Universität Hamburg
Fachbereich Mathematik

Zentrum für Modellierung und Simulation

Hamburger Beiträge
zur Modellierung und Simulation

Heft 12   Februar 1999

STRATEGIES OF COMPETITION IN CONSTANT AND FLUCTUATING ENVIRONMENTS

Johannes Mainik / Claus Peter Ortlieb

Mathematische Modellierung und Simulation

Die mathematisch-naturwissenschaftliche Methode, gegründet auf der Überzeugung, dass „das Buch der Natur in der Sprache der Mathematik geschrieben“ sei (Galilei), findet heute weit über ihren ursprünglichen Gegenstandsbereich hinaus Verwendung. *Mathematische Modellierung*, also der Versuch, das Nachdenken über eine Fragestellung in mathematische Termini zu übersetzen, verfolgt den Zweck, sich die Stringenz mathematischer Argumente auch für die Bearbeitung von Problemen außerhalb der Mathematik zu sichern. Im Begriff der *Simulation* ist in diesem Zusammenhang der Anspruch enthalten, dass die Analyse eines mathematischen Modells oder sein Nachvollzug auf dem Computer immer auch auf Erkenntnisse zielt, die über die Mathematik hinausweisen.

Der Erfolg dieser Methode bei der Behandlung physikalischer und technischer Systeme hat es nahegelegt, ihr Anwendungsfeld zu erweitern. In den *Lebens- und Sozialwissenschaften* geht es bis in Bereiche hinein, die gesellschaftliches Handeln zum Gegenstand haben und ihrerseits beeinflussen. Dabei werden häufig nur die wissenschaftlichen Ergebnisse wahrgenommen, während den Methoden, mit denen sie zustandekommen, blind vertraut wird. Doch die Mathematik als „höchste Form der Rationalität“ anzupreisen, wie es auch mathematische Fachwissenschaftler gerne tun, besagt noch nichts über ihre Bedeutung für die Erkenntnis gesellschaftlicher und natürlicher Phänomene und Zusammenhänge. Zu hinterfragen ist insbesondere die verbreitete Auffassung, bei mathematischen Modellen handele es sich in aller Schlichtheit um „Abbilder der Wirklichkeit“.

Das Zentrum für Modellierung und Simulation und diese Schriftenreihe haben zum Ziel, die *methodischen* Fragestellungen zu behandeln und zu durchleuchten, die die mathematische Bearbeitung „realer“ Probleme aufwirft. Die Frage nach dem „richtigen“ Einsatz mathematischer Modellierung im Einzelfall gehört ebenso dazu dazu wie die Frage nach Kriterien dafür im Allgemeinen. Gibt es eine „Methode“ der Modellierung und Simulation, und worin bestehen ihre Regeln, ihre Möglichkeiten, ihre Grenzen? Es ist klar, dass eine so komplexe Fragestellung mehr als nur einen Zugang erfordert. Gefragt sind u. a.

- Darstellungen und Untersuchungen von selbst entwickelten ebenso wie die Auseinandersetzung mit in der Literatur vorgefundenen mathematischen *Modellklassen* und *Fallstudien*,
- Untersuchungen zu spezifischen, am Modelltyp orientierten *Instrumenten und Methoden* der mathematischen Modellierung,
- *wissenschaftstheoretische und -historische* Abhandlungen zur gesellschaftlichen Bedeutung von Mathematisierungsprozessen.

Zentrum für Modellierung und Simulation
Fachbereich Mathematik der Universität Hamburg
Bundesstraße 55

D - 20146 Hamburg

Telefon 040 4123 5108
Fax 040 4123 5117
e -mail zms@math.uni-hamburg.de

Strategies of competition in constant and fluctuating environments

J. Mainik, C. P. Ortlieb

Centre for Modelling and Simulation, University of Hamburg,

Bundesstrasse 55, 20146 Hamburg.

E-mail: Mainik: mainik@gmx.de, Ortlieb: ortlieb@math.uni-hamburg.de

Abstract

The competitive exclusion principle which is formulated within the framework of the classic Lotka-Volterra model of species competing for the same resource has had a profound impact on ecological thinking. This principle is still an actual theme of mathematical and biological research.

In this paper we study the dynamics of several competition models with constant and variable environments. The competitive exclusion principle will be proved for a wide class of models with constant environments. In the case of variable environments we will show that the efficiency of different competition strategies (gleaner, exploiter and hunger resistance strategies) depends on the intensity of the environment's fluctuations.

Key words: exploitative competition - fluctuating environment - competitive exclusion - coexistence.

1 Introduction

The so-called competitive exclusion principle was formulated for the first time within the framework of the classic competition models by Volterra. It asserts that one of two species which compete for a single source must go extinct [16,28]. The interest and discussions aroused by this theme [12] prompted further research.

Traditionally, mathematicians distinguish between abiotic resource models (models with limiting factors)

$$
\begin{aligned}
x_i' &= u_i(y_1,\cdots,y_k)x_i, \quad i=1,\cdots,n,\\
y_j &= s_j(x_1,\cdots,x_n), \quad j=1,\cdots,k
\end{aligned}
\tag{1}
$$

and biotic resource models

$$
\begin{aligned}
x_i' &= u_i(y_1,\cdots,y_k)x_i, \quad i=1,\cdots,n,\\
y_j' &= g_j(x_1,\cdots,x_n,y_1,\cdots,y_k)y_j, \quad j=1,\cdots,k.
\end{aligned}
\tag{2}
$$

$y_1,\cdots,y_k$ are the concentrations of k resources, and $x_1,\cdots,x_n$ are the densities of n species competing for these resources, $k<n$. It holds that

$$\frac{\partial u_i}{\partial y_j}\geq 0, \quad \frac{\partial s_j}{\partial x_i}\leq 0, \quad \frac{\partial g_j}{\partial x_i}\leq 0. \tag{3}$$

Here and further t is the time and $' = \frac{d}{dt}$. The competition is purely indirect, because the species just share the food. There is no other mutual negative interference. The growth rates of the competitors depend only on the food supply. The classical Lotka-Volterra model belongs to the first group with $n=2$, $k=1$ and linear functions u_i and s_1.

The competitive exclusion principle can be formulated in different ways. We use the definition proposed by McGehee and Armstrong [1,17]. A system is said to exhibit persistence if it has a compact attractor $\mathcal{K}_0$ in the interior $R^n_+ = \{(x_1>0,\cdots,x_n>0)\}$ of the state space. It means that $\mathcal{K}_0$ has an open neighbourhood $\mathcal{U}_0\subset R^n_+$, so that any orbit starting in $\mathcal{U}_0$ remains in $\mathcal{U}_0$ and tends asymptotically to $\mathcal{K}_0$. The survival of the species in $\mathcal{U}_0$ is thus ensured. The competitive exclusion principle holds if there are no such attractors.

For abiotic resource models the competitive exclusion principle holds in the case $n=2$, $k=1$ or if all functions u_i, $1\leq i\leq n$, are linear. With the exception of special cases, at least $n-k$ consumers go extinct here and at most k competitors can survive on k resources. We say that the ith species goes extinct if $\lim_{t\to+\infty}x_i(t)=0$. For $n>2$ there are no point-attractors in the interior of the state space [1,9,14,17,21]. But in case $n\geq 3$ and $k=1$ the competitors can coexist [19] so that the competitive exclusion principle does not hold for these models in general.

For biotic resource models the competitive exclusion principle holds if all functions u_i, $1\leq i\leq n$, are linear. In general, n consumers can coexist on $k<n$ resources. An appropriate model for the case $n=2$ and $k=1$ is shown in [17].

