]] - eq0[[2]]}{x_1[t]x_2[t]}\, dt == 0,$
$x_2[t]], x_1[t] > 0\&\&\ x_2[t] > 0\&\&\ \mu > 0\&\&\ t \in Reals][[1]]$

$$\left\{x_2(t) \to e^{(\mu-1)t}x_1(t)^{\mu}\right\}. \quad (4)$$

Summing up three equations of the system (2) we obtain separable differential equation in relation to function u.

$sol2 = DSolve[u'[t] == 1 - u[t], u[t], t]/.u[t] \to s[t] + x_1[t] + x_2[t]//Flatten;$

We integrate this equation and find function $s(t)$ in the form (5)

$sol3 = Solve[sol2/.Rule \to Equal, s[t]]/.sol1//Simplify//Flatten$

$$\left\{s(t) \to e^{-t}\left(c_1 - e^{\mu t}x_1(t)^{\mu} - e^t x_1(t) + e^t\right)\right\}, \quad (5)$$

where c_1 is an arbitrary constant. Now we can find a differential equation of the first order which defines the function $x_1(t)$

$eq3 = sys[[2]]/.sol1/.D[sol3, t]/.sol3//Simplify$

$$x_1'(t) = x_1(t)\left(-\frac{m_1\left(-c_1 + e^{\mu t}x_1(t)^{\mu} + e^t x_1(t) - e^t\right)}{a_1 e^t + c_1 - e^{\mu t}x_1(t)^{\mu} - e^t x_1(t) + e^t} - 1\right). \quad (6)$$

Thus we have the next theorem.

THEOREM 2. Suppose that $a_1,\ m_1,\ \mu$ are positive numbers and $m_1 \neq 1$. Then the solution of the system (2) satisfies equalities (4)-(6). Namely, functions $x_2(t)$, $s(t)$ have the form

$$x_2(t) = e^{(\mu-1)t}x_1(t)^{\mu},$$

$$s(t) = e^{-t}\left(c_1 - e^{\mu t}x_1(t)^{\mu} - e^t x_1(t) + e^t\right),$$

where c_1 is an arbitrary constant and function $x_2(t)$ satisfies the first order differential equation (6).

Remark 1. Solution of the equation (6) with the known values of parameters $a_1,\ m_1,\ \mu$ we obtain with the command NDSolve [4]. We can show this by using the following Module.

3 Module for Examples

We make Module which allows visualizing the solutions of the system (2) for the known values of parameters $a_1,\ m_1,\ \mu$, initial condition for function x_1 while the values of parameters are being selected from the intervals determined by the biological conditions of the problem. We set that the arbitrary constant c_1 is equal to one.

$$Manipulate[Module[\{sol, x1, t\}, sol = First[NDSolve[\{$$

$$x1'[t] == \frac{x1[t](E^t a_1 + (-1 + m_1)(1 - E^t + E^t x1[t] + E^{t\mu}x1[t]^{\mu}))}{1 - E^t - E^t a_1 + E^t x1[t] + E^{t\mu}x1[t]^{\mu}}, x1[0] == \alpha\}, x1, \{t, 0, tt\},$$

$$MaxSteps \to 10^6]];\ \ If[plot, Plot[1 - E^{-t} - x1[t] - E^{-t+t\mu}x1[t]^{\mu}/.sol, \{t, 0, tt\},\ AxesOrigin \to$$

$$\{0, 0\}, PlotStyle \to \{Thick\}, AxesLabel \to \{Style[time, 18], Style[s, 18]\},\ AxesStyle \to$$

$$\{\{Thickness[0.006], Directive[14]\}, \{Thickness[0.006], Directive[14]\}\}], Plot[x1[t]/.sol, \{t, 0, tt\},$$

$AxesOrigin \to \{0, 0\}, PlotStyle \to \{Thick\}, AxesLabel \to \{Style[time, 18], Style[x_1, 18]\},$
$AxesStyle \to \{\{Thickness[0.006], Directive[Black, 14]\}, \{Thickness[0.006], Directive[14]\}\}],$
$Plot[E^{-t+t\mu} x1[t]^{\mu} /.sol, \{t, 0, tt\}, AxesOrigin \to \{0, 0\}, PlotStyle \to \{Thick\},$
$AxesLabel \to \{Style[time, 18], Style[x_2, 18]\}, AxesStyle \to \{\{Thickness[0.006], Directive[14]\},$
$\{Thickness[0.006], Directive[14]\}\}]]], \{plot, \{True \to$ "`nutrient` " s, $False \to$
"`predator` " x_1, $Indeterminate \to$ "`predator` " $x_2\}\}, \{\{\mu, 0.8,$ "`Parameter` μ"$\}, 0.5, 2.5\},$
$\{\{a_1, 0.01,$ "`Parameter` a_1"$\}, .001, .9\}, \{\{m_1, 2,$ "`Parameter` m_1"$\}, 1.5, 10\}, \{\{\alpha, 10^{-3},$
"`the initial concentration of the` x_1"$\}, 10^{-6}, 10\}, \{\{tt, 2,$ "`time`"$\}, 10^{-2}, 10^{2}\}]$

Remark 2. Thus for a given parameters $a_1 = a_2 = 0.01$, $m_1 = 2$, $m_2 = 1.99$, we get that break-even concentration of predators x_1 and x_2 has the following values $\lambda_1 = 0.01$ and $\lambda_2 = 0.010101$, which are almost equal. For this values of the parameters we can see that short period of the coexistence occurs between competing predators. Hence, results got according to the Module and Theorem 1 coinside. This occurrence is displayed on the graphs of functions x_1 and x_2 (Fig. 2, 3).

