

Linearized stability of structured population dynamical models

PhD thesis

József Zoltán Farkas

Supervisor: Prof.Dr. Miklós Farkas

Budapest University of Technology
Department of Differential Equations

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1 Introduction

Although 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 such 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 the 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 β and mortality μ 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 $\gamma = \beta - \mu$.

The solution of this differential equation is $P(t) = P(0)e^{\gamma t}$, that is the population survives if $\gamma \geq 0$ and goes to extinction if $\gamma < 0$.

Such a simple model does not distinguish, for example, young and old individuals what is very unrealistic and that way we cannot expect any interesting and difficult behaviour, of course. Thus, after the first attempts the interest of applied mathematicians focused on much more complicated models which may reproduce by greater certainty the behaviours observed by biologists.

A significant class of population models, in which we are interested, are the structured models. They describe the distribution of individuals through different classes determined by 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 case of a discrete structuring variable we have to investigate matrix population models, see [3] (such as the well-known Leslie-matrix model). The advantage of discrete matrix models is that they are relatively easy to construct

from life-cycle information about individuals. They are often used in the case if we can differentiate easily the individuals in the population regarding to distinct stages with respect to the structuring variable, e.g. in the case of several types of insects with different life-cycle stages.

In the case of continuous structuring variables we get partial differential equations which are more difficult to handle than matrix models but in many cases they reflect biological phenomena in a more realistic way.

Structured models have many advantages. Making a connection between the individual and the population level they can show such dynamical behaviour which other models cannot. 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 tools have been used to formulate and investigate deterministic structured population models.

Because we are interested in the continuous ones we mention here a few valuable references which treat those structured models mainly: [8],[21],[28],[3],[17].

1.1 The linear McKendrick model

The types of models which we will treat have their roots in the so called McKendrick equation, introduced in [24] to model mainly medical and demographical problems. We can find a very good overview of the linear theory of age-structured models in [21] Sect. 1-2.

The McKendrick equation is a linear PDE containing age dependent vital rate functions. We denote the density of individuals of age a at time t by $p(a,t)$ which means that the total population quantity at time t is given by

$$P(t) = \int_0^{\infty} p(a,t) da = \int_0^m p(a,t) da. \quad (1.1)$$

Here m denotes the maximal age. Usually, in this type of models migration is excluded, that is the density of individuals of age a at time $t + dt$ is given by those of age $a - dt$

who lived at time t minus those who died. If we denote the mortality at age a with $\mu(a)$ we get the following equation

$$p(a, t + dt) = p(a - dt, t) - \mu(a - dt)p(a - dt, t)dt. \quad (1.2)$$

We can rewrite equation (1.2) as

$$p(a, t + dt) - p(a, t) + p(a, t) - p(a - dt, t) = -\mu(a - dt)p(a - dt, t)dt. \quad (1.3)$$

Dividing by dt and taking into account that $da = dt$ we obtain

$$\frac{p(a, t + dt) - p(a, t)}{dt} + \frac{p(a, t) - p(a - da, t)}{da} = -\mu(a - dt)p(a - dt, t), \quad (1.4)$$

if we take the limit $da, dt \rightarrow 0$ in (1.4) we arrive at

$$p'_t(a, t) + p'_a(a, t) = -\mu(a)p(a, t). \quad (1.5)$$

If we denote the fertility of individuals of age a with $\beta(a)$ then the number of newborns is given by

$$p(0, t) = \int_0^m \beta(a)p(a, t)da. \quad (1.6)$$

Further we have to prescribe an initial age distribution, $p(a, 0) =: p_0(a)$, which has to satisfy the compatibility condition

$$p_0(0) = p(0, 0) = \int_0^m \beta(a)p(a, 0)da = \int_0^m \beta(a)p_0(a)da.$$

From the vital rate functions μ, β we may derive biologically meaningful quantities, namely

$$\pi(a) = e^{-\int_0^a \mu(s)ds}$$

measures the probability for an individual to survive the age a .

Furthermore we introduce

$$R = \int_0^m \beta(a)\pi(a)da, \quad (1.7)$$

which is the expected number of newborns to be produced by an individual in his reproductive lifetime and it is a crucial quantity as we will see.

With the method of the characteristics this linear model (1.5)-(1.6) can be reduced to a Lotka integral equation which corresponds to the case $t > a$. For the case $a \geq t$ we have an explicit solution, as follows.

The ODE system of characteristics is

$$\frac{dt}{d\tau} = 1, \quad \frac{da}{d\tau} = 1, \quad \frac{dp}{d\tau} = -\mu(a)p(a,t). \quad (1.8)$$

For $t = 0$, $a = a_0$ we have $p(a_0, 0) = p_0(a_0)$ so we choose the initial conditions as follows $(t(0), a(0), p(0)) = (0, a_0, p_0(a_0))$. Thus the solution is

$$t = \tau, \quad a = \tau + a_0 = t + a_0, \quad p = p_0(a_0)e^{-\int_0^t \mu(s+a_0)ds}. \quad (1.9)$$

Finally substituting from the second equation $a_0 = a - t$ into the third one we obtain the solution for $a \geq t$

$$p(a,t) = p_0(a-t)e^{-\int_0^t \mu(s+a-t)ds}. \quad (1.10)$$

To get a more meaningful formula rewrite (1.10) as

$$\begin{aligned} p_0(a-t)e^{-\int_0^t \mu(s+a-t)ds} &= p_0(a-t)e^{-\int_{a-t}^a \mu(s)ds} = p_0(a-t) \frac{e^{-\int_0^a \mu(s)ds}}{e^{-\int_0^{a-t} \mu(s)ds}} = \\ &= p_0(a-t) \frac{\pi(a)}{\pi(a-t)}. \end{aligned} \quad (1.11)$$

We can see from (1.11) that the boundary condition (1.6) doesn't play any role in this case, of course.