Another important example is given by the so-called chemostat model which belongs to the most cited ones. In simple cases it is described by the following system of differential equations

$$\begin{aligned} x_i' &= (\frac{w_i y}{h_i + y} - m_i)x_i, \quad 1 \le i \le n. \\ y' &= (y_0 - y)D - \sum_{i=1}^{n} \frac{f_i y}{h_i + y} x_i \end{aligned} \tag{4}$$

Here $x_1, \cdots, x_n$ are the densities of the consumers, and y is the nutrient concentration. The growth rates of the competing species are given by Michaelis-Menten functions (Monod model [18]). y_0 is the input concentration, D is the dilution rate, w_i, m_i and h_i are the rates of growth, mortality and the half-saturation constant for the ith species. In a simple case these parameters are constant.

The chemostat technique is very popular in laboratory research in microbiology and biology of populations [24]. The dynamics' high correspondence with the empirical data for this model is shown in [8]. The competitive exclusion principle for the case $D = m_1 = \cdots = m_n$ has been proved in [10]. The winner is the consumer with the lowest persistence threshold λ_i. The persistence threshold of the ith species is the lowest nutrient concentration necessary for survival in the absence of competitors, i.e. $x_i'(\lambda_i) = 0$. This threshold criterion has been discussed and tested empirically many times [13,27].

Theoretical ecology accepts that the principle of competitive exclusion is very important, but other mechanisms of competition must be evaluated, too. For example, a distinction can be made between the so-called gleaner and exploiter species which have different competition strategies [2,5,25,26]. The former are efficient at a low food level (low persistence threshold); the latter have high growth rates when the food is abundant.

The vast majority of mathematical models, for which the competitive exclusion principle was proved, considered the environment as constant. The temporal variability of the parameters and the environment is a real factor which can have a decisive effect on competition processes. It is important for the population dynamics, whether external (e.g. seasonal) oscillations make it possible to avoid the competitive exclusion. Looking at it from a mathematical point of view, we must analyze the simplifying assumptions which allow us to prove the competitive exclusion principle [1,12]. Here we recall to mind several results that belong to this research direction.

The existence of positive periodic solutions for a model of the Lotka-Volterra type is demonstrated in [3]. But it is not clear whether these periodic solutions are stable. In this respect, the results of the paper [4] are interesting. The existence of periodic solutions for the chemostat model is proved in

[7,11]. Interesting results of numerical simulations for the chemostat model in a variable environment are shown in [6]. An informative survey of other possible competition mechanisms for plankton communities can be found in [22].

2 Statement of the models

The competition models we consider cannot be assigned exactly to the described types. In general, the dynamics is described by the following system of $n+1$ differential equations

$$\begin{aligned} x_1' &= r_1(y)x_1 \\ &\vdots \\ x_n' &= r_n(y)x_n \\ y' &= C(y) - (g_1(y)x_1 + \cdots + g_n(y)x_n) \end{aligned} \tag{5}$$

The functions $r_i(y)$, $g_i(y)$, $i = 1, \cdots, n$, and $C(y)$ are Lipschitz continuous here; furthermore, the following conditions are satisfied:

1. $r_i(y)$, $1 \leq i \leq n$, increase monotonously, $r_i(0) < 0$ and $r_i(y) > 0$ for sufficiently large y,
2. $g_i(y)$, $1 \leq i \leq n$, increase monotonously and $g(0) = 0$,
3. $C(y)$ is a non-increasing function, $C(0) > 0$.

Here $x_1, \cdots, x_n$ are the densities of the n species competing for a single source, y is the density of this nutrient. $r_i(y)$ is the growth rate and $g_i(y)$ is the attack rate of the ith species, $i = 1, \cdots, n$. The term $C(y)$ determines the speed of the food input. The case $C(y) = C_0 > 0$ is especially interesting for us. On these conditions the process described by (5) can be considered as an external food input with the constant speed C_0.

In the following we will use the term "species x_i" besides "ith species". This will not create any misunderstandings because it is always clear whether the species itself or its density is meant. The persistence threshold λ_i for x_i is the positive solution of the equation $r_i(\lambda_i) = 0$. Further we assume $\lambda_1 < \lambda_i$, $i = 2, \cdots, n$, and $C(\lambda_1) > 0$ because otherwise all the species will obviously go extinct.

The system (5) is an autonomous system of differential equations corresponding to a constant environment. We will prove the exclusion principle for this system on some additional conditions. Anyway, they are satisfied for two especially important models. These models are described by the following systems of differential equations.

The first one has the form

$$\begin{aligned} x_1' &= r_1(y)x_1 \\ &\vdots \\ x_n' &= r_n(y)x_n \\ y' &= C(y) - (f_1x_1 + \cdots + f_nx_n)y \end{aligned} \tag{6}$$

with

$$r_i(y) = \frac{w_i y}{h_i + y} - m_i, \quad i = 1, \cdots, n. \tag{7}$$

The parameters m_i, w_i and h_i in the Michaelis-Menten terms are positive. The parameter $m_i > 0$ determines the maximum mortality rate of x_i (for $y = 0$). The maximum growth rate of x_i (for $y \to \infty$) equals $w_i - m_i$, and we assume $w_i > m_i$, $1 \leq i \leq n$. The persistence threshold for the species x_i equals

$$\lambda_i = \frac{m_i h_i}{w_i - m_i}, \quad i = 1, \cdots, n.$$

The second system has the form

$$\begin{aligned} x_1' &= r_1(y)x_1 \\ &\vdots \\ x_n' &= r_n(y)x_n \\ y' &= C(y) - (g_1(y)x_1 + \cdots + g(y)x_n) \end{aligned} \tag{8}$$

with the same growth rates $r_i(y) = w_i y/(h_i + y) - m_i$, $i = 1, \cdots, n$, as before. The attack rates $f_i y/(h_i + y)$ are here, unlike (6), saturated functions as in the chemostat model. The quotient w_i/f_i is the yield factor for the ith species, $i = 1, \cdots, n$. The system (8) is a generalization of the system (4).

In the case $C(y) = C_0$ these systems differ from the chemostat model in an important detail. The term $-Dy$, which describes in the chemostat model the loss of food because of dilution, is absent here. In real models (e.g. with rivers transporting food into the sea) there is no such loss indeed, so that our model is biologically sensible. There are also other biological communities which this model seems to fit.

Later these models will be considered in inconstant environments. The environment's variability will be modeled by pulsing food supply. Source fluctuations of this kind are characteristic of the semi-continuous cultures and correspond to a gradual delivery of nutrients. They appear in many empirical studies, e.g. [22,23]. It is shown in [23] that pulsations of this kind are an important factor for competing communities. Such source pulsations (that can be caused by climate) can also be found in real systems where they must have similar effects on the real dynamics.

So we will see that the variability of sources can support coexistence of consumers or allow some other species to win the competition. Furthermore, it can be seen that the competition strategies distinguished by population ecologists are really adapted to the intensity of the oscillations. Besides the persistence threshold and the maximum growth rate, the hunger resistance of a species also proved to be a very important factor in our competition models. The hunger resistance of the ith species is determined by the decrease speed of the density x_i if there is not enough food for survival. Fig. 1 shows the growth rates $r_1(y)$ and $r_2(y)$ of two species . The first one has a lower persistence threshold ($\lambda_1 < \lambda_2$), the second one has a higher growth rate if the nutrient is abundant ($r_2(y) > r_1(y)$ for large y) and also a better hunger resistance ($r_2(y) > r_1(y)$ for small y).

