Continuous Models and its Simulation

Tibor Kmeť

February 26, 2014

*

*study material
in press

Contents

Preface

This Workbook for Students is designed to teach students how to apply mathematics by formulating, analysing, criticizing, and simulating mathematical models. The book requires elementary calculus, matrix theory, elementary differential equations, and knowledge of programming in MATLAB. Although the level of mathematics required is not high, this is not an easy text: Setting up and manipulating models requires thought, effort, and usually discussion - purely mechanical approaches often end in failure. Since firmly believe in learning by doing, all the problems require creating and studying models by students. Possible fields of application of mathematics are physics, technology, chemistry, economics, management, geography, demography, biology/medicine, and sport. The book concentrates on mathematical modelling and simulation of biological systems, mainly on continuous population models, chemostat models and application of control theory. The core of the book, which should be included in any beginers modelling course are $Chapters$ 2, 3, and 4. Students find numerical methods quite interesting and useful. Computer calculations using MATLAB are presented in the form of graphs whenever possible so that the resulting numerical simulations are easier to visualize and interpret. The book is meant to be an introduction to the principle and practice of mathematical modelling and simulation in biological sciences a give short description and analysis of mathematical model.

Acknowledgements. Particular thanks are due to the following people who reviewed this book when it was in manuscript form: Pavol Flak, Jaroslav Křivánek and Anton Pokrivčák.

Chapter 1

Teaching and learning mathematical modelling

The world to which mathematics is applied is in a process of dynamic change. Besides the traditional physical sciences and engineering, the social, biological and ecological sciences, and, it seems, all areas of human endeavour, are also susceptible to quantitative reasoning or mathematical modelling.

The unifying theme for application of mathematics to these subjects is the translation of the "real world" problem to the mathematical one by formulation of a mathematical model. The process of modelling is illustrated in *Table* 1.1 [25].

The left-hand column represents the real world, the right-hand column the mathematical world and the middle column provides translation between the two states. The art of the good applied mathematician is to get an optimum balance between manageability and reality.

If a mathematical model is too simple, there would be poor agreement between the observed and predicted data at the validation stage and the cycle must be traversed again with an improved model. On the other hand, as the model becomes more complicated so does the resulting mathematics. Let us introduce the following definition [25].

Definition 1.1 *Model is an object or concept that is used to present something else. It is reality scaled down and converted to a form we can comprehend.*

Definition 1.2 *A mathematical model is a model whose parts are mathematical concepts, such as constants, variables, functions, equations, inequalities,*

Table 1.1: Process of modelling

Formulate the real problem	$\longrightarrow$	Assumption made	$\longrightarrow$	Formulate the mathematical problem
$\uparrow$				$\downarrow$
Validate and refining model	$\longleftarrow$	Interpret solution	$\longleftarrow$	Solve the mathematical problem

etc.

Mathematical models can be divided into two categories: descriptive and prescriptive. A descriptive model describes or predicts how something actually works or how it will work. A prescriptive model is meant to help us choose the best way for something to work. Alternative names which are sometimes used for prescriptive models are *normative* or *optimisation* models. The differences between descriptive and prescriptive models do not lie primarily in mathematics. The main difference is in what a model is used for. A prescriptive model is a tool for human decision-making, while a descriptive model just tells us "what makes it tick". Often a descriptive model can be turned into a prescriptive one.

Mathematical modelling is a process that involves responding to a real situation, abstracting a problem using some simplification and assumption, establishing a response to the problem (which may involve the use of mathematical visualization and symbols), and evaluating and communicating that response to self and others.

Modelling cannot be done mechanically. Nevertheless, there are some guidelines for how to do it. We can divide the modelling process into three main steps:

- formulation
- mathematical manipulation
- evaluation

. Formulation can, in turn, be divided into three smaller steps.

Formulation

1. Starting the question. The question we start with is often too vague or too "big". If it is vague, make it precise. If it is too big, subdivide it into manageable parts.
2. Identifying relevant factors. Decide which quantities and relationships are important for your question and which can be neglected.
3. Mathematical description. Each important quantity should be represented by a suitable mathematical entity, e.g., a variable, a function, a geometric figure, etc. Each relationship should be represented by an equation, inequality, or other suitable mathematical assumption.

Mathematical Manipulation
The mathematical formulation rarely gives us answers directly. We usually have to do some mathematics. This may involve a calculation, solving an equation, proving a theorem, etc.

Evaluation
In deciding whether our model is a good one, there are many things we could take into account. The most important question concerns whether or not the model gives correct answer. If the answers are not accurate enough or if the model has other shortcomings, then we should try to identify the sources of the shortcomings. It is possible that mistakes have been made in the mathematical manipulation. But in many cases we need a new formulation. For example, it can occur that some quantity or relationships which we neglected, were more important than we thought. After a new formulation we need to do new mathematical manipulations and a new evaluation. Thus, mathematical modelling can be a repeated cycle of the three modelling steps.

Amongst the activities undertaken in mathematical modelling are the following: formulating a real-world problem, formulating a mathematical problem and, solving the mathematical problem. In order to solve a modelling problem we need a number of skills, amongst which are the ability to *abstract* a mathematical problem from real-world situation, to *identify* appropriate mathematical tools needed to solve the problem, and to *use* appropriate mathematical tools to solve problems.

Mathematics is often thought to consist of finding formulas for quantities of interest to us. In that approach, called the analytical *approach*, we rely heavily on mathematical theory. There is another approach, that might almost be called *experimental mathematics*, which can sometimes be used. One form of mathematical experiment is called *simulation*. There are two great pillars upon which the experimental sciences rest, theory and experiments. By contrast, the mathematical manipulation in a mathematical model often seems to be based wholly on one pillar, the theory. This is largely true, but not completely. In fact, the experimental approach finds some use when we do mathematics.

Definition 1.3 *An analytic solution involves finding a formula that relates the quantity we are trying to estimate to other quantities known to us (We rely heavily on mathematical theory). A simulation solution attempts to estimate the value of a quantity by mimicking (simulating) the dynamic behaviour of the system involved (It needs less theory but lots of patience and/or computer time).*

Mathematical modelling is the activity of translating a real problem into a mathematical form. The mathematical form is solved and then interpreted back to help explain the behaviour of the real problem.

When a model is used, it may lead to incorrect prediction. The model is often modified, frequently discarded, and sometimes used anyway because it is better than nothing. This is the way science develops. What makes mathematical models useful? If we "speak in mathematics" then:

1. We must formulate our ideas precisely and thus we are less likely to let implicit assumption slip by.

2. We have a concise "language" which encourages manipulation.

3. We have a large number of potentially useful theorems available.

4. We have high-speed computers available for carrying out calculations.

There is a trade-off between items 3 and 4: Theory is useful for drawing general conclusions from simple models and computers are useful for drawing specific conclusions from complicated models.

There are two approaches to teaching a syllabus in applied mathematics.

One way is to consider a particular mathematical topic and to illustrate its application in a variety of different situation. For examples, the differential equation

$$dy/dx = ky$$

has not only an impotent application in carbon carbon dating, but it is also the governing equation for mathematical models which represent (i) the population changes of a single species, (ii) the way in which a drug loses its concentration in the body and (iii) the manner in which water cools.

This is one of the powers of mathematical analysis: the actual governing equations can be representative for many situations in different disciplines, so that by solving this one equation we have effectively solved a wide range of problems.

A second approach to teaching applied mathematics is to consider the application of mathematics to different disciplines divided up on a subject basis.

There are many good reasons to include modelling in the school curriculum. In general, five arguments have been presented as a rationale for modelling in schools: motivation, facilitation of learning, preparation for the use of mathematics in different areas, development of general competencies, and comprehension of the socio-cultural role of mathematics. Modelling literature has characterized modelling activities according to the duration and extent of the task as the teacher poses it.

Like problem solving, modelling is a difficult skill to teach. In authentic modelling situation, modellers typically:

1. extract the problem from the underlying real-word situation,
2. construct a simplified version of the initial problem,
3. construct a mathematical model of the simplified problem,
4. identify solution within the framework of the mathematical model,
5. interpret these solutions in terms of the simplified problem,

6. verify that the solutions generated for the idealised problem are solutions to the initial problem.

We can speak about three cases afforded by a modelling task as it is presented to students. In case 1, the teacher presents problem with quantitative and qualitative information, and the students are expected to investigate the situation. Case 2 provides other different possibilities for students engagement. The teacher poses an initial question to the students and they become responsible for collecting data and for presenting their solutions. In this case, the students are mostly responsible for regulating their own activities. The third case entails project with non-mathematical themes that may be chosen either by a teacher or students. The students are responsible for formulating a problem, collection of information, and solving the problem.

Freudenthal rightly demands that pupils should not learn applied mathematics, but should learn how to apply mathematics. Only their own active engagement can, in the end, make a difference for pupils. The well-known quotation from Chinese philosopher Confucius points out:

1. Tell it to me and I forget it.

2. Show it to me and I recall it.

3. Let me do it and I remember it.

Chapter 2

Continuous Single Population Models

The purpose of this chapter is to establish the continuous population models. We will start with mathematical model of exponential growth, then enlagre this simple model to the model of logistic growth, logistic growth with delay and partial functional logistic model. We will give qualitative analysis of the model analysis using analytical and numerical methods realize by MATLAB. Based on exterimental date we also verified the model of logistic growth. This chapter is based on the works [2], [8], [24], [30].