For the case $t > a$ we have to choose the initial values $(t(0), a(0), p(a)) = (t_0, 0, p(t_0, a))$. This way we obtain the equations

$$t = \tau + t_0, \quad a = \tau, \quad p = p(0, t_0)e^{-\int_0^\tau \mu(s)ds}. \quad (1.12)$$

From (1.12) we get the solution

$$p(a, t) = p(0, t - a)e^{-\int_0^a \mu(s) ds} = p(0, t - a)\pi(a) = \pi(a) \int_0^m \beta(s)p(s, t - a) ds. \quad (1.13)$$

As we can see the solution cannot be written more explicitly.

If we wish to get a rough picture of the phase space we can search for age distributions which are constant over time. Motivated from the classical theory of ODE's first we look for solutions of the form $p(a, t) = p_*(a)e^{\lambda t}$. Substituting this into (1.5) we get the ODE

$$p'_*(a) = -(\lambda + \mu(a))p_*(a), \quad (1.14)$$

and from this we get easily the solution

$$p_*(a) = p_*(0)e^{-\int_0^a (\lambda + \mu(s)) ds} = p_*(0)e^{-\lambda a}\pi(a), \quad (1.15)$$

and for the density of newborns we have

$$p_*(0) = \int_0^m \beta(a)p_*(a) da. \quad (1.16)$$

Substituting the solution (1.15) into (1.16) and dividing by $p_*(0)$ we get

$$1 = \int_0^m e^{-\lambda a}\beta(a)\pi(a) da, \quad (1.17)$$

which is the characteristic equation of the linear model (1.5)-(1.6). Comparing equation (1.17) with (1.7) we conclude that the population may survive at a constant level if and only if $R = 1$, ($Re(\lambda) = 0$).

1.2 A linear model with constant death rate

Consider the following example containing vital rate functions with infinite life span [15].

In the case of vital rate functions with infinite span the integration, for example, in (1.17) goes from 0 to infinity, that is (1.17) becomes a Laplace transform.

If we choose

$$\hat{\beta}(a) := a^6(40 - a)^2 e^{-a}, \quad \mu(a) := 0.2,$$

we get $\pi(a) = e^{-0.2a}$ for the survival probability.

The constant mortality rate seems to be very unrealistic on the face of it. But think about a population without any competition between the individuals for food and the individuals are caught by any "predator" roughly with the same probability, e.g. a fast growing fish population at a fishery.

In the case of the vital rates above the net reproduction rate becomes

$$\hat{R} = \int_0^\infty \hat{\beta}(a)\pi(a)da \sim 235544.910265203475.$$

In order to have 1 as the net reproduction rate we renorm the function $\hat{\beta}$ as follows $\beta := \frac{\hat{\beta}}{\hat{R}}$. With this new fertility function β we get a continuum number of stationary solutions of the linear model.

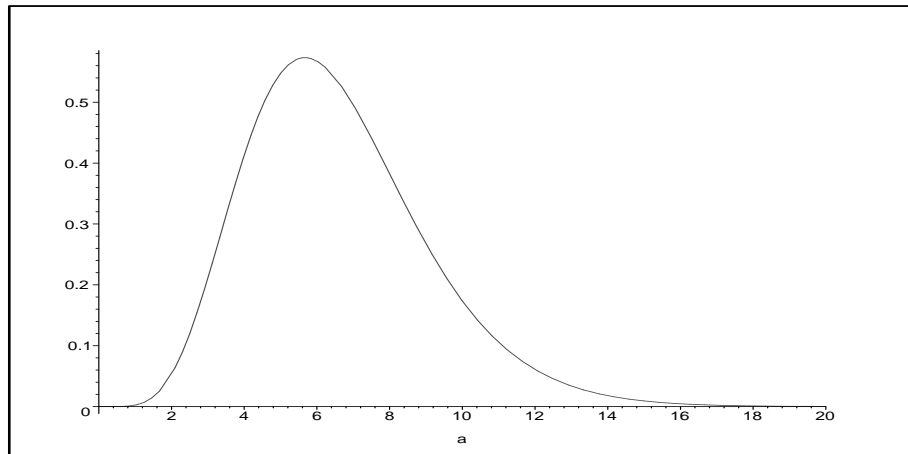


Fig.1. $\beta(a) := \frac{a^6(40-a)^2 e^{-a}}{235544.91026520347508}$

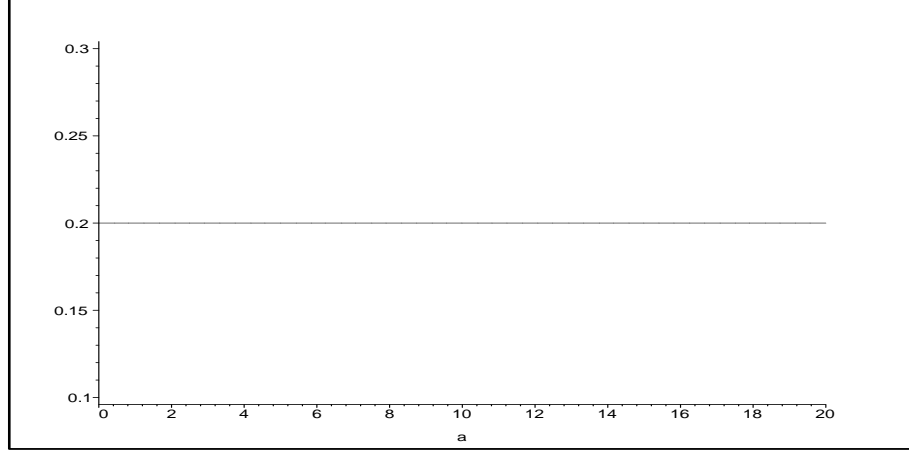


Fig.2. $\mu(a) := 0.2$

The characteristic function (1.17) assumes the form

$$\begin{aligned}
 K(x) - 1 &\sim \int_0^\infty 0.42454748815165876777 \cdot 10^{-5} e^{-xa} a^6 (40 - a)^2 e^{-a} e^{-0.2a} da - 1 \sim \\
 &\sim \frac{4.8907870635071090047}{(x + 1.2)^7} - \frac{1.7117754722274881516}{(x + 1.2)^8} + \frac{0.17117754722274881516}{(x + 1.2)^9} - 1.
 \end{aligned} \tag{1.18}$$