3 Dynamics in a constant environment

Theorem 1. *If for the system (5) constants $a_2, \cdots, a_n$ exist, such that*

$$a_i r_i(y) \leq g_i(y) r_1(y), \quad i = 2, \cdots, n, \tag{9}$$

then the point $P_0 = (C(\lambda_1)/g_1(\lambda_1), 0, \cdots, 0, \lambda_1)$ is globally asymptotically stable in the domain $S = \{(x_1, \cdots, x_n, y) : x_1 > 0, x_2 \geq 0, \cdots, x_n \geq 0, y \geq 0\}$.

Proof. It is easy to see that each solution of the system (5) remains in the domain S, if the start point $P = (x_1(0), \cdots, x_n(0), y(0))$ lies in S. The coefficients $a_2, \cdots, a_n$ obviously are positive. We consider a certain Ljapunov function V on S with the following gradient

$$\nabla V = (-\frac{C(\lambda_1)}{x_1} + g_1(\lambda_1), a_2, \cdots, a_n, r_1(y)). \tag{10}$$

Due to $a_2 > 0, \cdots, a_n > 0$, from (10) follows immediately that for any real number α the domain

$$S_\alpha = \{(x_1, \cdots, x_n, y) : V(x_1, x_2, \cdots, x_n, y) \leq \alpha\}$$

is compact. It holds for each solution of (5) that

$$\begin{aligned} V' &= \frac{d}{dt} V(x_1(t), \cdots, x_n(t), y(t)) = r_1(y)[C(y) - C(\lambda_1)] \\ &+ x_1 r_1(y)[g_1(\lambda_1) - g_1(y)] + \sum_{2 \leq i \leq n} x_i [a_i r_r(y) - g_i(y) r_1(y)] \leq 0, \end{aligned}$$

since all the summands on the right side are nonpositive. The term $x_1 r_1(y)[g_1(\lambda_1) - g_1(y)]$ equals 0 if $x_1 = 0$ or $y = \lambda_1$. Thus we have $V' \leq 0$, and S_α is positively invariant. Then the ω-limit $\omega(P)$ is a non-empty compact subset of S for any initial point P, $P \in S$, [9]. For $(x_1, \cdots, x_n, y) \in \omega(P)$ we have $V'(x_1, \cdots, x_n, y) = 0$. Due to $x_1 > 0$ one obtains $y = \lambda_1$, and $r_i(\lambda_1) < 0$, $i = 2, \cdots, n$, yields $x_2 = \cdots = x_n = 0$. Since $y' = 0$ here, the last equation of the system (5) yields $x_1 = C(\lambda_1)/g_1(\lambda_1)$. For every orbit starting in S the ω-limit consists only of the point P_0 which is therefore globally asymptotically stable on S. ■

Remark. The exact form of the attack rate $g_1(y)$ does not matter here. It only needs to grow strictly (strictly even in λ_1).

Corollary 1. *The exclusion principle holds for the system (6).*

Proof. It must be shown that in this case constants a_i, $i = 2, \cdots, n$, do exist, so that (9) is satisfied. We begin with a simple remark which also will be useful later.

Let $p_1(y)$ be a convex function and let $p_2(y)$ be a concave one. Let the graph of $p_i(y)$ intersect the x-axis at the point $y_i > 0$, $i = 1, 2$, increasing there strictly. If $y_1 < y_2$, then a positive coefficient a exists, such that $ap_1(y) < p_2(y)$.

For smooth functions we can determine $a > 0$, for example, by means of the parallelity of the tangents at the points $(y_1, 0)$ and $(y_2, 0)$, i.e. $ap_1'(y_1) = p_2'(y_2)$. Generally we can use the appropriate one-sided tangents. For the system (6) the function

$$p_1(y) = f_i y r_1(y) = f_i y(\frac{w_1 y}{h_1 + y} - m_1) \tag{11}$$

is convex ($p_1'(y) = 2f_i w_i h_i^2/(h_i + y)^3 \geq 0$), and

$$p_2(y) = r_i(y) = \frac{w_i y}{h_i + y} - m_i) \tag{12}$$

is concave ($p_2''(y) = r_2''(y) = -2w_i h_i/(h_i + y)^3 \leq 0$). Since $\lambda_1 < \lambda_i$, there is an $a_i > 0$, such that $a_i r_i(y) < f_i y r_1(y)$. ■

Remarks. 1. We have not used the exact form of $r_i(y)$, $i = 2, \cdots, n$ in the proof, so that they can be optional concave functions.

2. The statement holds also if, for example, $r_1(y)$ is linear, $r_1(y) = by - m_1$, $b > 0$. In this case each function $p_1(y) = f_i y r_1(y)$, $i = 2, \cdots, n$, is convex.

Corollary 2. *In (5) let*

$$g_i(y) = \frac{f_i y}{b_i + y}, \quad r_i(y) = \frac{w_i y}{h_i + y} - m_i, \quad i = 1, \cdots, n.$$

Then the exclusion principle holds if $b_i \geq h_i$, $i = 1, \cdots, n$.

Proof. We must show again the existence of coefficients a_i, $i = 2, \cdots, n$, such that (9) is satisfied, i.e.

$$a_i(\frac{w_i y}{h_i + y} - m_i) \leq \frac{f_i y}{b_i + y}(\frac{w_1 y}{h_1 + y} - m_1), \quad 2 \leq i \leq n.$$

This is equivalent to

$$a_i(b_i + y)(\frac{w_i y}{h_i + y} - m_i) \leq f_i y(\frac{w_1 y}{h_1 + y} - m_1), \quad 2 \leq i \leq n.$$

Let

$$p_1(y) = f_i y(\frac{w_1 y}{h_1 + y} - m_1), \quad p_2(y) = (b_i + y)(\frac{w_i y}{h_i + y} - m_i).$$

$p_1(y)$ is convex (see (11)). We have $p_2''(y) = -2w_i h_i(b_i - h_i)/(h_i + y)^3 \leq 0$ exactly if $b_i \geq h_i$. Then $p_2(y)$ is concave. The coefficient a_i exists because $\lambda_1 < \lambda_i$. ■

Remarks. 1. The exclusion principle holds for the system (8) and especially for the chemostat model (4). Here we have $b_i = h_i$.

2. The exclusion principle holds also if some functions $g_i(y)$ are linear here. In this case the corresponding growth rates $r_i(y)$ can be linear, too.

3. Instead of (12) the following forms of attack and growth rates can be used

$$g_i(y) = \frac{f_i \phi(y)}{b_i + \phi(y)}, \quad r_i(y) = \frac{w_i \phi(y)}{h_i + \phi(y)} - m_i, \quad i = 1, \cdots, n.$$

where $\phi(y)$ is an optional strictly increasing function with $\phi(0) = 0$. For example, $\phi(y) = y^n$ with $n > 1$ is used quite often. The existence of the coefficient a_i is obvious, because after the substitution $z = \phi(y)$ we obtain the necessary estimations.

Thus the exclusion principle has been proved for important classes of competition models. But we still could not find a Ljapunov-function for the general case. Therefore the question whether exclusion principle holds in general remains open. The following theorem allows us to take a look at the dynamics of the system (5) without additional restrictions. We are going to confine ourselves to a short sketch of the proof.