2.1 Exponential Growth

In this section we look at a population in which all individuals develop independently of one another. For detail explanation see [2]. For this situation to occur these individuals must live in an unrestricted environment, where no form of competition is possible. The population size of a single species at time t will be denoted by $x(t)$, where it is assumed that x is an everywhere differentiable, that is a *smooth* function on t. The rate of change of population size can be computed if the births and deaths and the migration rate are known. A *closed* population has no migration either into or out of population. For microorganisms, which reproduce by splitting, it is reasonable to assume that the rate of births of new organisms is proportional to the number of organisms present. In mathematical terms, this assumption can be expressed by saying that if the population size at time t is x, then over a short time interval of duration h from time t to $t+h$, the number of births is approximately bhx for some constant b, the *per capacity birth rate*. Similarly, we may assume that the number of deaths over the same time interval is approximately μhx for some constant μ, the *per capacity dealt rate*. Hence, the net change in population size from time t to time $t+h$, which is $x(t+h) - x(t)$ may be approximated by $(bh - \mu h)x(t)$.

We obtain the approximate equations

$$\frac{x(t+h) - x(t)}{h} \approx (b - \mu)x(t) \tag{2.1}$$

and passage to the limit as $h \to 0$ gives

$$\frac{dx}{dt} = (b - \mu)x(t) \tag{2.2}$$

under the assumption that the function $x(t)$ is differentiable.

If the net growth rate is naturally defined as

$$r \equiv b - \mu$$

then we arrive again at the differential equation

$$\frac{dx}{dt} = rx(t) \tag{2.3}$$

This differential equation has the infinite of solution given by the one parameter family of function

$$x(t) = ke^{rt} \tag{2.4}$$

The most convenient way to impose a condition that will describe the population dynamics of a specific population is by specifying the initial population size at time $t = 0$ as

$$x(0) = x_0 \tag{2.5}$$

this choose select the solution,

$$x(t) = x_0 e^{rt}. \tag{2.6}$$

Condition (2.5) is called an *initial condition* and the problem consisting of the differential equation (2.3) together with the initial condition (2.5) is called an *initial value problem*. The above initial value problem has a unique solution

$$x(t) = x_0 e^{rt},$$

where $r > 0$ implies that the population size will grow as $t \to \infty$, while $r < 0$ implies that population size will approach zero as $t \to \infty$. Populations that first grow exponentially are commonly observed in nature. However, their growth rates usually tend to decrease as population size increases. In fact, exponential growth or decay may be considered as *typical* local behaviour. The next section considers nonlinear assumptions on the population growth rate, which lead to quite different qualitative prediction.

2.2 The Logistic Population Model

As before, $x(t)$ denotes the size of a population at time t, and dx/dt, or $\dot{x}$ the rate of change of population size. Here we study models in which the growth rate depends only on population size, because, in spite of their shortcoming, these do predict qualitative behaviour of many real problems. The *per capacity growth rate* is given by $\dot{x}/x(t)$, which we assume to be a function of $x(t)$. The simplest population model in which per capacity growth rate is a decreasing function of population size is $\nu \ - \ ax$. This assumption leads to the *logistic* differential equation

$$\dot{x} = x(\nu \ - \ ax).$$

This equation is commonly written in the form

$$\dot{x} = rx(1 - \frac{x}{K}). \tag{2.7}$$

In analysing the equation (2.7), we first observe that the constant function $x(t) = 0$ and $x(t) = K$ are solutions. In seeking the remaining solutions, we can assume that $x(t) \neq 0$ and $x(t) \neq K$. We rewrite equation (2.7) as

$$\frac{\dot{x}}{x(1-x/K)} = r.$$

By the method of partial fractions, we transform this to

$$\frac{\dot{x}}{x} + \frac{\dot{x}}{K\ -\ x} = r.$$

Integrated we get

$$\int \frac{\dot{x}}{x} dt + \int \frac{\dot{x}}{K\ -\ x} dt = \int r dt + c.$$

A little more algebra yields the logistic function for initial value $x(0) = x_0$

$$x(t) = \frac{x_0 K}{x_0 + (K - x_0)e^{-rt}}. \tag{2.8}$$

The parameters r and K appearing in equation 2.8 can be fitted for a given set of experimental data using the following two $M - files$:

```
%logistic.m - file
global t x
t=[0,1,2,3,4,5,6,7,8,9];
x=[9.6,29.0,71.1,174.6,350.7,513.3,594.4,640.8,655.9,661.8];
start=[1,10];
estimates = fminsearch(@expfun,start)
plot(t,x,'*')
z=x(1)*estimates(2)./(x(1)+(estimates(2)-x(1)).*exp(-estimates(1)*t));
z1=(z-x)^2;
tt=0:0.25:9;
z=x(1)*estimates(2)./(x(1)+(estimates(2)-x(1)).*exp(-estimates(1)*tt));
hold on
plot(tt,z,'r')
plot(t,z1,'+')
xlabel('t')
ylabel('Number of yeast cells x(t)')
```

```
hold off

%expfun.m - file
function sse = expfun(params)
global t x
r = params(1);
K= params(2);
FittedCurve = x(1)*K./(x(1)+(K-x(1)).*exp(-r*t));
ErrorVector=FittedCurve - x;
sse= sum(ErrorVector.^2);
end
```

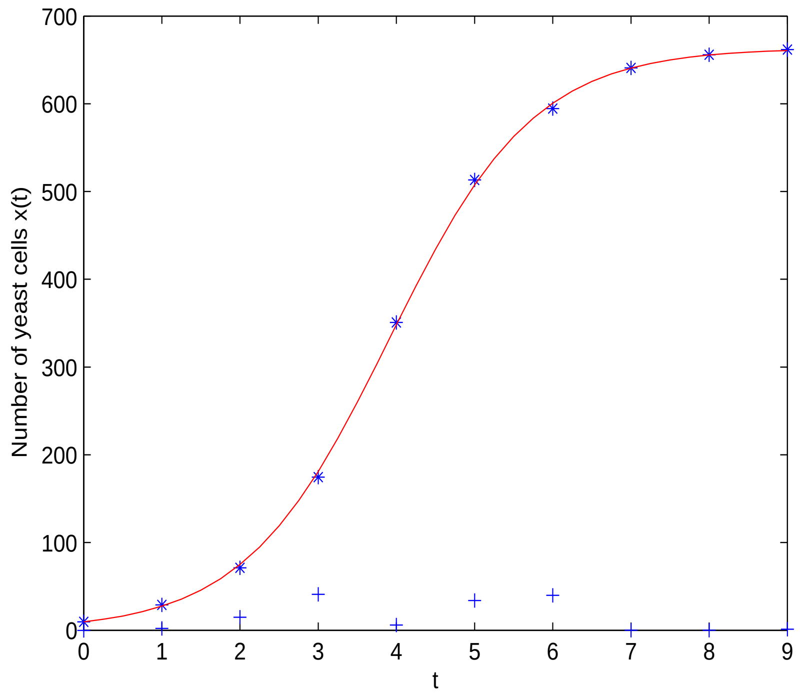

Figure 2.1: Actual yeast growth [25] compared to logistic function (2.8) ($K = 663$, $r = 1.08$)

2.3 Qualitative Analysis

Definitions and results presented in this section you can find in basic literature of differential equations and dynamical systems, for example [1], [21]. Differential equations are often used for mathematical modelling in science and engineering. Let us consider the equation

$$\dot{x} = f(x,t), \tag{2.9}$$

where $x \in R^n$ and $f : R^n x R \to R^n$. It is a differential equation because it involves the derivative dx/dt of the *unknown* function $x(t)$. Only the independent variable t appears on the right side of equation (2.9)

Definition 2.1 *A solution of the initial value problem $\dot{x} = f(x,t)$ with $x(0) = x_0$ on the interval $[0,b]$ is a differentiable function $x = x(t)$ such that $x(0) = x_0$ and $\dot{x}(t) = f(x(t),t)$ for all $t \in [0,b]$.*

Suppose that $n = 1$. At each point (t,x) in the rectangular region

$$G = \{(t,x) : 0 \le t \le b, c \le x \le d\},$$

the slope of the solution curve $x = x(t)$ can be found using the implicit formula $m = f(x(t),t)$. Hence the values $m_{i,j} = f(x_i,t_j)$ can be computed throughout the rectangle, and each value $m_{i,j}$ represents the slope of the line tangent to a solution curve $x(t)$ that passes through the point (t_j,x_i). It can be used to visualise how a solution curve $fits$ the slope constraint. Sketches of the slope field and solution can be constructed by using the MATLAB. The following $M-file$ will generate a graph analogous to $Figure$ 2.3.

```
[t,x] = meshgrid(0:1.:8,1:-0.25:0);
dt=ones(5,9);
K=0.5; % satutation coefficient
r=0.3; %growth rate
x1=0.2; %initial condition
x2=0.9; %initial condition
dx=r*(x-x.^2/K)
quiver(t,x,dt,dx);
hold on
```

```
y=0:0.01:8;
z1=0.;
z2=0.5;
z3=x1*K ./(x1+(K-x1)*exp(-r*y));
z4=x2*K ./(x2+(K-x2)*exp(-r*y));
plot(y,z1,y,z2,y,z3,y,z4)
hold off.
```

Definition 2.2 *Given the rectangle $G = \{(t,x) : 0 \leq t \leq b, c \leq x \leq d\}$, assume that $f(x,t)$ is continuous on G. The function f is said to satisfy a Lipschitz condition in the variable x on G provided that a constant $L > 0$ exists with the property that*

$$|f(x_1,t) - f(x_2,t)| \leq L\,|x_1 - x_2|$$

Theorem 2.1 *Assume that $f(x,t)$ is continuous in a region G. If f satisfies a Lipschitz condition on G in the variable x and $(t_0, x_0) \in G$, then the initial value problem has a unique solution $x = x(t)$ on the some subinterval $t_0 \leq t \leq t_0 + \delta$.*

Intuitively, a dynamic system is said to be in equilibrium if it does not change as time proceeds. Thus, a population is in equilibrium if it stays the same size. The mathematical way to put this would be: let $x(t)$ denote the population at time t; if $x(t)$ is a constant function, equally if $dx/dt = 0$ for all t, then the population is in equilibrium. Here is the formal definition used for the kinds of differential equations of interest to us.