The roots of (1.18) are approximately

$$\begin{aligned}
 x_{1,2} &\sim -2.3769875708071973591 \pm 0.54573322061635669689i, \\
 x_{3,4} &\sim -1.5278878025666194594 \pm 1.2267171157973694549i, \\
 x_{5,6} &\sim -1.0250000479503587998 \pm 0.066144214038681117910i, \\
 x_{7,8} &\sim -0.47012457867582438167 \pm 0.98443820499399594419i, \\
 \mathbf{x_0} &\sim \mathbf{0.27901552980952792594 \cdot 10^{-21}}.
 \end{aligned}$$

(Calculations were done by Maple 7.)

In the case of a linear model if there exists a non-trivial stationary solution $p_*(a)$ then we get a whole class I of stationary solutions, namely for every positive constant c we have a stationary solution as follows

$$\widehat{p}_*(a) := \pi(a), \quad I = \{c \cdot \widehat{p}_*(a) \mid c \in \mathbf{R}^+\}.$$

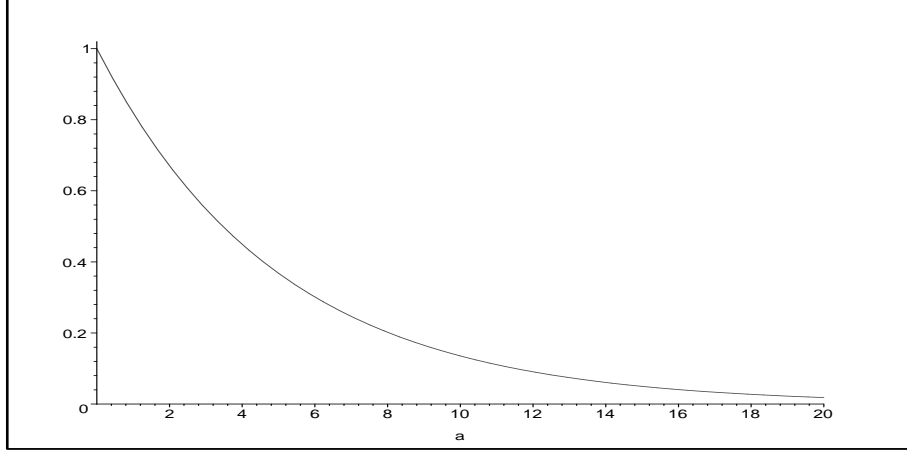


Fig.3. $\hat{p}_*(a) = \pi(a) = e^{-0.2a}$

1.3 Nonlinear models

The much more interesting nonlinear version of the McKendrick model was introduced by Gurtin and MacCamy in 1974 (see [18]) where the vital rate functions β -fertility and μ -mortality depend not only on the age a but on the total population quantity P , or more generally on a finite number of such weighted population sizes S_i . This new model allowed to investigate a wide spectra of nonlinear biological phenomena.

Denote the density of individuals of age a at time t with $p(a, t)$. Then the following model can be derived similarly to the linear model (1.5)-(1.6).

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

$$p(0, t) = \int_0^m \beta(a, P(t))p(a, t)da, \quad t > 0, \quad (1.19)$$

with initial condition $p(a, 0) =: p_0(a)$ and total population quantity $P(t) = \int_0^m p(a, t)da$.

The dynamics of the system depends on the vital rates $\beta(a, P), \mu(a, P)$ which are supposed to satisfy the following assumptions, in general.

$$\forall P \in [0, \infty), \forall a \in [0, m] \quad 0 \leq \beta(a, P) \leq k < \infty, \quad \mu(a, P) \geq 0, \quad (1.20)$$

$$\forall P \in [0, \infty), \int_0^m \mu(a, P) da = \infty, \quad \forall P \in [0, \infty) \forall a \in [0, m) \mu(a, P) < \infty. \quad (1.21)$$

m is the maximal age which can be infinite or finite. These two cases can be handled in different ways but the case of the finite life span is more realistic in the biological sense. We will treat mainly this case in the following.

Gurtin and MacCamy proved the existence and uniqueness of the solutions of the system (1.19) 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 (see the next section), but they did not use it to prove stability results besides the following very special example when the model can be reduced to a pair of ordinary differential equations as follows [19].

Consider the following vital rate functions with infinite life span

$$\mu(a, P) = \mu(P), \quad \beta(a, P) = \beta(P)e^{-\alpha a},$$

with $\mu(P), \beta(P) > 0, \alpha \geq 0$.

First we need the following lemma.

Lemma[19] Let $p(a, t)$ be a solution of (1.19), and let g be a (sufficiently smooth) function of age with

$$g(a)p(a, t) \rightarrow 0, \quad \text{as } a \rightarrow \infty.$$

Let

$$G(t) = \int_0^\infty g(a)p(a, t) da, \quad H(t) = \int_0^\infty g'(a)p(a, t) da.$$

Then

$$\dot{G} + \mu(P(t))G - g(0)B(P, t) = H(t). \quad (1.22)$$

Here $B(P, t)$ denotes the birth rate, $B(P, t) = \int_0^\infty \beta(a, P(t))p(a, t) da$.

