Linearized stability of structured population dynamical models

Selected results from the thesis
József Zoltán Farkas

Supervisor: Prof. Dr. Miklós Farkas

Budapest University of Technology
Department of Differential Equations
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1 Introduction

Altough the use of mathematical tools in modelling biological populations is quite old, the golden age of population dynamics was the first half of the twentieth century. The results of this period, the many classical models as the Lotka-Volterra equations and the fundamental phenomena such as exponential growth, carrying capacity, Allée-effect, competitive exclusion determined the evolution of this wide field of research.

Most of this basic models suppose some kind of homogeneity to avoid difficult mathematical problems. In fact, the main characteristic of population biology is that we only consider the dynamics at the population level not in the level of individuals. For example if we suppose that our population lives in a closed habitat with no limit of resources, and every member of the population has the same "fitness" namely fertility $\beta$ and mortality $\mu$ which are positive constants then the growth is governed by the following equation

$$\frac{d}{dt}P(t) = \beta P(t) - \mu P(t) = \gamma P(t),$$

where $\gamma = \beta - \mu$.

Thus, because of $P(t) = P(0)e^{\gamma t}$ the population survives if $\gamma \geq 0$ and goes to extinction if $\gamma < 0$, of course. Such a simple model doesn’t distinguish, for example, young and old individuals which is very unrealistic and that way we cannot expect any interesting and difficult behaviour, of course. Thus, after the first attempts the interest of mathematicians focused on much more complicated models which reproduce by greater certainty the behaviours observed by theoretical biologists.

A significal class of population models, in which we are interested, are the structured models. They describe the distribution of individuals through different classes, which classes are determined upon individual differences related to the decisive factors of the dynamics. This structure can be based on age, size, life cycle stages, biomass, etc. and it can be discrete or continuous. In the first case we have to investigate the so called matrix population models (such as the well-known Leslie-matrix model), in the second case we get partial differential equations.

Structured models have many advantages. Making a connection between the individual and the population level they can show such dynamical behaviour which other models can’t. Furthermore the many important biological factors such as environmental influences
on individuals corresponding to different classes can act completely differently.

Many different types of mathematical models have been used to formulate structured population models. Because we are interested in the continuous ones we mention here a few valuable monographies which treat those structured models mainly: [7],[20],[25],[3],[16].

The types of models which we will treat have it roots in the so called McKendrick model, introduced by the author in [23] to model mainly medical and demographical problems. This equation is a linear PDE containing age dependent vital rate functions. The much more interesting nonlinear model was introduced by Gurtin and MacCamy in 1974 (see [17]) where the vital rate functions, fertility $\beta$ and mortality $\mu$ depend not only on the age $a$ (or size $s$) but on the total population quantity $P$, or more generally on a finite number of weighted population sizes $S_i$.

Denote with $p(a,t)$ the density of individuals of age $a$ at time $t$. Then the following model can be derived from fundamental principles as a continuity equation.

$$p_t'(a,t) + p'_a(a,t) = -\mu(a,P(t))p(a,t), \quad 0 \leq a < m \leq \infty,$$

$$p(0,t) = \int_0^m \beta(a,P(t))p(a,t)da, \quad t > 0, \quad (1.1)$$

with initial condition $p(a,0) =: p_0(a)$ and total population quantity $P(t) = \int_0^m p(a,t)da$. Here $m$ is the maximal age which can be infinite or finite. These two cases can be handled differently regarding some aspects, but the case of the finite life span is more realistic in the biological sense. We treat this case in the following. Gurtin and MacCamy proved the existence and uniqueness of the solutions of system (1.1) under certain conditions. Moreover, they investigated the asymptotic behaviour of solutions through the existence and stability of stationary solutions. They deduced a characteristic equation for the stability of the stationary solution, but did not proved stability results except in some very simple examples. In a recent paper [15] the author deduced a characteristic equation in a completely different form. This equation became the origin of our investigations, because it seemed to be very useful to establish stability results under very general conditions on the vital rates.
2 Selected results from the dissertation

In this section we summarize very briefly some of our results according to the topic.