Definition 2.3 *For the differential equation of the form*

$$\frac{dx}{dt} = f(x) \tag{2.10}$$

the value $\bar{x}$ is called an equilibrium if $f(\bar{x}) = 0$.

Observe that if $\bar{x}$ is an equilibrium, then the constant function $x(t) = \bar{x}$ satisfies equation (2.10) and so $x(t) = \bar{x}$ is called an equilibrium solution of (2.10).

In order to describe the behaviour of the solution near an equilibrium, we will consider linear system. If $\bar{x}$ is an equilibrium of the differential equation

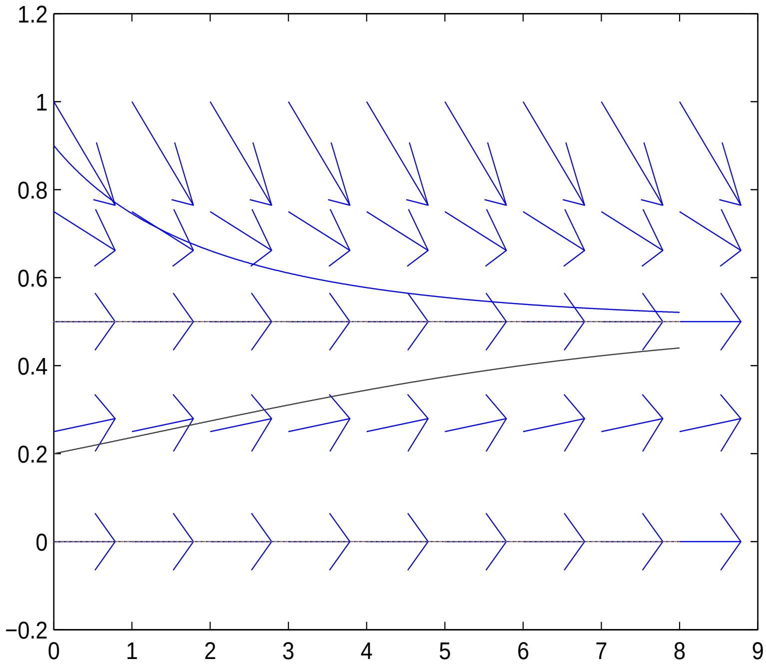

Figure 2.2: The slope field for the differential equation (2.7)

$\dot{x} = f(x)$ so that $f(\bar{x}) = 0$, we make the change of variable $u(t) = x(t) - \bar{x}$. Substitution gives

$$\frac{dx}{dt} = f(u(t) + \bar{x})$$

The *linearization* of the differential equation at the equilibrium $\bar{x}$ is defined to be the linear homogeneous differential equation

$$\frac{dv}{dt} = \frac{df(\bar{x})}{dx} v \tag{2.11}$$

The importance of the linearization lies in the fact that the behaviour of its solution is easy to analyse.

Theorem 2.2 *If all solution of the linearization* (2.11) *at an equilibrium* $\bar{x}$ *tend to zero as* $t \to \infty$*, then all solution of* (2.10) *with x(0)sufficiently close to* $\bar{x}$ *tend to the equlibrium* $\bar{x}$ *as* $t \to \infty$*.*

Definition 2.4 *An equilibrium* $\bar{x}$ *is said to be stable if for every* $\epsilon > 0$ *there exists* $\delta > 0$ *such that* $|x(0) - \bar{x}| < \delta$ *implies* $|x(t) - \bar{x}| < \epsilon$ *for all* $t > 0$*. An equilibrium is said to be asymptotically stable if it is stable and if in addition* $|x(0) - \bar{x}| < \delta$ *implies* $\lim_{t\to\infty} x(t) = \bar{x}$*.*

For differential equation $\dot{x}(t) = f(x(t))$ an equilibrium $\bar{x}$ is asymptotically stable if and only if

$$\frac{df(x)}{dx}_{x=\bar{x}} = \frac{df(\bar{x})}{dx} < 0.$$

If the population governed by logistic equations (2.7) is at equilibrium K at some point of time, say $t = 0$ for convenience, then it will stay at the equilibrium and the function $x(t) = K$ is a solution with the initial condition $x(0) = K$. We get

$$\frac{df(x)}{dx} = r\left(1 - \frac{x}{K}\right) - \frac{xr}{K}.$$

For $\bar{x} = 0$ $\frac{df(0)}{dx} = r > 0$ and for $\bar{x} = K$ $\frac{df(K)}{dx} = -r < 0$. As follows from $Figure$ 2.3, all solutions of the logistic equation tend to equilibrium $\bar{x} = K$ as $t \to \infty$ and the only solution that tends to $\bar{x} = 0$ is the identically zero solution $x(t) = 0$.

2.4 Continuous Single-Species Population Models with Time Delay

Up to now in our study of continuous population models we have been assuming that $\dot{x}(t)$, the growth rate of population size at a same time t, depends only on $x(t)$. For detail explanation see [2]. However, there are situations in which the growth rate does not respond instantaneously to change in population size. If we assume that the per capacity growth rate $\dot{x}(t)/x(t)$ is a function of $x(t - \tau)$, as may be approximate for example in modelling a population whose food supply requires a time τ, we are led to a model of the form

$$\dot{x}(t) = x(t)g(x(t-\tau)), \tag{2.12}$$

a differential-difference equation. For example, the delay logistic equation is

$$\dot{x}(t) = rx(t)(1 - \frac{x(t-\tau)}{K}) \tag{2.13}$$

Definition 2.5 *An equilibrium of the differential-difference equation*

$$\dot{x}(t) = x(t)g(x(t-\tau))$$

is a value such that $\bar{x}(t)g(\bar{x}) = 0$, so that $x(t) \equiv \bar{x}$ is a constant solution of the differential-difference equation.

Observe that for the differential-difference equation (2.12) implies that $x = 0$ is always an equilibrium. The delay logistic equation have two equilibria $\bar{x} = 0$ and $\bar{x} = K$. For differential equation $\dot{x}(t) = x(t)g(x(t))$, an equilibrium $\bar{x}$ is asymptotically stable if and only if

$$\frac{d\,(xg(x))}{dx}_{x=\bar{x}} = \bar{x}\frac{dg(\bar{x})}{dx} + g(\bar{x}) < 0,$$

so that the equilibrium $x = 0$ is asymptotically stable if $g(0) < 0$ and an equilibrium $\bar{x}$ is asymptotically stable if $g'(\bar{x}) < 0$. The asymptotic stability of equilibrium $\bar{x}$ of the differential-difference equations

$$\dot{x}(t) = x(t)g(x(t-\tau))$$

requires additional condition. We let $u(t) = x(t) - \bar{x}$ and obtain the equivalent differential-difference equation

$$\begin{aligned}
\dot{u}(t) &= (\bar{x}(t) + u(t))g(\bar{x} + u(t-\tau)) \\
&= (\bar{x}(t) + u(t))(g(\bar{x}) + g'(\bar{x})u(t-\tau)) + \frac{g''(c)}{2}u(t-\tau)^2 \\
&= u(t))(g(\bar{x}) + \bar{x}g'(\bar{x})u(t-\tau)) + h(u(t), u(t-\tau))
\end{aligned}$$

The linearization of the differential-difference equation $\dot{x}(t) = x(t)g(x(t-\tau))$ is defined to be the linear differential-difference equation

$$\dot{v}(t) \quad = \quad g(\bar{x})v(t) + \bar{x}g'(\bar{x})v(t-\tau))$$

Theorem 2.3 *If all solutions of the linearization*

$$\dot{v}(t) = g(\bar{x})v(t) + \bar{x}g'(\bar{x})v(t-\tau))$$

at an equilibrium $\bar{x}$ tend to zero as $t \to \infty$, then every solutions $x(t)$ of $\dot{x}(t) = x(t)g(x(t-\tau))$ with $|x(t) - \bar{x}|$ sufficiently small for $-\tau \leq t \leq 0$ tends to the equilibrium $\bar{x}$ as $t \to \infty$.

In order to describe the behaviour of solution of linearization, we must study a more general problem

$$\dot{v}(t) = av(t) + bv(t-\tau)$$

We look for solution of the form $v(t) = ce^{\lambda t}$ and obtain the *characteristic equation*

$$\lambda = a + be^{-\lambda\tau}$$

In order that all solutions of $\dot{v}(t) = av(t) + bv(t-\tau)$ tend to zero as $t \to \infty$, all solutions of the characteristic equation must have negative real part. It is possible to prove the following results [8].

Theorem 2.4 *All roots of the equation $(z+A)e^z + B = 0$, where A and B are real, have negative real parts if and only if*

$$\begin{aligned} A &> -1 \\ A + B &> 0 \\ B &< \zeta \sin\zeta - A\cos\zeta \end{aligned}$$

where ζ is the root of $\zeta = -A\tan\zeta$, $0 < \zeta < \pi$, if $A \neq 0$ and $\zeta = \frac{\pi}{2}$ if $A = 0$.