Theorem 2. *Let in the system (5) $x_i(0) > 0$ at least for a single species with $C(\lambda_i) > 0$. Then $y(t)$ and the sum $x_1(t) + \cdots + x_n(t)$ are permanent.*

The permanence of $x(t) = y(t)$ or $x(t) = x_1(t) + \cdots + x_n(t)$ means that the following estimations hold

$$\lim_{\tau\to+\infty} \inf_{t\geq\tau} x(t) \geq \tau, \quad \lim_{\tau\to+\infty} \sup_{t\geq\tau} x_(t) \leq D,$$

and the positive constants do not depend on the initial conditions [9]. Further we assume $C(\lambda_i) > 0$ for all $i = 1, \cdots, n$. As a general rule, we could consider the sum of the species x_i with $C(\lambda_i) > 0$. All other species go extinct.

Let $\lambda = min\{\lambda_1, \cdots, \lambda_n\}$, $M = max\{-r_1(0), \cdots, r_n(0)\}$, and let $\mathcal{K}$ be the following compactum in $R_+^{n+1} = \{(x_1, \cdots, x_n, y)\}$

$$\mathcal{K} = \{(x_1, \cdots, x_n, y) : x_1 \geq 0, \cdots, x_n \geq 0, y \geq 0,$$
$$S_1 \leq x_1 + \cdots + x_n \leq S_2, \quad y_1 \leq y \leq y_2\}$$

The parameters S_1, S_2, y_1 and y_2 are chosen so that

$$S_1 < min_{1\leq i\leq n} \frac{C(\lambda)}{g_i(\lambda)}, \quad S_2 > max_{1\leq i\leq n} \frac{C(\lambda)}{g_i(\lambda)}, \quad y_2 > max \lambda_1, \cdots, \lambda_n.$$

and

$$0 < y_1 < \lambda, \quad S_2 max_{1\leq i\leq n} g_i(y_1) < 0.5C(\lambda), \quad y_1 < 0.5C(\lambda) \frac{S_2 - S_1}{MS_2}.$$

First we can prove that any orbit $X(t) = (x_1(t), \cdots, x_n(t), y(t))$ enters the interior of this compactum $\mathcal{K}$. After that it can be shown that the supremum return time τ_0 for orbits starting in K is finite. Therefore the set

$$\mathcal{K}_1 = \{X(t) : \quad X(0) \in \mathcal{K}, \quad 0 \leq t \leq \tau_0\}$$

is compact in R_+^{n+1} and separate from $y = 0$ and $x_1 = cdots = x_n = 0$. Any orbit remains in $\mathcal{K}_1$ for large t, and therefore $y(t)$ and $x_1(t) + \cdots + x_n(t)$ are permanent.

The previous theorem confirms that the dynamics of the system (5) shows realistic traits also in the general case. In this context there is an interesting statement that we can prove only for models with 2 species.

Theorem 3. *In the system (5) let* $n = 2$, $\lambda_1 < \lambda_2$ *and* $C(\lambda_1) > 0$. *Then the species* x_1 *with the lowest persistence threshold is permanent.*

Proof. Let $x_1(0) > 0$. Theorem 2 yields that we can assume $g_2(\lambda_2) > 0$ and $x_2(0) > 0$. First we will show that x_1 does not go extinct.

Let $\lim_{t\to+\infty} x_1 = 0$. According to theorem 2 the species x_2 is permanent here, and $x_2(t) \geq \delta_2$, $\delta_2 > 0$, for large t. Obviously, constants $a_2 > 0$ and y_0,

$y_0 > \lambda_2$, exist, such that the inequation $r_1(y) - a_2 r_2(y) > 0$ is satisfied for $0 \le i \le y_0$. We consider a certain function V with the following gradient

$$\nabla V = (-\frac{\mu}{x_1}, -\frac{C(\lambda_2)}{x_2} + g_2(\lambda_2) + \frac{\mu a_2}{x_2}, r_2(y)), \tag{13}$$

where the constant μ is positive. The function V will serve as Ljapunov function. We have

$$V' = r_2(y)[C(y) - C(\lambda_2)] + x_2 r_2(y)[g_2(\lambda_2) - g_2(y)] - \mu[r_1 - a_2 r_2] - x_1 g_1(y) r_2.$$

The terms $r_2(y)[C(y) - C(\lambda_2)]$ and $x_2 r_2(y)[g_2(\lambda_2) - g_2(y)]$ are obviously not positive, and the last of them equals 0 exactly for $y = \lambda_2$. For $y \to \infty$ it tends to $-\infty$.

Since $-[r_1(y) - k_2 r_2(y)]$ is negative for $0 \le y \le y_0$ and bounded for $y \ge 0$, it holds for sufficiently small $\mu > 0$ that

$$r_2(y)[C(y) - C(\lambda_2)] + x_2 r_2(y)[g_2(y) - g_2(\lambda_2)] - \mu[r_1(y) - k_2 r_2(y)] \le -2\epsilon$$

with $\epsilon > 0$. The term $-x_1 g_1(y) r_2(y)$ is negative for $y > \lambda_2$, and for $0 \le y \le \lambda_2$ we have $-x_1 g_1(y) r_2(y) \le K x_1$ with $K = sup_{0 \le y \le \lambda_2} g_1(y) r_2(y) < \infty$. Then for $x_1 < \epsilon / K$ we obtain $\lim_{t \to +\infty} V(t) = -\infty$. Nevertheless, any orbit remains for large t in a compactum $\mathcal{K}_1$ in R_+^{n+1}. Due to (13) $V(t) \to \infty$ on $\mathcal{K}_1$ if $x_1 \to 0$. Thus we have a contradiction.

Herefrom follows the existence of a positive threshold δ, such that every orbit always returns into the domain $\mathcal{U} = \{(x_1, x_2, y) : x_1 > \delta\}$. We define a function on $\mathcal{K}_1$ that determines the time of the return into $\mathcal{U}$,

$$\tau_1(P) = inf\{t : \quad t > 0, X(0) = P \in \mathcal{K}_1, X(t) \in \mathcal{U}\}.$$

$\tau_1(P)$ is an upper semi-continuous function, and its supremum is finite on the compactum $\mathcal{K}_1$. Thus we can conclude the existence of a threshold $\delta_1 > 0$ which x_1 does not fall below,

$$\lim_{t \to +\infty} \inf_{\tau \ge t} x_1(\tau) \ge \delta_1,$$

and δ_1 is independent on $x_1(0) > 0$. The necessary upper estimation follows from the theorem 2. ■

4 Dynamics in a variable environment.

Up to now we have viewed systems with constant environments. Now let the nutrient enter the system in portions. We restrict ourselves to the case $n = 2$

and begin with the system (6). It must be replaced by the following

$$\begin{array}{rcl} x_1' & = & r_1(y)x_1 \\ x_2' & = & r_2(y)x_2 \\ y' & = & -(f_1x_1+f_2x_2)y \end{array} \tag{14}$$

where y changes with the step τ. First we consider the case

$$y(t_k+) = y(t_k-) + \Delta_\tau, \quad t_k = k\tau, \quad k = 1, 2, \cdots. \tag{15}$$

The quotient Δ_τ/τ determines the average food supply, corresponding to a constant food input speed $C(y) = C_0$. We analyse the system (14-15) numerically.

In the next simulations we will change τ and Δ_τ without changing the average food supply. For higher τ the pulsations of food are stronger and the periods with low food concentration are longer.

In all cases $x_1(t)$, $x_2(t)$ and $y(t)$ converge for $t \to +\infty$ asymptotically to periodic oscillations that we denote by $\tilde{x}_1(t)$, $\tilde{x}_2(t)$ and $\tilde{y}(t)$. The period of these oscillations is denoted by T. T is not always equal τ.