Proof.

Multiply the first equation in (1.19) by g and integrate from $a = 0$ to $a = \infty$, then we arrive at

$$\dot{G}(t) + \int_0^\infty g(a)p'_a(a,t)da + \mu(P(t))G(t) = 0.$$

Finally integrating the second term by parts and making use of the condition $g(a)p(a,t) \rightarrow 0$ we arrive at (1.22). \square

From (1.22) with the choice of $g \equiv 1$ we get

$$\dot{P} + \mu(P)P - B = 0,$$

and with $g(a) = e^{-\alpha a}$ we have

$$\dot{G} + \mu(P)G - B + \alpha G = 0,$$

where now

$$G(t) = \int_0^\infty e^{-\alpha a} p(a,t) da = \frac{B(t)}{\beta(P(t))}.$$

Thus we get the pair of differential equations:

$$\dot{P} = -\mu(P)P + \beta(P)G, \quad \dot{G} = (-\mu(P) + \beta(P) - \alpha)G. \quad (1.23)$$

The relevant initial conditions are

$$P(0) = \int_0^\infty p_0(a) da, \quad G(0) = \int_0^\infty e^{-\alpha a} p_0(a) da.$$

The analysis of the system (1.23) leads to the necessary and sufficient condition $\mu'(P_*) > \beta'(P_*)$ for the linearized stability of the stationary solution $p_*(a)$ with total population quantity P_* (see [18],[19],[16]).

As we mentioned we can get a more general model if we allow for the vital rate functions to depend on a finite number of weighted size populations, namely if we replace $\beta(a,P), \mu(a,P)$ with $\beta(a, S_1, \dots, S_n), \mu(a, S_1, \dots, S_n)$, where $S_i = \int_0^m \gamma_i(a)p(a,t) da$,

$i = 1 \dots n$, where the weight functions γ_i are positive. [21] mainly discusses these type of models. In the more general class of models we can allow for the vital rates to depend on any functional of the solution $p(a, t)$ ([25],[8],[6]).

In [26],[27] J. Prüss investigated an n species Gurtin-MacCamy type model, where the vital rates β and μ depend on the age and on the standing population $\mathbf{p}(a, t) = (p_1(a, t), \dots, p_n(a, t))$. He proved the existence of nonzero equilibrium solutions under very general assumptions. Analogously to the special example of Gurtin and MacCamy he showed that for some very special kind of vital rates the n -dimensional PDE system can asymptotically be described by means of an ODE system.

Another commonly used model is the size structured model, which we will treat in section 4, where the variable a denotes the size of an individual. In this case a third vital rate function occurs, namely $\gamma \geq 0$ which is the growth rate and depends on a or in a more general setting it depends on the total population quantity P too. See [25],[8],[6],[7].

2 Characteristic equations for the age structured model

In this thesis we treat mainly the linearized stability of structured population models according to the following definition.

Definition The stationary solution $p_*(a)$ is said to be stable if for every $\varepsilon > 0$ there exists $\delta > 0$ such that, if $p(0, \cdot)$ satisfies $|p(0, \cdot) - p_*(\cdot)|_{L^1} \leq \delta$ then the solution $p(t, a)$ satisfies $|p(t, \cdot) - p_*(\cdot)|_{L^1} \leq \varepsilon \quad \forall t \geq 0$. It is said to be asymptotically stable if it is stable and δ can be chosen such that $\lim_{t \rightarrow \infty} |p(t, \cdot) - p_*(\cdot)|_{L^1} = 0$.

The classical method of linearization can be described shortly by the following way. First we introduce the variation $u(a, t) = p(a, t) - p_*(a)$ and linearize the differential equation satisfied by $u(a, t)$. Then we search for solutions in the form $U(a)e^{\lambda t}$. If such a solution exists we can substitute it into the linearized differential equation satisfied by $u(a, t)$. From this we get an equation for λ which is the characteristic equation. If all the (complex) roots of the characteristic function are in the left half-plane then $u(a, t) = U(a)e^{\lambda t} \rightarrow 0$ as t tends to infinity exponentially what means that the stationary solution is stable. If the characteristic function has any roots in the right half-plane then the stationary solution is unstable. In the case of pure imaginary roots further analysis is needed to analyze the weakly nonlinear dynamics of the system.

We can find an approach for this in [2] where a parametrized class of systems for which $Re\{\lambda\} = 0$ holds is studied in the special case when the vital rates assume the form $\mu(a, P) = \mu(P)$, $\beta(a, P) = \beta(P)e^{-\alpha a}$ as in [18].

If the system (1.19) admits a stationary solution $p_*(a)$ (a solution which does not depend on time) it has to satisfy the following equations

$$p'_*(a) = -\mu(a, P_*)p_*(a), \quad p_*(0) = \int_0^m \beta(a, P_*)p_*(a)da. \quad (2.1)$$

From (2.1) we get easily the solution

$$p_*(a) = p_*(0)e^{-\int_0^a \mu(s, P_*)ds}. \quad (2.2)$$

Substituting (2.2) into the boundary condition of (2.1) we get

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

(Here π is the survival probability function and R is the net reproduction function as in the linear case.) Thus (2.3) is a necessary condition for the existence of a stationary solution with population quantity P_* . We can solve equation (2.3) for the single variable P and from the following equation we have the initial value $p_*(0)$

$$P_* = \int_0^m p_*(a) = p_*(0) \int_0^m \pi(a, P_*) da. \quad (2.4)$$

Then we have the stationary solution as $p_*(a) = p_*(0)\pi(a, P_*)$. Thus, we proved the following