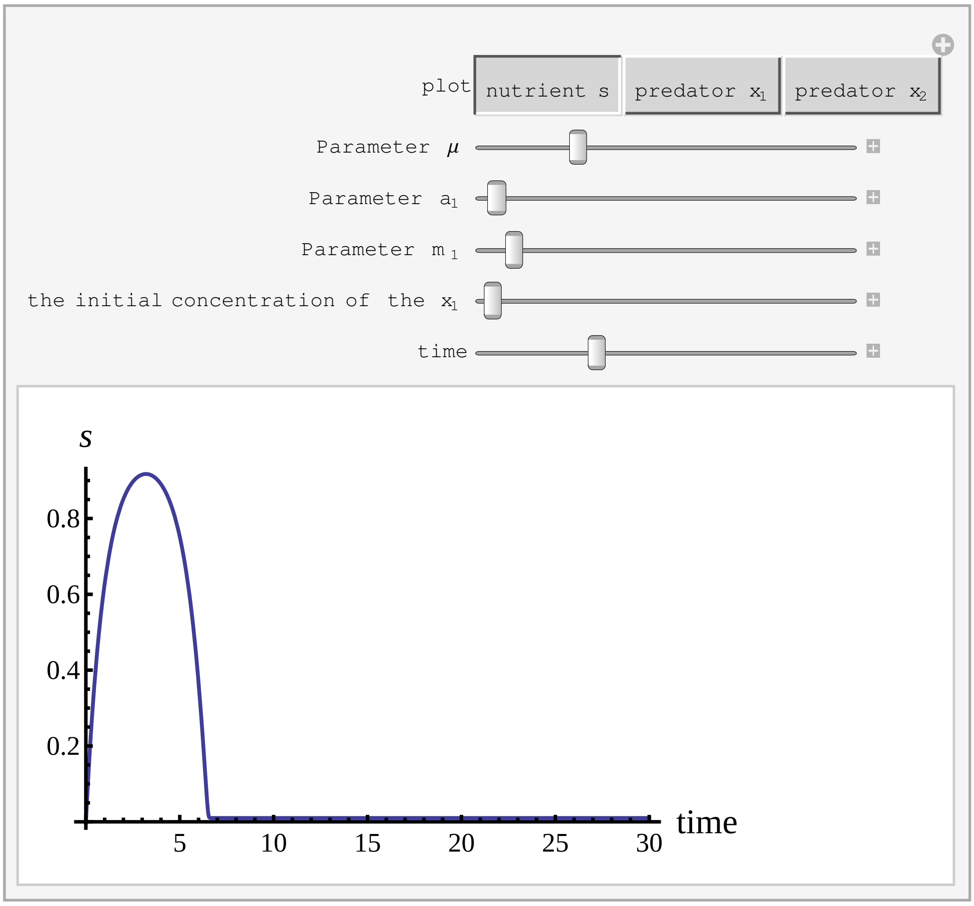

Figure 1: Graphic of the function $s(t)$ for $\mu = 0.995$, $a_1 = 0.01$, $m_1 = 2$, $x_1(0) = 10^{-3}$, $t = 30$.

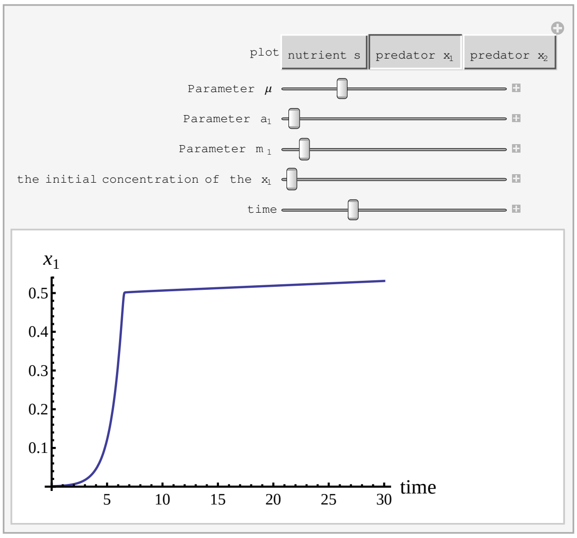

Figure 2: Graphic of the function $x_1(t)$ for $\mu = 0.995$, $a_1 = 0.01$, $m_1 = 2$, $x_1(0) = 10^{-3}$, $t = 30$.

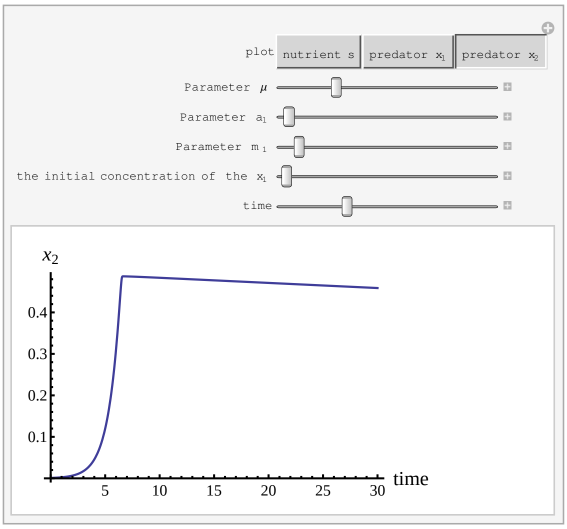

Figure 3: Graphic of the function $x_2(t)$ for $\mu = 0.995$, $a_1 = 0.01$, $m_1 = 2$, $x_1(0) = 10^{-3}$, $t = 30$.

References

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[4] *http://reference.wolfram.com/mathematica/ref/NDSolve.html*