Figs. 2–4 represent the results of simulations for different steps τ if $f_1 = 5$, $f_2 = 4$ and the species grow in the following manner

$$r_1(y) = \frac{2.5y}{1+y} - 1.82, \quad r_2(y) = \frac{2y}{5+y} - 0.8. \tag{16}$$

The graphs of $r_1(y)$ and $r_2(y)$ are shown in Fig. 1, and we have $\lambda_1 < \lambda_2$. The average food supply is constant, $\Delta_\tau/\tau = 1.25$.

For smaller τ the species x_1 is the superior competitor due to its lower persistence threshold λ_1. The dynamics of the system (14-15) is still similar to that of (6). If $\tau = 4$, then $x_2(t)$ tends to 0, x_1 and y converge asymptotically to oscillations $\tilde{x}_1$ and $\tilde{y}$, see Fig. 2. Their period T equals τ. The species x_2 goes extinct because of competition. If x_1 is absent, $x_1(0) = 0$, then x_2 does not tend to 0. Dynamics of this kind is repeatedly shown by the simulations for $\tau \leq 6$.

At further increase of τ the result changes in the following way. First the species x_1 and x_2 become capable of coexistence, and after that the species x_2 can win in spite of higher persistence threshold. Oscillations $\tilde{x}_1$, $\tilde{x}_2$ and $\tilde{y}$ for $\tau = 7$ are shown in Fig. 3. Here we obtain a doubling of the period, $T = 2\tau$, that will appear in some other cases, too. For $\tau = 8$ the species x_1 goes extinct, $\tilde{x}_2$ and $\tilde{y}$ can be seen in Fig. 4. Here the extinction of x_1 is caused by competition; x_1 does not go extinct if x_2 is absent, $x_2(0) = 0$. For larger τ we obtain the same dynamics.

Thus these simulations show that the threshold criterion cannot be the only decisive factor in oscillating environments. In the last cases we had $m_2 < m_1$ and $w_2 - m_2 > w_1 - m_1$, so that x_2 had a better hunger resistance and a higher growth rate for a higher food concentration. Therefore x_2 could win the competition for higher τ.

In the next example we have $m_1 = m_2$ and still $f_1 = 5$, $f_2 = 4$. The other parameters are chosen so that

$$r_1(y) = \frac{1.48y}{2.834 + y} - 0.8, \quad r_2(y) = \frac{2y}{5 + y} - 0.8. \tag{17}$$

In this case we still have $\lambda_1 < \lambda_2$. The dynamics depends again on the intensity of the fluctuations. Fig. 5 shows the graphs of $r_1(y)$, $r_2(y)$ and a single period of the function $\tilde{x}_2$ for $\tau = 10$. The simulations yield in this case that x_1 goes extinct. Here the species x_2 is the superior competitor because $w_2 > w_1$.

In order to show that hunger resistance is a significant factor, too, we consider one more example with

$$r_1(y) = \frac{4y}{1.35 + y} - 2.8, \quad r_2(y) = \frac{2y}{5 + y} - 0.8. \tag{18}$$

We have $\lambda_1 < \lambda_2$, $w_1 - m_1 = w_2 - m_2$, but x_2 has a better hunger resistance, $r_2(y) > r_1(y)$ for small y. In the case $\tau = 8$ the simulations yield indeed that x_2 wins. Since $r_2(y) < r_1(y)$ holds for $y > \lambda_1$, it is caused only by a better hunger resistance of x_2. The graphs $r_1(y)$, $r_2(y)$ and $\tilde{x}_2$ are shown in Fig. 6. If other parameters are the same, x_1 wins the competition in the case $\tau = 2$ (i.e. if the oscillations are small), and in the case $\tau = 4$ the species can coexist.

Simulations also yield analogous results, if the food is reset to the same level after a certain time span. Then we have instead of (15)

$$y(t_k+) = \Delta_\tau, \quad t_k = k\tau, \quad k = 1, 2, \cdots. \tag{19}$$

The frequency τ is varied again, the quotient Δ_τ/τ remains constant. Oscillations of this kind are used for example in experimental biological studies of competition [23]. They are produced by periodic replacing of the culture medium by a fresh food suspension. The results of these simulations are absolutely analogous to the last ones, they have the same sense and biological cause. This was to be expected, since asymptotical periodic oscillations of the nutrient concentration have already been found in the previous simulations.

If (8) is used as the basic system for constant environments, then (14) must be replaced by the following system

$$\begin{aligned} x_1' &= r_1(y)x_1 \\ x_2' &= r_2(y)x_2 \\ y' &= -(\frac{f_1 y}{h_1 + y}x_1 + \frac{f_2 y}{h_2 + y}x_2) \end{aligned} \tag{20}$$

where (15) holds for y. The simulations' results correspond to the former ones.

Let $f_1 = 5$, $f_2 = 4$, $\Delta_\tau/\tau = 1.25$, and at first let $r_1(y)$, $r_2(y)$ be defined as in (16), see Fig. 1. It still holds $\lambda_1 < \lambda_2$. Figs. 7-9 show the nontrivial asymptotical oscillations for $\tau = 4$, $\tau = 6$ and $\tau = 8$, respectively. At the lowest τ the species x_1 wins, for $\tau = 6$ both species can coexist and for $\tau = 8$ the winner is the species x_2. This demonstrates again that different strategies of adaptation to oscillating external conditions are possible.

If in (20) $r_1(y)$ and $r_2(y)$ are defined as in (17), see Fig. 5, and $\tau = 10$, then x_2 is the superior competitor, too. Fig. 10 shows the periods of $\tilde{x}_2$ and $\tilde{y}$. The species x_2 wins because it has a higher growth rate when the food concentration is high. If $r_1(y)$ and $r_2(y)$ are defined by means of (18), see Fig. 8, and $\tau = 8$, then $x_1(t) \to 0$. Here the species x_2 is the superior competitor because it has a better hunger resistance. The periods of $\tilde{x}_2$ and $\tilde{y}$ can be found in Fig. 11.

5 Discussion

Our analytic results refer to the case of constant environments. The competitive exclusion principle has been proved for a wide class of models. We have also taken a look at the dynamics of the system (5) in the general case. It is significant that the species with the lowest persistence threshold can never lose the competition in a constant environment. In comparison with this case the results for oscillating environments demonstrate a decisive change of the dynamics. For this aim we employ numerical simulations.

The results of our analytical and numerical research can be summarized in the following way. The outcome of the competition cannot be forecast by means of a single concept (e.g. gleaner, exploiter or hunger resistance). It seems more reasonable to distinguish some competition strategies that allow species an adaptation to the environment's oscillations. It must be remarked that "strategy" does not mean any conscious activity. The gleaner strategy is better for small oscillations, and if the environment's variability is low, the species with this competition strategy is the superior competitor. The other strategies both have some advantages in environments with strong oscillations, so that they can be successful in environments with high variability. Furthermore, it can be seen that slight changes in climatic conditions can have a drastic influence on the dynamics of competing communities.

Acknowledgement. This research was supported by DFG, project OR82/1-1 Mathematical Methods of Detecting Climatic Ecological Bifurcations.