Theorem 2.1 (M.E.Gurtin-R.C.MacCamy[18]) Any stationary solution $p_*(a)$ of the system is determined uniquely by the root P_* of the following equation

$$R(P) = 1.$$

Now recall the characteristic equation from [18]

$$1 = \int_0^m r(a) e^{-\gamma a} da + g_\gamma \left(\frac{\kappa}{B_0} - \int_0^m r(a) f_\gamma(a) da \right), \quad (2.5)$$

where $r(a) = \beta_0(a)\pi_0(a)$,

$$\kappa = B_0 \int_0^m \beta'_0(a)\pi_0(a) da, \quad f_\gamma(a) = \int_0^a e^{-\gamma(a-\alpha)} \lambda'_0(\alpha) d\alpha \quad (2.6)$$

and

$$g_\gamma = \frac{B_0 \int_0^m e^{-\gamma a} \pi_0(a) da}{1 + B_0 \int_0^m \pi_0(a) f_\gamma(a) da}, \quad B_0 = \int_0^m \beta_0(a) p_0(a) da. \quad (2.7)$$

With our notations

$$\lambda_0(\alpha) = \mu(\alpha, P_*), \quad \pi_0(a) = \pi(a, P_*), \quad \beta_0(a) = \beta(a, P_*), \quad \gamma = \lambda.$$

The equations (2.5)-(2.7) seem to be extremely complicated and the analysis of the characteristic equation was left as a question in [18], and as we know it was not used to prove stability results.

Some results about the characteristic equation was proved in [21] Ch. 4.4.

In [16] Miklós Farkas deduced a characteristic equation in a completely different form.

$$K(\lambda) = A_{11}(\lambda)A_{22}(\lambda) - A_{12}(\lambda)A_{21}(\lambda) + A_{12}(\lambda) + A_{21}(\lambda) = 1, \quad (2.8)$$

where

$$A_{11}(\lambda) = \int_0^m e^{-\lambda a} e^{-\int_0^a \mu(s, P_*) ds} da,$$

$$A_{12}(\lambda) = -p_*(0) \int_0^m e^{-\lambda a} e^{-\int_0^a \mu(s, P_*) ds} \int_0^a \mu'_P(s, P_*) e^{\lambda s} ds da,$$

$$A_{21}(\lambda) = \int_0^m e^{-\lambda a} \beta(a, P_*) e^{-\int_0^a \mu(s, P_*) ds} da,$$

$$A_{22}(\lambda) = p_*(0) \int_0^m \beta'_P(a, P_*) e^{-\int_0^a \mu(s, P_*) ds} da$$

$$-p_*(0) \int_0^m \left(e^{-\lambda a} \beta(a, P_*) e^{-\int_0^a \mu(s, P_*) ds} \int_0^a \mu'_P(s, P_*) ds \right) da$$

and $P_* = \int_0^m p_*(a) da$ is the total population quantity of the stationary solution.

At the first look we also cannot believe that this characteristic equation can be handled more easily.

Remark that the coefficients $A_{ij}(\lambda)$ become Laplace transforms in the case of vital rates with infinite life span.

Let us now check the equivalence of the two mainly different forms of the characteristic equation [15].

Substituting the expressions (2.6)-(2.7) into the equation (2.5), changing the notations and making use of the formula $p_*(0) = \frac{P_*}{\int_0^m \pi(a, P_*) da}$ we arrive, after straightforward calculations, at the following equation:

$$1 = \int_0^m e^{-\lambda a} \beta(a, P_*) \pi(a, P_*) da +$$

$$\begin{aligned}
 & + \left(\frac{\frac{P_*}{\int_0^m \pi(a, P_*) da} \int_0^m e^{-\lambda a} \pi(a, P_*) da}{1 + \frac{P_*}{\int_0^m \pi(a, P_*) da} \int_0^m \pi(a, P_*) \int_0^a e^{-\lambda(a-s)} \mu'_P(s, P_*) ds da} \right) \int_0^m \beta'_P(a, P_*) \pi(a, P_*) da - \\
 & - \left(\frac{\frac{P_*}{\int_0^m \pi(a, P_*) da} \int_0^m e^{-\lambda a} \pi(a, P_*) da}{1 + \frac{P_*}{\int_0^m \pi(a, P_*) da} \int_0^m \pi(a, P_*) \int_0^a e^{-\lambda(a-s)} \mu'_P(s, P_*) ds da} \right) \\
 & \quad \cdot \int_0^m \beta(a, P_*) \int_0^a e^{-\lambda(a-s)} \mu'_P(s, P_*) ds da. \tag{2.9}
 \end{aligned}$$

Now introducing the new coefficients $A_{ij}(\lambda)$ we get

$$\begin{aligned}
 1 & = \left(\frac{p_*(0)A_{11}(\lambda)}{1 + p_*(0)\frac{A_{12}(\lambda)}{-p_*(0)}} \right) \int_0^m \beta'_P(a, P_*) \pi(a, P_*) da - \\
 & - \left(\frac{p_*(0)A_{11}(\lambda)}{1 + p_*(0)\frac{A_{12}(\lambda)}{-p_*(0)}} \right) \int_0^m e^{-\lambda a} \beta(a, P_*) \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da. \tag{2.10}
 \end{aligned}$$

From (2.10) we have

$$1 = A_{21}(\lambda) + \left(\frac{p_*(0)A_{11}(\lambda)}{1 - A_{12}(\lambda)} \right) \frac{A_{22}(\lambda)}{p_*(0)}, \tag{2.11}$$

and a simple transformation leads to (2.8).

From [18] recall the stability criterion of the stationary solution $p_*(a)$ based on the characteristic equation (2.5).

Theorem 2.2 [18],[16] The stationary solution of the problem (1.19) is asymptotically stable if all the roots of equation (2.5) have negative real part. If (1.19) has a root with positive real part then the stationary solution is unstable.