The following similar theorem holds [8]

Theorem 2.5 *If A,B are real numbers, then all roots z of*

$$Ae^z + B - ze^z \quad = \quad 0$$

have negative real parts if and only if $A < 1$ and $A < -B < \sqrt{\alpha^2 + A^2}$, where α is a root of $\alpha = A \tan \alpha$, such that $0 < \alpha < \pi/2$. If $A = 0$, then take $\alpha = \pi/2$.

For the equilibrium $\bar{x} = 0$ the linearization is

$$\dot{v}(t) \quad = \quad g(\bar{x})v(t).$$

Since $g(0) > 0$ for the most models of this type, the equilibrium $\bar{x} = 0$ is unstable. For the equilibrium $\bar{x} > 0$, $g(\bar{x}) = 0$ end the linearization is

$$\dot{v}(t) \quad = \quad \bar{x}g'(\bar{x})v(t - \tau))$$

or in general form with $a = 0$

$$\dot{v}(t) \quad = \quad bv(t - \tau))$$

Using $Theorem$ 2.4 it is possible to show that the condition that all roots of the characteristic equation have negative real part is

$$0 < -b\tau < \frac{\pi}{2}.$$

For the delay-logistic equation this stability condition is $0 < r\tau < \frac{\pi}{2}$.
A graphic display of the solution is often helpful to obtain insights into the behavior of the solution. For delay-logistic equation, here is a display of the solution with $r = 1,\ K = 2, \tau = 1$.

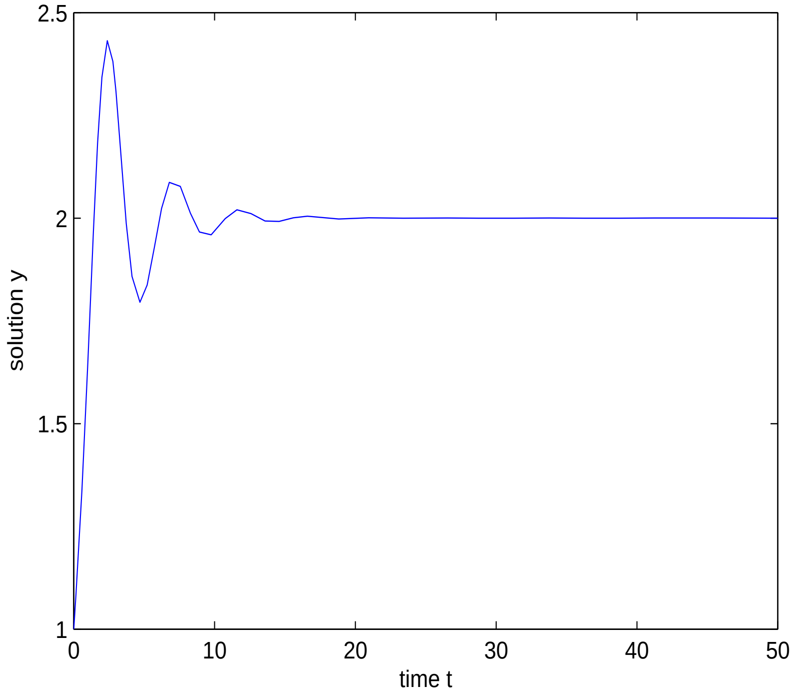

Figure 2.3: Numerical solution of logistic-delay equation

```
%    logist_delay

%    The differential equations
%
%          y'(t) = r* y(t)*(1- y(t-1)/K)
%
%
%    are solved on [0, 10] with history y = 1 for
%    t <= 0.
%
%    The lags are specified as a vector [1], the delay differential
%    equations are coded in the subfunction DDEfun, and the history is
%    evaluated by the function DDEHIST. Because the history is constant it
```

```
%   could be supplied as a vector:
%       sol = dde23(@ddefun,[1],1,[0, 10]);
%       K=2, T=1, r=1
global r K
r=0.5;
K=2;
sol = dde23(@ddefun,[1],@ddehist,[0, 50]);
figure;
plot(sol.x,sol.y)
xlabel('time t');
ylabel('solution y');

function s = ddehist(t)
% Constant history function.
s = 1;

function dydt = ddefun(t,y,Z,r,K)
% Differential equations function.
global r K
ylag1 = Z(:,1);
dydt =  r*y(1)*(1-ylag1(1)/K);
```

Chapter 3

The Lotka-Volterra Equations

The central subject of this chapter are mathematical models of more interacting species. We will begin with predator-prey models and analyse its properties. In section (3.2) we will examine the stability equilibrium for two species competition model. In the next we give qualitative analysis of more than two species models, describe competition partial differential model and predator-prey partial functional differential model. This chapter is based on the work [2], [7], [10], [17], [30].

3.1 Predator-Prey Model

In the 1920s Vito Volterra was asked if it were possible to explain the fluctuation which had been observed in the fish population of tha Adriatic-sea. Volterra [28] constructed the model which has become known as the Lotka-Volterra model, because Lotka [20] constructed a similar model in a different context.

Let $x(t)$ be the number of fish and $y(t)$ the number of sharks at time t. We assume that plankton, which is a food supply for the fish, is unlimited, and thus that a per capita growth rate of the fish population in the absence of sharks would be constant. Thus, if there were no sharks the fish population would satisfy a different equation of the form

$$\frac{dx}{dt} = \lambda x$$

Shark, on the other hand, depend on fish as their food supply, and we assumed that if there were no fish the sharks would have a constant per capita death rate, thus, in the absence of fish, the shark population would describe a differential equation of the form

$$\frac{dy}{dt} = -\mu y$$

We assumed that the presence of fish increases the shark growth rate, changing the growth rate form $-\mu$ to $-\mu + cx$. The presence of sharks reduces the fish population, changing the growth rate from λ to $\lambda - by$. This gives Lotka-Volterra equations

$$\begin{aligned} \frac{dx}{dt} &= x(\lambda - by) \\ \frac{dy}{dt} &= y(-\mu + cx) \end{aligned} \tag{3.1}$$

We cannot solve this system of ordinary differential equations analytically, but we can obtain some information about the behavior of this solution. To solve for $x(t)$ and $y(t)$ as a function of t, we eliminate t. We look for orbits, or trajectories of the solution-curve in the phase-plane representing the functional relation between x and y with the time t as the parameter [2]. We may eliminate t from the equation in the following way

$$\frac{dy/dt}{dx/dt} = \frac{dy}{dx} = \frac{y(-\mu + cx)}{x(\lambda - by)}$$

We may solve this differential equations by separation of variables:

$$\begin{aligned} \int \frac{-\mu + cx}{x} dx &= \int \frac{\lambda - by}{y} dy \\ -\mu \log x + cx &= \lambda \log y - by + h \end{aligned}$$

where h is a constant of integration, or

$$-\mu \log x - \lambda \log y + cx + by = h$$

The minimum value of the function

$$V(x, y) = -\mu \log x - \lambda \log y + cx + by$$

is obtaining by setting

$$\frac{\partial V}{\partial x} = 0, \qquad \frac{\partial V}{\partial y} = 0$$

Then $\bar{x} = \frac{\mu}{c}$ and $\bar{y} = \frac{\lambda}{b}$, which is an *equilitrium* point of (3.1). Every orbit of the system is given implicitly by an equation $V(x(t), y(t)) = h$, for some constants h, which is determined by the initial conditions, i.e.