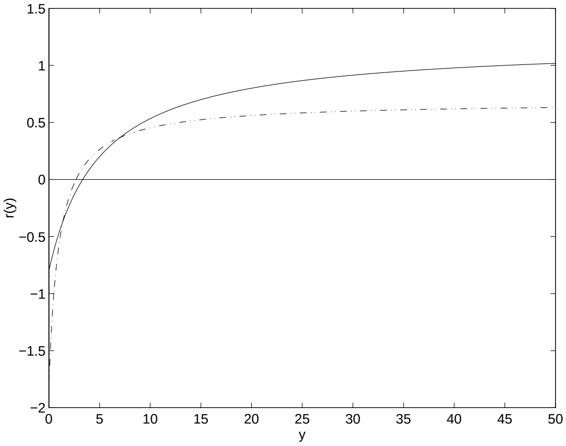

Fig. 1. Growth rates $r_1(y) =$ - - - and $r_2(y) =$ —, $\lambda_1 < \lambda_2$.

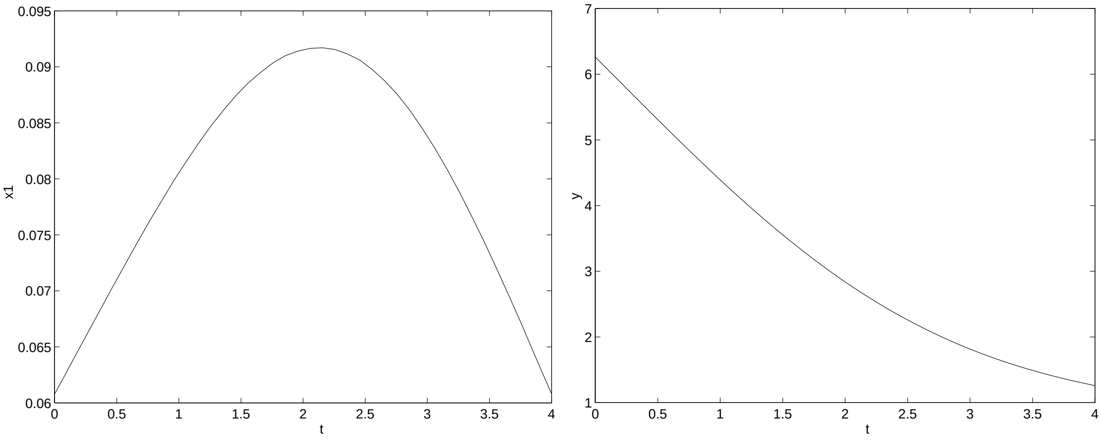

Fig. 2. $\tau = 4$: asymptotical oscillations $\tilde{x}_1$ (left) and $\tilde{y}$ (right).
$x_2 \to 0$, $T = \tau$.

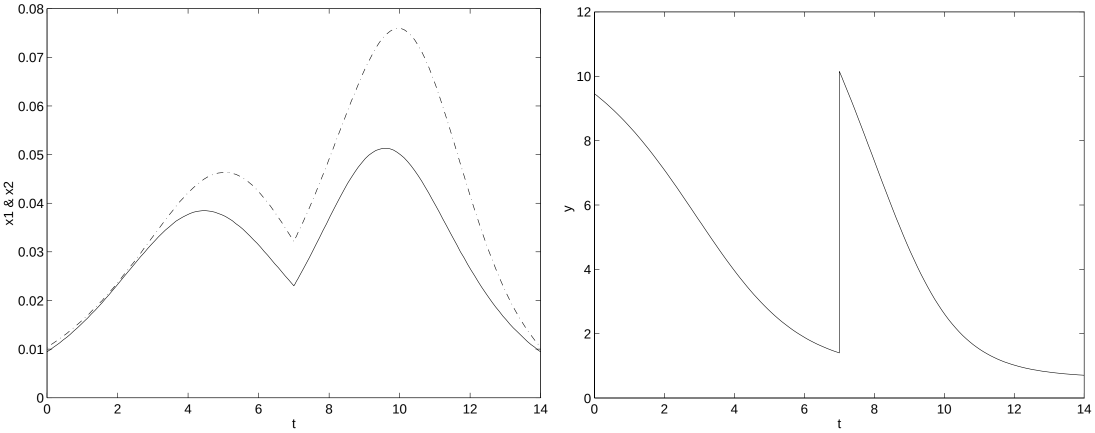

Fig. 3. $\tau = 7$: oscillations $\tilde{x}_1 =$ - - - , $\tilde{x}_2$= — (left), $\tilde{y}$ (right), $T = 2\tau$.

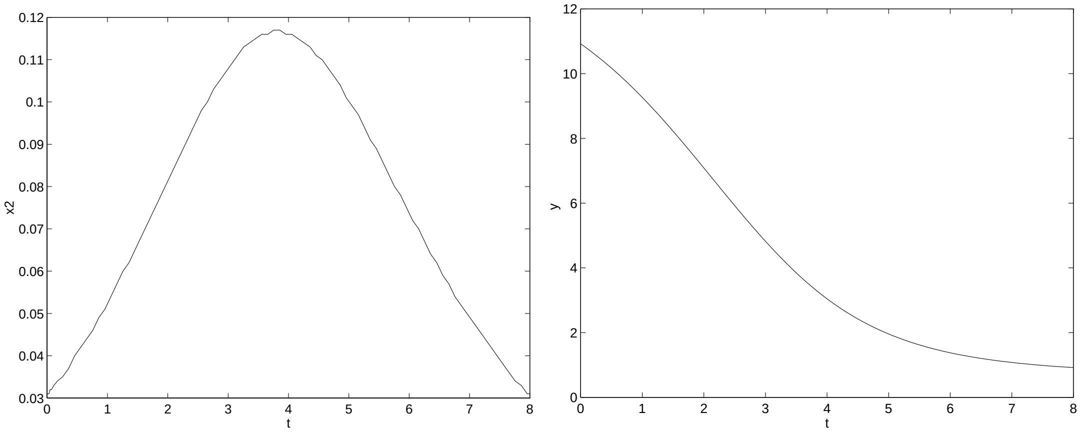

Fig. 4. $\tau = 8$: oscillations $\tilde{x}_2$ (left) and $\tilde{y}$ (right). $x_1 \to 0$, $T = \tau$.

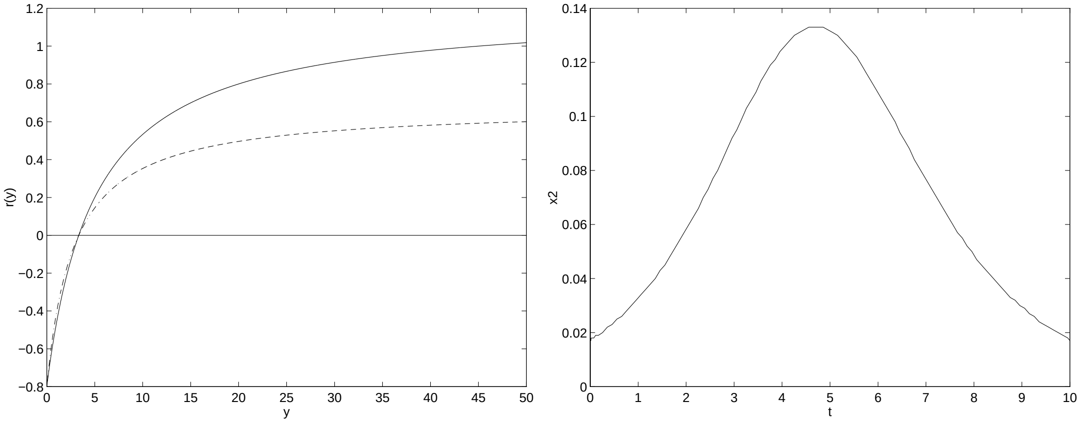

Fig. 5. $r_1(y) =$ - - - , $r_2(y) =$ —, $m_1 = m_2$, $\lambda_1 < \lambda_2$, $w_1 < w_2$ (left); $\tau = 10$: asymptotical oscillations $\tilde{x}_2$ (right). $x_1 \to 0$, $T = \tau$.