3 Stability of the age structured model

In this section we investigate the asymptotic stability of stationary solutions $p_*(a)$ of the Gurtin-MacCamy age structured model (1.19). Our results are based on the localization of the roots of equation (2.8) and on Th.2.2. First we treat the case of an age dependent mortality function and we suppose a factorization property for the fertility function β , motivated from the special example of Gurtin and MacCamy. Then we consider a general mortality function $\mu(a, P)$ and suppose the factorization property for the fertility β . In this section the maximal age is denoted by M .

3.1 μ does not depend on P

Now suppose that $\mu(a, P) = m(a)$ and $\beta(a, P) = b(a)f(P)$ where $b(\cdot), m(\cdot), f(\cdot) \in C^1$.

Theorem 3.1 [9] The characteristic function $K(\lambda) - 1$ for any stationary solution $p_*(a)$ is stable if and only if $R'(P_*) < 0$.

Proof. Under the assumptions for the vital rates above the characteristic equation (2.8) reduces to the following

$$\int_0^M e^{-\lambda a} \pi(a) \beta(a, P_*) da + \int_0^M e^{-\lambda a} \pi(a) da \int_0^M \beta'_P(a, P_*) p_*(0) \pi(a) da = 1, \quad (3.1)$$

and obviously

$$\int_0^M \beta'_P(a, P_*) p_*(0) \pi(a) da = \int_0^M f'(P_*) p_*(0) b(a) \pi(a) da \quad (3.2)$$

holds. Furthermore we have for any stationary solution

$$\int_0^M \beta(a, P_*) \pi(a) da = \int_0^M f(P_*) b(a) \pi(a) da = 1, \quad (3.3)$$

and with

$$p_*(0) = \frac{P_*}{\int_0^M \pi(a) da} \quad (3.4)$$

we can rewrite equation (3.1) as follows

$$K(\lambda) = 1 = \int_0^M e^{-\lambda a} \pi(a) b(a) f(P_*) da + \int_0^M e^{-\lambda a} \pi(a) da \left(\frac{P_*}{\int_0^M \pi(a) da} \frac{f'(P_*)}{f(P_*)} \right). \quad (3.5)$$

Now suppose that $f'(P_*) > 0$ holds. Then it is easy to see that for $K(\lambda)$ in (3.5) we have

$$\lim_{\lambda \rightarrow -\infty} K(\lambda) = +\infty \quad \lim_{\lambda \rightarrow +\infty} K(\lambda) = 0$$

and $K(\lambda)$ is a strictly monotone decreasing function of λ , so there exists exactly one real λ for which $K(\lambda) = 1$ holds. Now we are going to show that $\lambda > 0$ holds. Contrary, suppose that $\lambda \leq 0$. Then for every $a \in [0, M]$ we have $e^{-\lambda a} \geq 1$.

That is we have

$$\int_0^M e^{-\lambda a} \pi(a) b(a) f(P_*) da \geq \int_0^M \pi(a) b(a) f(P_*) da = 1,$$

and

$$\int_0^M e^{-\lambda a} P_* \frac{\pi(a)}{\int_0^M \pi(a) da} \frac{f'(P_*)}{f(P_*)} da > 0.$$

This shows that $K(\lambda) > 1$ for every $\lambda \leq 0$.

On the other hand if $f'(P_*) < 0$ then suppose that there exists a solution $\lambda = x + iy$ with $x \geq 0$. Then the characteristic equation assumes the form

$$1 = \operatorname{Re}(K(\lambda)) = \int_0^M e^{-xa} \cos(ya) \pi(a) b(a) f(P_*) da + \int_0^M e^{-xa} \cos(ya) \pi(a) da \left(\frac{P_*}{\int_0^M \pi(a) da} \frac{f'(P_*)}{f(P_*)} \right),$$

$$\operatorname{Im}(K(\lambda)) = 0.$$

If $x \geq 0$ then $e^{-xa} \leq 1$ and $|\cos(ya)| \leq 1$, so that

$$\operatorname{Re}(K(\lambda)) \leq \int_0^M \pi(a)b(a)f(P_*)da + P_* \frac{f'(P_*)}{f(P_*)} = 1 + P_* \frac{f'(P_*)}{f(P_*)} < 1,$$

a contradiction.

Finally observe that $R'(P_*) < 0 \iff f'(P_*) < 0$ because in this special case of vital rates $R(P) = \int_0^M b(a)f(P)\pi(a)da$ holds. \square

This result is in accordance with the example of Gurtin and MacCamy (see [16],[18]) which we treated at the end of the first section, because now $m'(P) \equiv 0$ and $-\beta'(P_*) > 0 \iff f'(P_*) < 0$.

3.2 μ does depend on P

Now consider the following more general vital rates, both of them depending on P

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

The characteristic equation is

$$K(\lambda) = A_{11}(\lambda)A_{22}(\lambda) - A_{12}(\lambda)A_{21}(\lambda) + A_{12}(\lambda) + A_{21}(\lambda) = 1,$$

where now

$$A_{11}(\lambda) = \int_0^M e^{-\lambda a} \pi(a, P_*) da,$$

$$A_{12}(\lambda) = -p_*(0) \int_0^M e^{-\lambda a} \pi(a, P_*) \int_0^a \mu'_P(s, P_*) e^{\lambda s} ds da,$$

$$A_{21}(\lambda) = \int_0^M e^{-\lambda a} b(a) f(P_*) \pi(a, P_*) da,$$

$$A_{22}(\lambda) = p_*(0) \int_0^M b(a) f'(P_*) \pi(a, P_*) da$$

$$-p_*(0) \int_0^M e^{-\lambda a} b(a) f(P_*) \left(\int_0^a \mu'_P(s, P_*) e^{\lambda s} ds \right) \pi(a, P_*) da.$$

Theorem 3.2 [9] The stationary solution $p_*(a)$ corresponding to the population quantity P_* is asymptotically stable if $f'(P_*) < 0$ and $\mu'_P(\cdot, P_*) > 0$.