$$h = -\mu \log(x(0)) - \lambda \log(y(0)) + cx(0) + by(0)$$

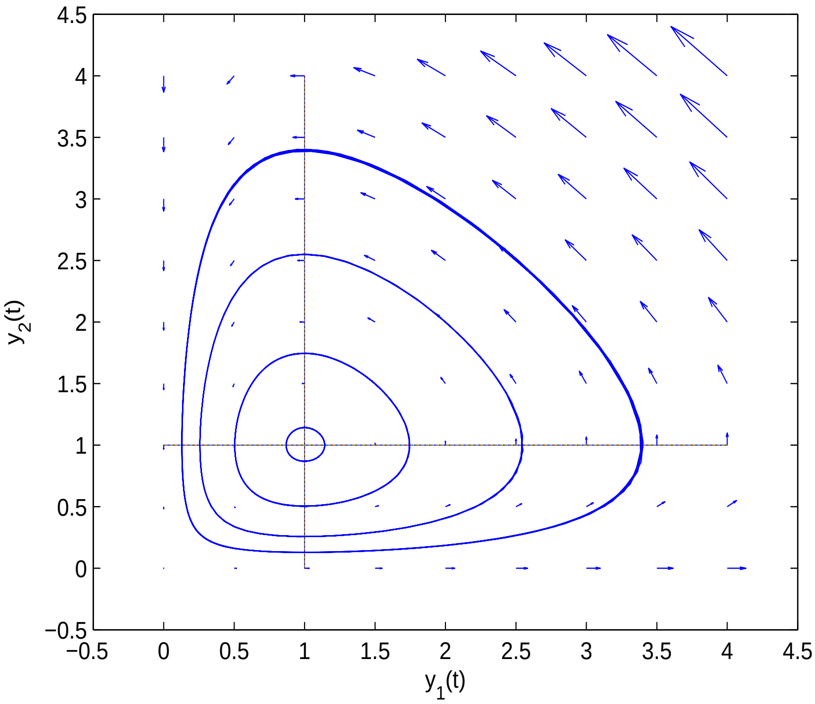

Figure 3.1: The slope field and trajectories of Lotka-Volterra equation

$Figure$ 3.1 is generated by the following $M - files$.

```
a=1.;b=1.;c=1.;d=1;
```

```
[y1,y2] = meshgrid(0:0.5:4,0:0.5:4)
Dy1Dt=y1.*(a-b.*y2);
Dy2Dt=y2.*(-d+c.*y1);
quiver(y1,y2,Dy1Dt,Dy2Dt);
hold on
z1=a/b;z2=d/c;
z=0:0.005:4;
plot(z,z1);
plot(z2,z);
options = odeset('AbsTol', 1e-7,'RelTol', 1e-4);
tspan = [0,50]; yzero=[1.5,1.5];
[t,y]=ode45(@LV,tspan,yzero,options,a,b,c,d);
plot(y(:,1),y(:,2)),title(''),grid

yzero=[1.1,1.1];
[t,y]=ode45(@LV,tspan,yzero,options,a,b,c,d);
plot(y(:,1),y(:,2)),title('')

yzero=[2.5,2.5];
[t,y]=ode45(@LV,tspan,yzero,options,a,b,c,d);
plot(y(:,1),y(:,2)),title('')

yzero=[2,2];
[t,y]=ode45(@LV,tspan,yzero,options,a,b,c,d);
plot(y(:,1),y(:,2)),title('')
xlabel 'x'; ylabel 'y'
hold off

function yprime = LV(t,y,a,b,c,d)
%LV       LV predator-prey parammetrized
%         YPRIME = LV(T,Y,A,B,C)
yprime = [y(1)*(a-b*y(2)); y(2)*(c*y(1)-d)];
```

3.2 A competition equation

Let us return to ecology and model the interaction of two *competing species*. If x and y denote their densities, then the rates of growth $\dot{x}\ /x$ and $\dot{y}\ /y$ will be decreasing functions of both x and y, since competition will act both within and between the species [10]. The most simpleminded assumption would be that this decrease is linear. This leads to

$$\begin{aligned} \dot{x} &= x(a - bx - cy) \\ \dot{y} &= y(d - ex - fy) \end{aligned} \tag{3.2}$$

with positive constants a to f. Again, since the boundary of R^2_+ is invariant, so is R^2_+ itself. In fact, if one population is absent, the other obeys the familiar logistic growth law.

The $x-$ and $y-$isoclines are given by

$$a - bx - cy = 0$$
$$d - ex - fy = 0$$

in int R^2_+. These are straight with negative slopes.

There remains the case of unique intersection $\bar{F} = (\bar{x}, \bar{y})$ of the isoclines in int R^2_+ when

$$\bar{x} = \frac{af - cd}{bf - ce} \qquad \bar{y} = \frac{bd - ae}{bf - ce} \tag{3.3}$$

The Jacobian of (3.2) at F is

$$\mathbf{A} = \begin{bmatrix} -b\bar{x} & -c\bar{x} \\ -e\bar{y} & -f\bar{y} \end{bmatrix} \tag{3.4}$$

We have to distinguish two situations:
(a) If $bf > ce$ then the denominator in (3.3) is positive. This implies $af - cd > 0,\ bd - ae > 0$ and hence

$$\frac{b}{e} > \frac{a}{d} > \frac{c}{f}. \tag{3.5}$$

From the signs of $\dot{x}$ and $\dot{y}$ in the regions I, II, III, IV can be inferred that every orbit in int R^2_+ converges to $\bar{F}$. This agrees with the fact that the

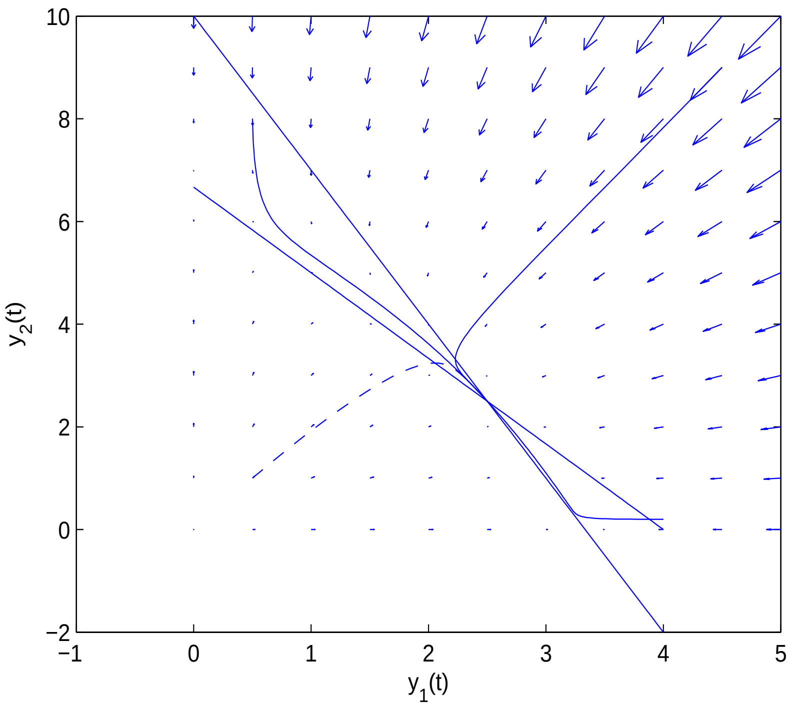

Figure 3.2: The slope field and trajectories of competition equation

eigenvalues of (3.4) are negative and $\bar{x}$, consequently, is a sink. This is the case of $stable\ coexistence$, $Figure3.2$.

(b) otherwise

$$\frac{c}{f} > \frac{a}{d} > \frac{b}{e}. \tag{3.6}$$

As seen from $Figure3.3$,all orbits in region I converge to the y-axis and all those of region III to the x-axis. Since $detA = \overline{xy}(bf - ce) < 0$, $\bar{F}$ is a saddle. Its stable manifold consists of two orbits converging to $\bar{F}$. One of them lies in region II, the other one in region IV. Together, they divide int R^2_+ into two basins of attraction. All orbits from one basin converge to $\bar{F}_2 = (0, \frac{d}{f})$, all those from the other one to $\bar{F}_1 = (\frac{a}{e}, 0)$. This means that - depending on the initial conditions - one or the other species gets eliminated. This is the so-called *bistable case*.

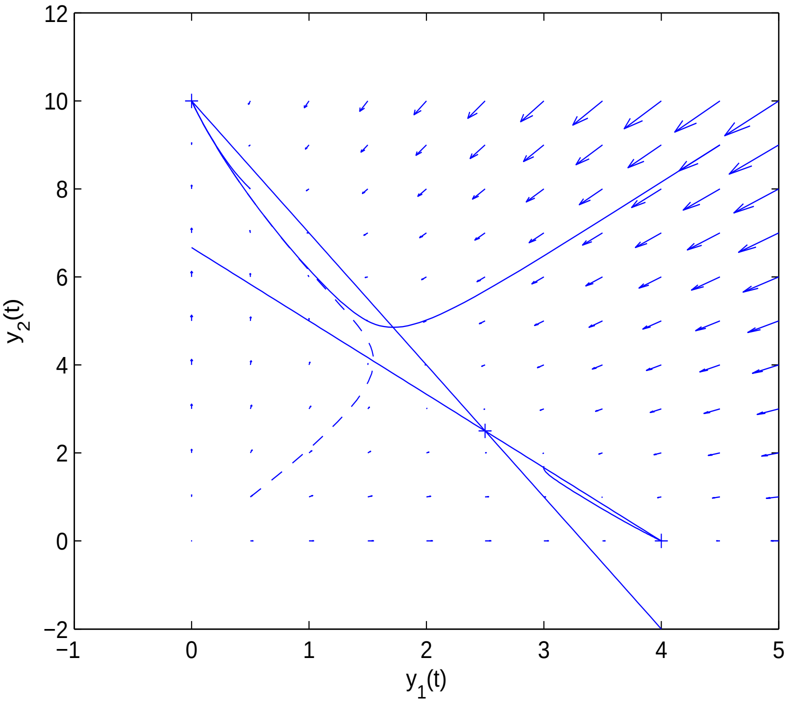

Figure 3.3: The slope field and trajectories of competition equation

The following M files generates *Figure* 3.2, 3.3.

```
%interior equilibrium point a=10.;b=3.;c=1.;d=10;e1=2.5;f=1.5;
a=10.;b=2.5;c=1.5;d=10.;e1=3.;f=1.;
[y1,y2] = meshgrid(0:0.5:5,0:1:10);
Dy1Dt=y1.*(a-b.*y1-c.*y2);
Dy2Dt=y2.*(d-e1.*y1-f.*y2);
quiver(y1,y2,Dy1Dt,Dy2Dt);
hold on
z=0:0.05:4;
z1=(a-b*z)/c;z2=(d-e1*z)/f;
plot(z,z1,'r');
```

```
plot(z,z2,'c');
plot(a/b,0,'+');
plot(0,d/f,'+');
z3=(a*f-c*d)/(b*f-c*e1)
z4=(b*d-a*e1)/(b*f-c*e1)
plot(z3,z4,'+');
tspan = [0,50]; yzero=[0.5,1];
options = odeset('AbsTol', 1e-7,'RelTol', 1e-4);
[t,y]=ode45(@comp_equat,tspan,yzero,options,a,b,c,d,e1,f);
plot(y(:,1),y(:,2),'--'),title(''),grid

yzero=[0.5,8];
[t,y]=ode45(@comp_equat,tspan,yzero,options,a,b,c,d,e1,f);
plot(y(:,1),y(:,2)),title(''),grid

yzero=[4.5,9];
[t,y]=ode45(@comp_equat,tspan,yzero,options,a,b,c,d,e1,f);
plot(y(:,1),y(:,2)),title(''),grid

yzero=[3.,1.7];
[t,y]=ode45(@comp_equat,tspan,yzero,options,a,b,c,d,e1,f);
plot(y(:,1),y(:,2)),title(''),grid
xlabel y_1(t),ylabel y_2(t)
hold off

function yprime = comp_equat(t,y,a,b,c,d,e1,f)
%comp_equat    competition equations
%          YPRIME = comp_equat(t,y,a,b,c,d,e,f)
yprime = [y(1)*(a-b*y(1)-c*y(2)); y(2)*(d-e1*y(1)-f*y(2))];
```