If system (1.1) admits a stationary solution (a solution which does not depend on the time) denoted by \( p_*(a) \) then it has to satisfy the equations

\[
p_*(a) = -\mu(a, P_*) p_*(a) \tag{2.1}
\]

with total population quantity \( P_* = \int_0^m p_*(a) da \), and

\[
p_*(0) = \int_0^m \beta(a, P_*) p_*(a) da. \tag{2.2}
\]

From (2.1) we get easily the solution \( p_*(a) = p_*(0) e^{-\int_0^a \mu(s,P_*)ds} \) and substituting this solution into (2.2) we get the equation

\[
1 = \int_0^m \beta(a,P_*) e^{-\int_0^a \mu(s,P_*)ds} da = \int_0^m \beta(s,P_*) \pi(a,P_*) da = R(P_*). \tag{2.3}
\]

Here \( \pi(a,P_*) \) is the probability for an individual to survive the age \( a \), and \( R(\cdot) \) is the inherent net reproduction number, the expected number of newborns. That is, we can solve equation (2.3) for \( P_* \) and then we can determine the stationary solution with the following formula

\[
p_*(a) = p_*(0) \pi(a,P_*) = \frac{P_*}{\int_0^m \pi(a,P_*) da} \pi(a,P_*) da \tag{2.4}
\]

As we mentioned earlier Gurtin and MacCamy treated an example in [17] where the mortality does not depend on the age \( a \) (harsh environment) and the fertility is an exponential decreasing function of age, in fact \( \mu(a, P) = \mu(P), \ \beta(a, P) = \beta(P)e^{-\alpha a}, \ \alpha \geq 0. \)

In [15] the author handled this example with the newly deduced characteristic equation and arrived at the same condition of stability as in [17], namely, \( \mu'(P_*) - \beta'(P_*) > 0 \) guarantees the stability of \( p_*(a) \), as well.

Beside this very special example (see e.g. [16]) as we know there were no general criteria for the stability (resp. instability) of stationary solutions of the system (1.1). In [8] we used the new characteristic equation to treat the stability of the model (1.1). First in the case of an only age dependent mortality function \( \mu(a,P(t)) = m(a) \) and \( \beta(a,P(t)) = b(a)f(P) \) where \( b(\cdot), m(\cdot), f(\cdot) \in C^1 \) we proved the following.

**Theorem 1** [8] The characteristic equation \( K(\lambda) = 1 \) for any stationary solution \( p_*(a) \) is stable if and only if \( R'(P_*) < 0. \)
The biological meaning of the conditions in this theorem seems to be very natural, it says that if at the equilibrium the growth of the population decreases the net reproduction number of individuals which, in general, decreases the number of newborns then this equilibrium solution is stable.

If the vital rate functions assume a more general form, both of them depending on $P$ the following way

$$\beta(a,P) = b(a) f(P), \quad \mu(a,P),$$

then the next theorem can be proven.

**Theorem 2** [8] The stationary solution $p_*(a)$ corresponding to the population quantity $P_*$ is asymptotically stable if $f''(P_*) < 0$ and $\mu'_P(.,P_*) > 0$.

This is not a surprising behaviour again, if for sufficiently close $P > P_*$ the fertility decreases and the mortality increases, which are supposed to involve the decrease of the total population, then the stationary solution is asymptotically stable.

Later on inspired by [3] and [20] our attention turned to the following more general size structured model.

$$p'_t(a,t) + (\gamma(a)p(a,t))'_a = -\mu(a,P(t))p(a,t), \quad 0 \leq a < m < \infty,$$

$$\gamma(0)p(0,t) = \int_0^m \beta(a,P(t))p(a,t) da, \quad t > 0,$$

with the initial condition $p(a,0) := p_0(a)$. This model describes the dynamics of a single species population with structuring variable $a$ which is now a measure of an individual’s “size” (volume, weight, biomass, etc.). The mortality and the fertility functions $\mu, \beta$ depend on the size $a$ and on the total population quantity $P(t)$ as before. The growth rate $\gamma > 0$ depends on the size $a$. This generalized model is equivalent to the Gurtin-MacCamy (or McKendrick) nonlinear age-structured model if $\gamma \equiv 1$.

This model enables us to investigate the behaviour of a much wider range of population models which occur more frequently in real world applications, e.g. tree, coral and fish populations.

In [10] we deduced a characteristic equation corresponding to the stationary solution of system (2.5). Then based on the analysis of the characteristic function we proved the following.
Theorem 3 [10] In the case of \( \mu(a,P) = m(a), \beta(a,P) \) general, \( \gamma(0) = 1 \), the stationary solution \( p_*(a) \) is asymptotically stable if \( \beta_p'(.,P_*) < 0 \), if instead \( \beta_p'(.,P_*) > 0 \) then it is unstable.

Analogously to \( R(P) \) in (2.3) an important function can be introduced in the size structured case, namely

\[
Q(P) = \int_0^M \beta(a,P) e^{-\int_0^a \frac{m(s,P) + q(s)}{\gamma(s)} ds} da,
\]

(2.6)

which determines the number of stationary solutions of the system (2.5). Because our investigations were motivated from the beginning by the importance of the behaviour of these \( R \) and \( Q \) functions so much, we were glad to being able to prove the next result for the most general vital rate functions \( \beta(a,P), \mu(a,P) \).