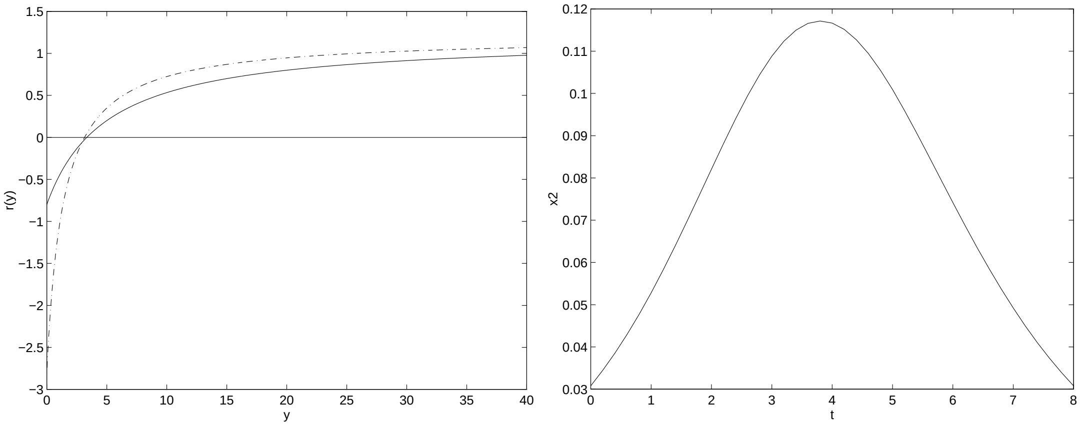

Fig. 6. Growth rates $r_1(y) =$ - - - , $r_2(y) =$ —, $m_1 > m_2$, $\lambda_1 < \lambda_2$, (left); $\tau = 8$: asymptotical oscillations $\tilde{x}_2$ (right). $x_1 \to 0$, $T = \tau$.

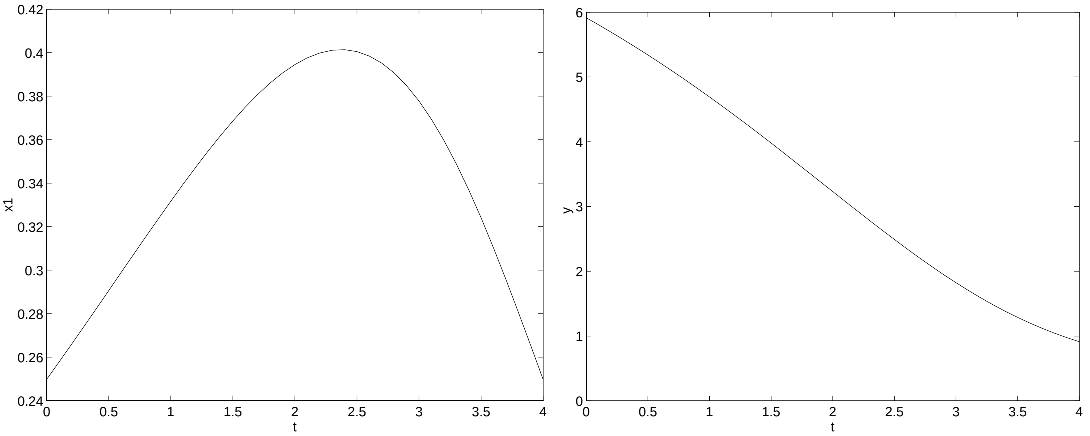

Fig. 7. $\tau = 4$: oscillations $\tilde{x}_1$ (left) and $\tilde{y}$ (right), $x_2 \to 0$, $T = \tau$.

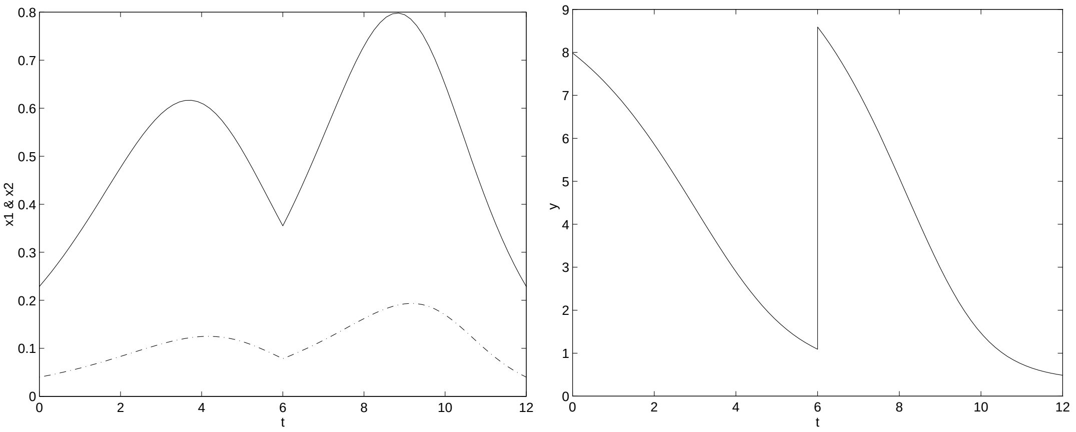

Fig. 8. $\tau = 6$: oscillations $\tilde{x}_1 =$ - - -, $\tilde{x}_2$= — (left), $\tilde{y}$ (right). $T = 2\tau$.

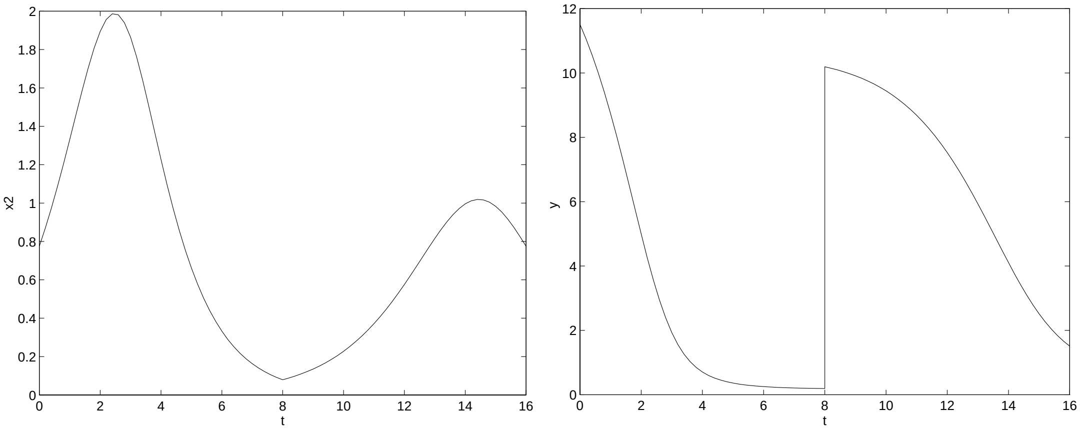

Fig. 9. $\tau = 8$: oscillations $\tilde{x}_2$ (left) and $\tilde{y}$ (right). $x_1 \to 0$, $T = 2\tau$.