3.3 Lotka-Volterra Equations for More Than Two Populations

The general Lotka-Volterra equation for n populations is of the form [7], [10],[27]

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j) \qquad i = 1, \ldots, n. \tag{3.7}$$

The x_i denote the densities; the r_i are intrinsic growth (or decay) rates, and the a_{ij} describes the effect of the j-th upon the i-th population, which is positive if it enhances and negative if it inhibites the growth. All sorts of interactions can be modelled in this way, as long as one is prepared to assume that the influence of every species upon the growth rates is linear. The matrix $A = (a_{ij})$ is called the *interaction matrix*.

The state space is, of course, the positive orthant

$$\mathbf{R^n_+} = \{\mathbf{x} = (x_1, \ldots, x_n) \in \mathbf{R^n} : x_i \geq 0 \text{ for } i = 1, \ldots, n\}.$$

The boundary points of $\mathbf{R^n_+}$ lie on the coordinate planes $x_i = 0$, which correspond to the states where species i is absent. These "faces" are invariant, since $x_i(t) \equiv 0$ is the unique solution of the i-th equation of (3.7) satisfying $x_i(0) = 0$. In such a model, a missing species cannot "immigrate". Thus the boundary bd $\mathbf{R^n_+}$ and consequently $\mathbf{R^n_+}$ itself are invariant under (3.7). So is the interior int $\mathbf{R^n_+}$, which means that if $x_i(0) > 0$ then $x_i(t) > 0$ for all t. The density $x_i(t)$ may approach 0, however, which means extinction.

The ecological equations of the last chapter were examples of (3.7) with $n = 2$. We shall see that all possible two dimensional cases can be classified. In higher dimensions, many open questions remain. In particular, numerical simulation shows that even the case of 3 populations may lead to some kind of *chaotic motion*, and the asymptotic behaviour of the solution consists of highly irregular oscillations and depends in a very sensitive way upon the initial conditions. The long term outcome, in such a case, is unpredictable.

In this section, we will describe a few general results about (3.7) and then turn to some special cases of biological interest [10].

We will apply **LaSalle's extension theorem** of Lyapunov stability. We note the following definition and the theorem.

Let $\dot{x} = f(x)$ be a system of differential equations. The vector-valued function $f(x)$ is continuous in x for $x \in \bar{G}$ where G is an open set in R^n. Let V be a C^1 function on R^n to R.

Definition 3.1 *We say V is Lyapunov function in G for $\dot{x} = f(x)$ if $\dot{V} = gradV.f \leq 0$ on G.*

Let $E = \{x \in \bar{G} : \dot{V}(x) = 0\}$.

Theorem 3.1 *If V is a Lyapunov function in G for $\dot{x} = f(x)$, then each bounded solution $x(t) \subseteq G$ of $\dot{x} = f(x)$ approaches M where M is the largest invariant in set E.*

3.3.1 Interior equilibria

The equilibrium point of (3.7) in *int* $\mathbf{R^n_+}$ are the solutions of the linear equations

$$r_i + \sum_{j=1}^{n} a_{ij}x_j = 0 \quad i = 1, \ldots, n \tag{3.8}$$

whose components are postivie. (The equilibria on the boundary faces of $\mathbf{R^n_+}$ can be found in similar way: one has only to note that the restriction of (3.7) to any such face is again of Lotka-Volterra type.)

Theorem 3.2 *Int $\mathbf{R^n_+}$ contains α- or ω- limit points if and only if (3.7) admits an interior equilibrium.*

for proof see [10]. One direction of this proposition is trivial. A rest point coincides with its own α- and ω- limit. It is a converse which is of interest, since it is (in principle) not a hard check, if (3.8) admits positive solutions. If it does not, then every orbits has to converge to the boundary, or to infinity. In particular, if int $\mathbf{R^n_+}$ contains a periodic orbit, it must also contains a rest point.

In order to prove the converse, let $L : \mathbf{x} \to \mathbf{y}$ be defined by

$$y_i = r_i + \sum_{j=1}^{n} a_{ij}x_j \qquad i = 1, \ldots, n$$

If (3.7) admits no interior equilibrium, the set $K = L(int\ \mathbf{R^n_+})$ is disjoint from $\mathbf{0}$ A well known theorem from convex analysis implies that there exists a hyperplane H trough $\mathbf{0}$ which is disjoint from the convex set K. Thus there exists a vector $\mathbf{c} = (c_1, \ldots, c_n) \neq 0$ which is orthogonal to H ($\mathbf{c}.\mathbf{x} = 0$ for all $x \in H$) such that $\mathbf{c}.\mathbf{y}$ is positive for all $y \in K$. Setting

$$V(\mathbf{x}) = \sum c_i \log x_i, \tag{3.9}$$

we see that V is defined on int $\mathbf{R}^{\mathbf{n}}_{+}$. If $\mathbf{x}(t)$ is solution of (3.7) in int $\mathbf{R}^{\mathbf{n}}_{+}$, then the time derivative of $t \to V(\mathbf{x}(t))$ satisfies

$$\begin{aligned} \dot{V} &= \sum c_i \frac{\dot{x}_i}{x_i} \\ &= \sum c_i y_i = \mathbf{c}.\mathbf{y} > 0 \end{aligned}$$

Thus V is increasing along each orbit. But then no point $\mathbf{y} \in int\mathbf{R}^{\mathbf{n}}_{+}$ may belong to its ω- limit: indeed, by Lyapunov's theorem, the derivative $\dot{V}$ would have to vanish there. This contradiction completes the proof. It also shows:
Corollary: *If (3.7) admits no interior equilibrium, then it is gradient-like in int* $\mathbf{R}^{\mathbf{n}}_{+}$.

In general, (3.8) will admit one solution in int $\mathbf{R}^{\mathbf{n}}_{+}$, or none at all. It is only in the "degenerate" case $detA = 0$ that (3.7) can have more than one solution: these will form a continuum of rest points.

3.4 Equilibria and its stability

Definition 3.2 *For the differential equation of the form*

$$\frac{dx}{dt} = f(x) \tag{3.10}$$

the value $\bar{x}$ is called an equilibrium if $f(\bar{x}) = 0$.

Observe that if $\bar{x}$ is an equilibrium, then the constant function $x(t) = \bar{x}$ satisfies equation (2.10) and so $x(t) = \bar{x}$ is called an equilibrium solution of (3.17).

In order to describe the behaviour of the solution near an equilibrium, we introduce the process of *linearization*. If $\bar{x}$ is an equilibrium of the differential equation $\dot{x} = f(x)$ so that $f(\bar{x}) = 0$, we make the change of variable $u(t) = x(t) - \bar{x}$. Substitution gives

$$\frac{dx}{dt} = f(u(t) + \bar{x})$$

The *linearization* of the differential equation at the equilibrium $\bar{x}$ is defined to be the linear homogeneous differential equation

$$\frac{dv}{dt} = \frac{df(\bar{x})}{dx}v \tag{3.11}$$

The importance of the linearization lies in the fact that the behaviour of its solution is easy to analyse.

Theorem 3.3 *If all solution of the linearization* (3.18) *at an equilibrium $\bar{x}$ tend to zero as $t \to \infty$, then all solutions of* (3.17) *with x(0)sufficiently close to $\bar{x}$ tend to the equlibrium $\bar{x}$ as $t \to \infty$.*

Definition 3.3 *An equilibrium $\bar{x}$ is said to be stable if for every $\epsilon > 0$ there exists $\delta >)$ such that $|x(0) - \bar{x}| < \delta$ implies $|x(t) - \bar{x}| < \epsilon$ for all $t > 0$. An equilibrium is said to be asymptotically stable if it is stable and if in addition $|x(0) - \bar{x}| < \delta$ implies $\lim_{t\to\infty} x(t) = \bar{x}$.*

We now examine a concept called asymptotic stability in the context of linear system of ODEs. The following fundamental result applies to constant coefficient systems:

Theorem 3.4 *Let A be a constant matrix with eigenvalues*

$$\lambda_1, \lambda_2, \ldots, \lambda_n.$$

Equilibrium $\bar{x} = 0$ of linear differential equation $\dot{x}(t) = Ax(t)$ is asymptotically stable if and only if all eigenvalues of the matrix has negative real part.

Let us now recall some classic Hopf bifurcation theorem for the following system of ODDEs

$$\dot{x} = f(x, \mu),$$

where $f(0, \mu) = 0$ for μ in a neighborhood of 0.