Remark. We are to prove that under the conditions above the characteristic equation cannot have roots with positive or zero real part, and we refer to [21] Th.I.5.1, where it is proven that if there exists a root with positive real part then there exists a real positive root, too. This means that there exists a dominant real root of the characteristic equation (2.8). We only note here that these properties are often valid for population dynamical models, and they are based on the theory of positive operators and positive semigroups but these theories go beyond our goals in this thesis, for details see [25].

Proof. We are going to prove that under the conditions for the vital rates for any real $\lambda \geq 0$ we have $K(\lambda) < 1$.

Observe that $A_{21}(\lambda) \leq 1 \iff \lambda \geq 0$, so it is enough to prove

$$A_{11}(\lambda)A_{22}(\lambda) - A_{12}(\lambda)A_{21}(\lambda) + A_{12}(\lambda) < 0$$

or

$$-A_{11}(\lambda)A_{22}(\lambda) - A_{12}(\lambda) > -A_{12}(\lambda)A_{21}(\lambda). \quad (3.6)$$

Simplifying the first term of $A_{22}(\lambda)$ we get:

$$A_{22}(\lambda) = p_*(0) \left(\frac{f'(P_*)}{f(P_*)} - \int_0^M e^{-\lambda a} b(a) f(P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) \pi(a, P_*) da \right).$$

Now we are going to substitute the $A_{ij}(\lambda)$ into the inequality (3.6):

$$\begin{aligned} & -\frac{f'(P_*)}{f(P_*)} p_*(0) \int_0^M e^{-\lambda a} \pi(a, P_*) da + \\ & + p_*(0) \int_0^M e^{-\lambda a} \pi(a, P_*) da \left(\int_0^M e^{-\lambda a} b(a) f(P_*) \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da \right) + \end{aligned}$$

$$\begin{aligned}
& + p_*(0) \int_0^M e^{-\lambda a} \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da > \\
> p_*(0) \left(\int_0^M e^{-\lambda a} \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da \right) \left(\int_0^M e^{-\lambda a} \beta(a, P_*) \pi(a, P_*) da \right). \tag{3.7}
\end{aligned}$$

Omitting the first term of the left-hand side and dividing by $p_*(0)$ we get

$$\begin{aligned}
& \left(\int_0^M e^{-\lambda a} \pi(a, P_*) da \right) \left(\int_0^M e^{-\lambda a} \beta(a, P_*) \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da \right) + \\
& + \int_0^M e^{-\lambda a} \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da > \\
> \left(\int_0^M e^{-\lambda a} \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da \right) \left(\int_0^M e^{-\lambda a} \beta(a, P_*) \pi(a, P_*) da \right) \tag{3.8}
\end{aligned}$$

which implies (3.7).

Subtracting the second term of the left-hand side we get

$$\begin{aligned}
& \left(\int_0^M e^{-\lambda a} \pi(a, P_*) da \right) \left(\int_0^M e^{-\lambda a} \beta(a, P_*) \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da \right) > \\
> \left(\int_0^M e^{-\lambda a} \pi(a, P_*) \left(\int_0^a e^{\lambda s} \mu'_P(s, P_*) ds \right) da \right) \left(\int_0^M e^{-\lambda a} \beta(a, P_*) \pi(a, P_*) da - 1 \right). \tag{3.9}
\end{aligned}$$

Finally observe that for $\lambda \geq 0$ we have $e^{-\lambda a} \leq 1$ so that

$$\int_0^M e^{-\lambda a} \beta(a, P_*) \pi(a, P_*) da - 1 \leq 0.$$

The first factor of the right-hand side of (3.9) is positive because $\mu'(\cdot, P_*) > 0$, thus the right-hand side is negativ while the left-hand side is positive. This proves (3.8) wich implies (3.7) which completes the proof. \square

The conditions on the vital rates in the theorem are very natural. They say that if at the equilibrium population the growth of the population decreases the fertility of individuals and increases the mortality in each class then the stationary solution is asymptotically stable.

Remark. We can show easily that under the assumptions on the vital rates in the theorem $R'(P_*) < 0$ holds.

From

$$R(P(t)) = \int_0^M \beta(a, P(t)) \pi(a, P(t)) da$$

we have

$$R'(P_*) = \int_0^M \beta'_P(a, P_*) \pi(a, P_*) + \beta(a, P_*) \pi'_P(a, P_*) da,$$

and with

$$\pi'_P(a, P_*) = - \int_0^a \mu'_P(s, P_*) ds e^{-\int_0^a \mu(s, P_*) ds} = -\pi(a, P_*) \int_0^a \mu'_P(s, P_*) ds$$

we obtain

$$R'(P_*) = \int_0^M \beta'_P(a, P_*) \pi(a, P_*) da - \int_0^M \beta(a, P_*) \pi(a, P_*) \int_0^a \mu'_P(s, P_*) ds da.$$

If $\beta'_P(a, P_*) = b(a) f'(P_*) < 0$ and $\mu'_P(a, P_*) > 0$ for each $a \in [0, M]$ holds then $R'(P_*) < 0$.

4 The two species model

Let us consider the following two dimensional model introduced by Miklós Farkas in [16]. 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. This yields no restrictions in a biological sense setting M arbitrary large but lets us avoid some mathematical problems. 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.