Theorem 4 [10] Suppose \( \gamma(0) = 1 \), then if \( Q'(P_*) > 0 \) holds then the stationary solution \( p_*(a) \) with total population quantity \( P_* \) is unstable.

From this we get a general result for the age structured model (1.1) as an easy consequence.

Corollary 5 For general \( \beta(a,P), \mu(a,P) \) if \( R'(P_*) > 0 \) holds then the stationary solution \( p_*(a) \) with total population quantity \( P_* \) is unstable.

Next we review our main results according to a two species Gurtin-MacCamy type model. As we know the following model was treated first in [15].

Let \( p(a,t) \) and \( q(a,t) \) denote the density of the two species of age \( a \) at time \( t \geq 0 \), which means that the total population quantity at time \( t \) is given by

\[
P(t) = \int_0^M p(a,t) da, \quad Q(t) = \int_0^M q(a,t) da,
\]

with maximal age \( M \) for both species. The intrinsic mortality and fertility of the species is given by \( m(a,Q), b_p(a) \) and \( n(a,P), b_q(a) \) respectively, where the mortality of species \( p \) depends on the total population quantity of the other species \( q \) and vice-versa. The fertility function depends only on the age \( a \) for both species.

With these notations the functions \( p(a,t), q(a,t) \) have to satisfy the well-known balance equations

\[
\frac{\partial p(a,t)}{\partial a} + \frac{\partial p(a,t)}{\partial t} = -m(a,Q(t))p(a,t),
\]

5
\[
\frac{\partial q(a,t)}{\partial a} + \frac{\partial q(a,t)}{\partial t} = -n(a,P(t))q(a,t).
\]

The number of newborns at time \(t\) is given by

\[
p(0,t) = \int_0^M b_p(a)p(a,t)da, \quad q(0,t) = \int_0^M b_q(a)q(a,t)da.
\]  

(2.7)

The initial age distributions are denoted by \(p_0(a) := p(a,0), q_0(a) := q(a,0)\) and they have to satisfy the compatibility conditions

\[
p_0(0) = \int_0^M b_p(a)p(a,0)da, \quad q_0(0) = \int_0^M b_q(a)q(a,0)da.
\]  

(2.8)

We introduce the inherent net reproduction number functions,

\[
R_p(Q) = \int_0^M b_p(a)\pi_p(a,Q)da, \quad R_q(P) = \int_0^M b_q(a)\pi_q(a,P)da.
\]  

(2.9)

Based on the characteristic equation which is deduced similarly to the one-dimensional problem in [15], we proved the following result.

**Theorem 6** [11] If \(\text{sign}(R_p'(Q_*)) = \text{sign}(R_q'(P_*))\) holds then the stationary solution \((p_*(a), q_*(a))\) corresponding to the pair of population quantities \((P_*, Q_*)\) is unstable.

**Remark**

Note that if \(\text{sign}(m'_Q) = \text{sign}(n'_p)\) then \(\text{sign}(R_p'(Q_*)) = \text{sign}(R_q'(P_*))\) because

\[
R_p'(Q_*) = -\int_0^M b_p(a)\pi_p(a,Q_*)\int_0^a m'_Q(s,Q_*)dsda,
\]

and

\[
R_q'(P_*) = -\int_0^M b_q(a)\pi_q(a,P_*)\int_0^a n'_p(s,P_*)dsda,
\]

respectively. This means that in the case

\[
m'_Q > 0, n'_p > 0, \text{ resp. } m'_Q < 0, n'_p < 0
\]

(2.10)

every stationary solution of the system is unstable, and conditions (2.10) mean that the model is a competitive resp. a cooperative one.

Although, as we know, Theorem 6 is a first general stability result for such type of two-dimensional systems the much more interesting problem, namely the case of \(\text{sign}(R_p'(Q_*)) \neq \text{sign}(R_q'(P_*))\) remains open.
3 Outline of the dissertation

First we give a brief introduction and describe the basic properties of the well known linear McKendrick model. Then we show a simple example of the linear model. Finally we treat nonlinear models in which we are interested. We emphasize shortly some connections between our and related works.

In the second section we deal with the two different forms of the characteristic equations of the age-structured model.

In the third section we prove stability results for the non-linear age-structured model of Gurtin and MacCamy.

In the fourth section we give our first results according to a two species age-structured model.

In the fifth section we deal with the size structured model. We are able to deduce a characteristic function which enables us to prove stability results under very general assumptions on the vital rate functions. Then we shortly revisit our stability results for the age structured model.

In section seven we formulate the non autonomous version of the Gurtin-MacCamy equation. In this part the asymptotics of the solutions is investigated. We give biologically meaningful conditions for the stability of the trivial equilibrium.

Finally, in section eight we describe some bifurcations of equilibria of the nonlinear age-structured model as an application of our stability results.

References