Assume that $A(\mu) = \frac{df(0,\mu}{dx}$ has a pair of complex conjugate eigenvalues λ and $\bar{\lambda}$ such that $\lambda(\mu) = \alpha(\mu) + i\omega(\mu)$, where $\alpha(0) = 0$, $\omega(0) = \omega_0 > 0$, $\alpha'(0) \neq 0$, and the remaining $n-2$ eigenvalues have strictly negative real parts. Then the system has a family of periodic solution [22].

3.4.1 Eigenvalues

Let $\mathbf{A}$ be a square matrix of dimension n x n and let $\mathbf{v}$ be a vector of dimension n. The product $\mathbf{Y} = \mathbf{Av}$ can be viewed as a linear transformation from n-dimensional space into itself. We want to find scalars λ for which there exists a nonzero vector $\mathbf{v}$ such that

$$\mathbf{Av} = \lambda \mathbf{v}; \tag{3.12}$$

that is, the linear transformation $T(\mathbf{v}) = \mathbf{Av}$ maps $\mathbf{v}$ onto the multiple $\lambda\mathbf{v}$. When this ocours, we call $\mathbf{v}$ an eigenvector that corresponds to the eigenvalue λ, and together they form the eigenpair $\lambda, \mathbf{v}$ for $\mathbf{v}$. In general, the scalar λ and vector $\mathbf{v}$ can involve complex numbers. For simplicity, most of our illustrations will involve real calculations. However, the techniques are easily extended to the complex case [6]. The identity matrix $\mathbf{I}$ can be used to express equation (3.19) as

$$(\mathbf{A} - \lambda \mathbf{I})\mathbf{v} = 0. \tag{3.13}$$

The significance of equation (3.20) is that the product of the matrix $(\mathbf{A} - \lambda\mathbf{I})$ and the nonzero $\mathbf{v}$ is the zero vector! This linear system has nontrivial solutions if and only if the matrix $\mathbf{A} - \lambda\mathbf{I}$ is singular, that is,

$$det(\mathbf{A} - \lambda \mathbf{I}) = 0. \tag{3.14}$$

This determinant can be written in the form

$$\begin{vmatrix} a_{11} - \lambda & a_{12} & \dots & a_{1n} \\ a_{21} & a_{22} - \lambda & \dots & a_{2n} \\ \vdots & \vdots & \dots & \vdots \\ a_{n1} & a_{n2} & \dots & a_{nn} - \lambda \end{vmatrix} = 0. \tag{3.15}$$

When the determinant in (3.22) is expanded, it becomes a polynomial of degree n, which is called the characteristic polynomial

$$\begin{aligned} p(\lambda) &= det(\mathbf{A} - \lambda \mathbf{I}) \\ &= (-1)^n(\lambda^n + c_1\lambda^{n-1} + c_2\lambda^{n-2} + \ldots + c_{n-1}\lambda + c_n) \end{aligned} \tag{3.16}$$

There exists exactly n roots (not necessarily distinct) of a polynomial of degree n. Each root λ can be substituted into equation (5.31) to obtain an underdetermined system of equation that has a corresponding nontrivial solution vector $\mathbf{v}$. If λ is real, a real eigenvector $\mathbf{v}$ can be constructed. For emphasis, we state the following definitions.

Definition 3.4 ***Eigenvalue***. *If* $\mathbf{A}$ *is an* n *x* n *real matrix, then its* n *eigenvalues* $\lambda_1, \lambda_2, \ldots, \lambda_n$ *are the complex roots of the characteristic polynomial*

$$p(\lambda) = det(\mathbf{A} - \lambda \mathbf{I}). \tag{3.17}$$

Definition 3.5 ***Eigenvector***. *If* λ *is an eigenvalue of* $\mathbf{A}$ *and the nonzero vector* $\mathbf{v}$ *has a property that*

$$\mathbf{A}\mathbf{v} = \lambda \mathbf{v}, \tag{3.18}$$

then $\mathbf{v}$ *is called an eigenvector of* $\mathbf{A}$ *corresponding to the eigenvalue* λ.

Consider the characteristic equation

$$|\lambda \mathbf{I} - \mathbf{A}| = \lambda^n + b_1 \lambda^{n-1} + \ldots + b_{n-1}\lambda + b_n = 0$$

determining the n eigenvalues λ of each real n x n square matrix $\mathbf{A}$, where $\mathbf{I}$ is the identity matrix. Then all the eigenvalues λ have negative real parts if

$$\Delta_1 > 0, \Delta_2 > 0, \ldots, \Delta_n > 0,$$

where

$$\Delta_k = \begin{vmatrix} b_1 & 1 & 0 & 0 & 0 & 0 & \ldots & 0 \\ b_3 & b_2 & b_1 & 1 & 0 & 0 & \ldots & 0 \\ b_5 & b_4 & b_3 & b_2 & b_1 & 1 & \ldots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ldots & \vdots \\ b_{2k-1} & b_{2k-2} & b_{2k-3} & b_{2k-4} & b_{2k-5} & b_{2k-6} & \ldots & b_k \end{vmatrix}$$

Particularly for a given n we have the following Routh-Hurwitz condition:
n=1
The polynomial $P(x) = x + a$ is stable if $a > 0$.
n=2
$P(x) = x^2 + ax + b$ is stable if $a > 0, b > 0$.
n=3
$P(x) = x^3 + ax^2 + bx + c$ is stable if $a > 0, b > 0, 0 < c < ab$.
n=4
$P(x) = x^4 + ax^3 + bx^2 + cx + d$ is stable if $a > 0, b > 0, 0 < c < ab, 0 < d < \frac{(abc-c^2)}{a^2}$.

Chapter 4

The Chemostat

The purpose of this chapter is to describe and analyse of different type of chemostat. We will consider single chemostat, n species chemostat, chemostat with delayed response in growth and diffusive chemostat. All results in this chapter are taken from the work [2], [5], [11], [12] and [13].

4.1 Single Chemostat

A chemostat is a piece laboratory apparatus used to cultivate bacteria. It consists of a reservoir containing a nutrient, a culture vessel in which the bacteria are cultivated, and an output receptacle. For detail explanation see [2], [11], [12] and [13].

Nutrient is pumped from the reservoir to the culture vessel at a constant rate and bacteria are collected in receptacle by pumping the contents of the culture vessel out at the same constant rate. The process is called continuous culture of bacteria. We wish to describe the behavior of the chemostat by modeling the number of bacteria and nutrient concentration. We will obtain a model for two interacting population that describes a laboratory realization of a very simple lake. More complicated chemostats, in which two or more cultures are introduced, give multispecies models representing more complicated real word situations. We let y present the number of bacteria and C the concentration of nutrient in the chemostat, both functions of t. Let V be the volume of the chemostat and Q the rate of flow into the chemostat from the nutrient reservoir and also the rate of flow out from the chemostat. The fixed concentration of nutrient in the reservoir is a constant $C^{(0)}$.We assume that the average per capita bacterial birth rate is a function $b(C)$ of the nutrient concentration and that the rate of nutrient consumption of an individual bacterium is proportional to $b(C)$, say $\alpha b(C)$. Then the rate of charge of population is the birth rate $b(C)y$of bacteria minus the outflow rate $Q.y/V$. The rate of charge of nutrient volume is the replenishment rate $QC^{(0)}$ minus outflow rate QC minus the consumption rate $\alpha b(C)$. This gives the pair off differential equations

$$\begin{aligned}\dot{y} &= b(C).y - q.y\\ \dot{C} &= q(C^{(0)} - C) - \beta b(C).y,\end{aligned}$$

where $q = Q/V$ and $\beta = \alpha/V$.
It is reasonable to assume that the function $b(C)$ is zero if $C = 0$ and that it saturates when C becomes large. The simplest function with these properties is

$$b(C) = \frac{aC}{C+A},$$

where a and A are constants, and this was the choise originally made by Monod. The explicit chemostat model is now

$$\begin{aligned}\dot{y} &= \frac{aCy}{A+C} - qy \qquad (4.1)\\ \dot{C} &= q(C^{(0)} - C) - \frac{\beta aCy}{A+C},\end{aligned}$$

4.2 Limiting behavior for competing species

Two competition models concerning n species consuming a single, limited resource are discussed. One in based on the Holing-type functional response and other on the Lotka-Volterra-type. The focus of the paper is on the asymptotic behavior of solutions. LaSalle's extension theorem of Lyapunov stability theory is the main tool.

1. Introduction. The section is concerned with the limiting behavior, as $t \to +\infty$, for the solutions of the system

$$\begin{aligned}\dot{S}(t) &= (S^{(0)} - S(t))D - \sum_{i=1}^{n} \frac{k_i x_i(t)S(t))}{a_i + S(t)} \qquad (4.2)\\ \dot{x}_i(t) &= \frac{m_i x_i(t)S(t)}{a_i + S(t)} - D_i x_i(t), \qquad i = 1, \ldots, n\end{aligned}$$

where $S^{(0)}, D, k_i, a_i, m_i, D_i$ are positive. Only the positive solutions are analyzed, since they are of realistic interest.

The system (4.2) describes n species, with populations x_i, $i = 1, \ldots, n$, and death rates D_i competing for a single, limited resource S. This generalizes the model (4.1) by allowing species-specific death rates. The species are assumed to feed on the resource with a saturating functional response to the resource density. Specifically we assume that Michaelis-Menten kinetics or the Holling "disc" model describe how feeding rates and birth rates change in increasing resource density. Close parallels of this model in future are e.g. the planktonics communities of unicellular algae in lake and oceans.

The mathematical future of this section is to apply LaSalle's extension theorem of Lyapunov stability theory. This technique allows us to generalize the results and to give simple, elegant proof. In this section, we will discuss the limiting behavior of solution of the system (4.2). First we note the following lemmas, for proofs see [11] the proofs.