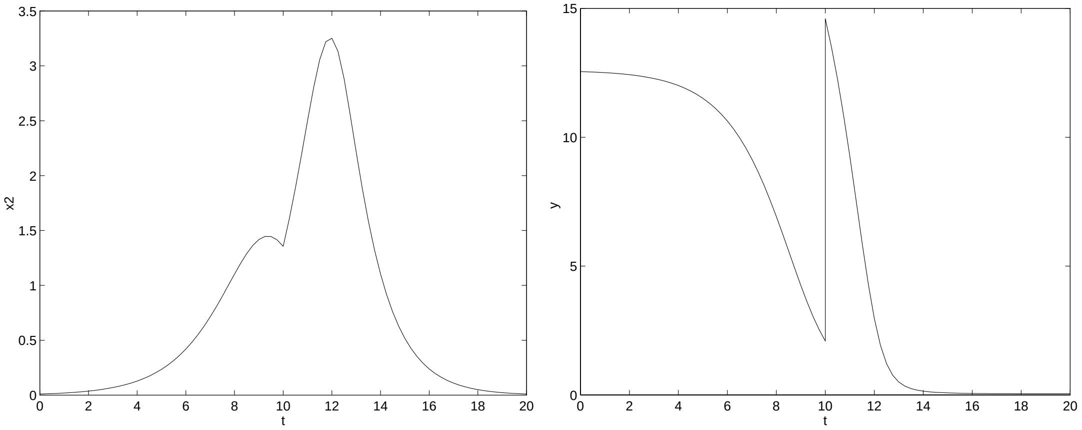

Fig. 10. $\tau = 10$: oscillations $\tilde{x}_2$ (left) and $\tilde{y}$ (right). $x_1 \to 0$, $T = 2\tau$.

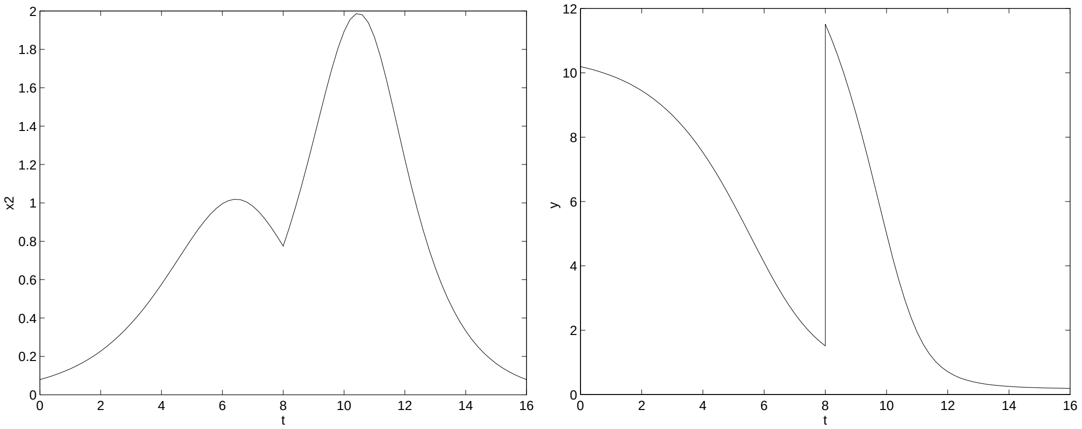

Fig. 11. $\tau = 8$: oscillations $\tilde{x}_2$ (left) and $\tilde{y}$ (right). $x_1 \to 0$, $T = 2\tau$.

References

1. Armstrong, R. A., McGehee, R., 1980. Competitive exclusion, Am. Nat., 115: 151-170.

2. Crowley, P. H., 1975. Natural selection and the Michaelis constant, J. Theor. Biol., 50: 461-475.

3. Cushing, J. M., 1980. Two species in periodic environment, J. Math. Biol., 10: 385-400.

4. Cushing, J. M., 1986. Periodic Lotka-Volterra competition equatios, J. Math. Biol., 24: 381-403.

5. Fredrickson, A. G., Stephanopoulos, G., 1981. Microbial competition, Science, 213: 972-979.

6. Grover, J. P., Resource competition in a variable environment: phytoplankton growing according to Monod's model, Am. Nat., 136: 771-789.

7. Hale, J. K., Somolinos, A. S., 1983. Competition for fluctuating nutrient, J. Math. Biol., 18: 255-280.

8. Hansen, S. R., Hubbel, S. P., 1980. Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes, Science, 207: 1491-1493.

9. Hofbauer, J., Sigmund, K., 1988. The theory of evolution and dynamical systems, Cambridge - New York - New Rochelle - Melbourne - Sydney: Cambridge University Press.

10. Hsu, S. B., Hubbell, S., Waltman, P., 1977. A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms, SIAM J. Appl. Math., 32: 366-383.

11. Hsu, S. B., 1980. A competition model for seasonally fluctuating nutrient, J. Math. Biol., 9: 115-132.

12. Hutchinson, G. E., 1961. The paradox of the plankton. Am. Nat. 95: 137-143.

13. Lampert, W., Gabriel, W., Rothhaupt, K. O., 1992. Ecophysiological models: A tool for understanding interactions in freshwater communities?, Verh. Dtsch. Zool. Ges., 85.2: 95-110.

14. Levin, S., 1970. Community equlibria and extension of the competitive exclusion principle, Am. Natur., 104: 413-423.

15. Levins, R., 1979. Coexisistence in a variable environment, Am. Nat., 114: 765-783.

16. Lotka, A., 1956. Elements of mathematical biology, Dover, New York.

17. McGehee R., Armstrong, R. A., 1977. Some mathematical problems concerning the ecological principle of competitive exclusion, J. Differ. Equations, 23: 30-52.

18. Monod, J., 1950. La technique de culture continue: théorie et applications, Ann. Inst. Pasteur, 79: 390-401.

19. Nitecki, Z., 1978. A periodic attractor determined by one function, J. Differ. Equations, 29: 214-234.

20. Powell, T., Richerson, P., 1985. Temporal variation, spatial heterogeneity, and competition for resources in plankton systems: a theoretical model, Am. Nat., 125: 431-464.

21. Rescigno, A., Richardson, I., 1965. On the competitive exclusion principle, Bull. Math. Biophys., special issue, 27: 85-89.

22. Rothhaupt, K. O., 1990. Resource competition of zooplankton: a review of approaches and perspectives, Arch. Hydrobiol., 118: 1-29.

23. Rothhaupt, K. O., 1993. Rotifers and continuous culture techniques: model system for testing mechanisms concepts of consumer-resource interactions. In Plankton regulation dynamics (Ed: Walz, N.), Springer, Berlin, Heidelberg, New York - London - Paris - Tokyo - Hong Kong - Barcelona - Budapest.

24. Smith, H. L., Waltman, P., 1995. The theory of the chemostat, dynamics of microbial competition, Cambridge Univer. Press, Cambridge - New York - Melbourne.

25. Sommer, U., 1985. Comparison between steady state and non-steady state competition: experiment with natural phytoplankton, Limnol. Oceanogr. 30: 335-346.

26. Stemberger, R. S., Gilbert, J. J., 1985. Body size, food concentration, and population growth in plankton rotifers, Ecology 66: 1151-1159.

27. Tilman, D., 1982. Resource competition and community structure, Princeton University Press, Princeton.

28. Volterra, V., 1928. Variations and fluctuations in animal species living together, J. Cons. Int. Explor. Mer. 3: 3-51.