Lemma 4.1 *The solutions* $S(t), x(t), i = 1, \ldots, n$ *of* (4.1) *are positive and bounded.*

Lemma 4.2 *Let* $b_i = m_i/D_i$, $\lambda_i = a_i/(b_i - 1), i = 1, \ldots, n$. *If*

$$(i) \qquad b_i \leq 1$$

or

$$(ii) \qquad \lambda_i > S^{(0)},$$

then $\lim_{t\to\infty} x_i(t) = 0$.

Our basic hypothesis is (H_n)

$$0 < \lambda_1 \leq \lambda_2 \leq \ldots \leq \lambda_n, \qquad \lambda_1 < S^{(0)}.$$

The equations in (4.2) may be relabeled without loss of generality, so that the parameters λ_i are nondecreasing in i.

Theorem 4.1 *Let* (H_n) *hold.*

(i) If $0 < \lambda_1 \leq \lambda_2 \leq \ldots \leq \lambda_n$*, then the solutions of (4.1) satisfy*

$$\begin{aligned} \lim_{t\to\infty} S(t) &= \lambda_1, \\ \lim_{t\to\infty} x_1(t) &= x_1^* = \frac{(S^{(0)} - \lambda_1)(a_1 + \lambda_1)D}{k_1\lambda_1}, \\ \lim_{t\to\infty} x_i(t) &= 0 \qquad i = 2, 3, \ldots, n. \end{aligned} \tag{4.3}$$

(ii) If $0 < \lambda_1 = \ldots = \lambda_j < \lambda_{j+1} \leq \ldots \leq \lambda_n$*, for some* $j, 2 \leq j \leq n$*, then the trajectory of (4.1) approaches* M*, where*

$$M = \left\{(\lambda_1, x_1, \ldots, x_j, 0, \ldots, 0) : (S^{(0)} - \lambda_1)D = \sum_{i=1}^{j} \frac{k_i\lambda_i}{\lambda_i + a_i} x_i, x_i \geq 0, \quad i = 1, \ldots, j\right\}$$

Proof. A rearrangement of (4.2) yields

$$\begin{aligned} \dot{S}(t) &= (S^{(0)} - S(t))D - \sum_{i=1}^{n} \frac{k_i x_i(t) S(t)}{a_i + S(t)}, \\ \dot{x}(t) &= (m_i = D_i)\frac{S(t) - \lambda_i}{a_i + S(t)} x_i(t). \end{aligned}$$

Let

$$V(S, x_1, \ldots, x_n) = S - \lambda_1 - \lambda_1 . \ln\left(\frac{S}{\lambda_1}\right) + c_1\left[(x_1 - x_1^*) - x_1^* . \ln\left(\frac{x_1}{x_1^*}\right)\right] + \sum_{i=2}^{n} c_i x_i,$$

and $G = \{(S, x_1, \ldots, x_n) : S > 0, \ x_i > 0, \ i = 1, \ldots, n\}$. Choose $c_i = k_i/(m_i - D_i), \ i = 1, \ldots, n$. Then time derivative of V computed along solution of the differential equation is

$$\dot{V} = (S - \lambda_1)\left[\frac{(S^{(0)} - S)}{S} D - \frac{k_1 x_1^*}{a_1 + S}\right] + \sum_{i=2}^{n} k_i(\lambda_1 - \lambda_i)\frac{x_i}{a_i + S}$$

or

$$\dot{V} = \frac{(S - \lambda_1)^2 D}{(a_1 + S)S\lambda_1}(-\lambda_1 S - a_1 S^{(0)}) + \sum_{i=2}^{n} k_i(\lambda_1 - \lambda_i)\frac{x_i}{a_i + S} \leq 0 \text{ on } G. \tag{4.4}$$

If $0 < \lambda_1 < \lambda_2 \leq \ldots \leq \lambda_n$, then

$$E = \{(\lambda_1, x_1, 0, \ldots, 0) : x_1 \geq 0\}$$

and the largest invariant set M in E is $\{(\lambda_1, x_1^*, 0, \dots, 0)\}$. Hence (4.4) follows directly from Lemma4.1 and LaSalle's theorem.

If $0 < \lambda_1 = \dots = \lambda_j < \lambda_{j+1} \leq \dots \leq \lambda_n$ for some $j,\ 2 \leq j \leq n$, then from (4.4) we have

$$E = \{(\lambda_1, x_1, \dots, x_j, 0, \dots, 0) : x_1, \dots, x_j \geq 0\}$$

and

$$M = \left\{(\lambda_1, x_1, \dots, x_j, 0, \dots, 0) : (S^{(0)} - \lambda_1)D = \sum_{i=1}^{j} \frac{k_i \lambda_1}{a_1 + \lambda_1} x_i, x_i \geq 0, \quad i = 1, \dots, j\right\}$$

Hence the trajectory approaches M.

Bibliography

[1] Bathia, N. P. and Szego, G. T. Stability Theory of Dynamic Systems. *Springer Verlag, New York* ,1970.

[2] Brauer, F.,Chastillo-Chavez, C. Mathematical Models in Population Biology and Epidemiology. *Springer Verlag, New York* ,2001.

[3] Clark, C., W. Mathematical Bio-economics:The optimal management of Renewable Resources. *Wiley, New York* ,1990.

[4] Clark, C.,W., Munro, G. The economics of fishing and modern capital theory:A simple approach. *J. Environmental Econom. and Management* 2, 92-106, 1975.

[5] Ellermeyer, S. F. Competition in the Chemostat:Global Asymptotic Behavior of a Model with Delayed Response in Growth. *SIAM J. APPL. MATH.* 54:456–465, 1994.

[6] Gantmacher, F. R. The theory of matrices. vol. 2. *New York, Chelsea* , 1959.

[7] Goh, B.S. Global Stability in Many-Species Systems The economics of fishing and modern capital theory:A simple approach. *The American Naturalist* 977, 135–143, 1977.

[8] Hale, L. S.,Verduyn Lunel, S. M. Introduction to Functional Differential Equations. *Springer Verlag, New York* ,1993.

[9] Higham, J. D.,Higham, J. n., Matlab guide. *SIAM, Philadelphia* ,2000.

[10] Hofbauer, J., Sigmund K. The Theory of Evolution and Dynamic Systems:Mathematical Aspects of Selection. *Athenaeum Press Ltd, Newcastle*,1988.

[11] Hsu, S. B. Limiting Behavior for Competing Species. *SIAM J. APPL. MATH.* 34:1026–1044, 1978.

[12] Hsu, S. B., Waltman, P. On a system of Reaction-Diffusion Equations Arising from Competition in an Unstirred Chemostat. *SIAM J. APPL. MATH.* 53:1026–1044, 1993.

[13] Hsu, S. B., Hubebell, S., Waltman, P. A Mathematical Theory for Single-nutrient Competition in Continuous Cultures of Micro-organisms *SIAM J. APPL. MATH.* 32:366–383, 1977.

[14] Jerry, M., Raissi, N. The optimal strategy for a bioeconomical model of a harvesting renewable resource problem. *Mathematical and Computer Modelling* 36, 1293-1306, 2002.

[15] Kmet, T˙How to accelerate the degradation of a nonpreferred substrate by microorganisms utilizing a preffered substrate. *Biologia Bratislava*, 45:249–258, 1990.

[16] Kmet, T; Straskraba, M. and Mauersberger P. A mechanistic model of the adaptation of phytoplankton photosynthesis. *Bull. Math. Biol.*, 55:259–275, 1993.

[17] Kmet, T; Holcik, J. The diffusive Lotka-Volterra model as applied to the population dynamics of the German carp and predator prey species in the Danube River basin. *Ecological Modelling*, 74:259–275, 1994.

[18] Kirk, D. E. Optimal Control Theory. *Dover publications, New York*, 2004.

[19] Lee, E. B.,Marcus, L. Foundation of Optimal Control Theory. *John Wiley and Sons, New York*,1967.

[20] Lotka, A. J. Elements of Physical Biology. *John Wiley and Sons, New York*,1925.

[21] Malkin, J. G. Stability Theory of Motion. *Nauka, Moscow* ,1966.

[22] Mardsen, I. J. E., McCracken, M. TheHopf Bifurcation and Its Applications. *New York, Springer*,1999.

[23] Mathews, J. H.,Fink, K. D. Numerical Methods Using MATLAB. *Prentice Hall, Saddle River*,1999.

[24] MATLAB User Guide *The MATHWORKS Inc*, 2004.

[25] Meyer, W. J. Concepts of Mathematical Modeling. *Dover publications, New York*, 2004.

[26] Pontryagin, L. S., Boltyanski, V. G., Gamkrelidze, R. V., Mischenko, E. F. The Mathematical Theory of Optimal Process. *Moscow: Nauka*, 1983, (In Russian).

[27] Solimano, F., Beretta, E. Graph Theoretical Criteria for Stability and Boundedness of Predator-Prey Systems. *Bull. Math. Biol.* 44:579–585, 1982.

[28] Volterra, V. Variazioni e fluttazioni del numero d'individiu in spesie animali conviventi. *Mem. Acad. Sci. Lincei*,2:31–43, 1926.

[29] Wang, J., Wang, K. Optimal control of harvesting for single population. *Applied Mathematics and Computation*, 156, 235-247, 2004.

[30] Wu, J. Theory and Applications of Partial Functional Diferential Equations. *Spinger, Applied Math. Sciences* , 119, 1996.