For the vital rate functions we make the following general assumptions, similarly to the case of a one species model:

$$\forall a \in [0, M] \quad 0 \leq b_q(a), b_p(a) \leq K < \infty, \forall a \in [0, M], x \in [0, \infty) \quad m(a, x), n(a, x) \geq 0$$

$$\forall x \in [0, \infty) : \int_0^M m(a, x) da = \int_0^M n(a, x) da = \infty, \quad b_q(\cdot), b_p(\cdot), m(\cdot, \cdot), n(\cdot, \cdot) \in C^1.$$

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

$$\begin{aligned} p'_a(a, t) + p'_t(a, t) &= -m(a, Q(t))p(a, t), \\ q'_a(a, t) + q'_t(a, t) &= -n(a, P(t))q(a, t). \end{aligned} \tag{4.1}$$

The number of newborns at time t is given by

$$p(0, t) = \int_0^M b_p(a)p(a, t) da, \quad q(0, t) = \int_0^M b_q(a)q(a, t) da. \tag{4.2}$$

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

$$p_0(0) = \int_0^M b_p(a)p(a, 0)da, \quad q_0(0) = \int_0^M b_q(a)q(a, 0)da. \quad (4.3)$$

Every positive equilibrium of the system (4.1)-(4.3) is a stationary age distribution denoted by $(p_*(a), q_*(a))$.

The asymptotic stability of stationary solutions of the two dimensional model above is given by the following definition analogously as at the beginning of section 2.

Definition The stationary solution $(p_*(a), q_*(a))$ is said to be asymptotically stable if for all $\varepsilon > 0$ there exists a $\delta > 0$ such that whenever $|p(\cdot, 0) - p_*(\cdot)|_{L^1} < \delta$, $|q(\cdot, 0) - q_*(\cdot)|_{L^1} < \delta$ then $|p(\cdot, t) - p_*(\cdot)|_{L^1} < \varepsilon$ and $|q(\cdot, t) - q_*(\cdot)|_{L^1} < \varepsilon$ for all $t \geq 0$ holds. Moreover δ can be chosen such that $\lim_{t \rightarrow \infty} |p(\cdot, t) - p_*(\cdot)|_{L^1} = \lim_{t \rightarrow \infty} |q(\cdot, t) - q_*(\cdot)|_{L^1} = 0$.

4.1 Stability by the characteristic equation

In [16] Miklós Farkas introduced this two species system and deduced a characteristic equation corresponding to the stationary solution $(p_*(a), q_*(a))$ analogously to the one dimensional case. In this case, after the linearization procedure, a four dimensional homogeneous system is obtained, with coefficients $A_{ij}(\lambda)$, which are Laplace transforms in the case of infinite maximal age.

Recall now the characteristic equation from [16]

$$(A_{11}(\lambda)A_{34}(\lambda) + A_{14}(\lambda)A_{31}(\lambda))(A_{22}(\lambda)A_{43}(\lambda) + A_{23}(\lambda)A_{42}(\lambda)) = A_{31}(\lambda)A_{43}(\lambda), \quad (4.4)$$

with the following notations

$$\begin{aligned} A_{11}(\lambda) &= \int_0^M e^{-\lambda a} \pi_p(a, Q_*) da, \\ A_{23}(\lambda) &= \int_0^M e^{-\lambda a} \pi_q(a, P_*) da, \\ A_{31}(\lambda) &= 1 - \int_0^M e^{-\lambda a} b_p(a) \pi_p(a, Q_*) da, \\ A_{43}(\lambda) &= 1 - \int_0^M e^{-\lambda a} b_q(a) \pi_q(a, P_*) da, \end{aligned}$$

$$\begin{aligned}
A_{14}(\lambda) &= p_*(0) \int_0^M e^{-\lambda a} \pi_p(a, Q_*) \int_0^a e^{\lambda s} m'_Q(s, Q_*) ds da, \\
A_{22}(\lambda) &= q_*(0) \int_0^M e^{-\lambda a} \pi_q(a, P_*) \int_0^a e^{\lambda s} n'_P(s, P_*) ds da, \\
A_{34}(\lambda) &= p_*(0) \int_0^M e^{-\lambda a} \pi_p(a, Q_*) b_p(a) \int_0^a e^{\lambda s} m'_Q(s, Q_*) ds da, \\
A_{42}(\lambda) &= q_*(0) \int_0^M e^{-\lambda a} \pi_q(a, P_*) b_q(a) \int_0^a e^{\lambda s} n'_P(s, P_*) ds da.
\end{aligned}$$

Here

$$\pi_p(a, Q) = e^{-\int_0^a m(s, Q) ds}, \quad \pi_q(a, P) = e^{-\int_0^a n(s, P) ds},$$

denote the survival probability of species p and q , respectively, while the total population quantities are denoted by $P_* = \int_0^M p_*(a) da$ and $Q_* = \int_0^M q_*(a) da$.

Recall from [16]

Theorem 4.1 If all the roots of the characteristic equation (4.4) have negative real part then the stationary solution $(p_*(a), q_*(a))$ is asymptotically stable, if instead it has a root with positive real part then (4.4) and consequently the stationary solution $(p_*(a), q_*(a))$ is unstable. \square

If the system (4.1)-(4.3) admits a stationary solution $(p_*(a), q_*(a))$ at total population quantities $(P_*, Q_*) \neq (0, 0)$ it has to satisfy the following equations

$$p'_*(a) = -m(a, Q_*)p_*(a), \quad q'_*(a) = -n(a, P_*)q_*(a), \quad (4.5)$$

$$p_*(0) = \int_0^M b_p(a)p_*(a)da, \quad q_*(0) = \int_0^M b_q(a)q_*(a)da. \quad (4.6)$$

Substituting the solutions of (4.5) into (4.6) we obtain

$$1 = R_p(Q_*) = \int_0^M b_p(a)\pi_p(a, Q_*)da, \quad 1 = R_q(P_*) = \int_0^M b_q(a)\pi_q(a, P_*)da. \quad (4.7)$$

As earlier $R_p(Q), R_q(P)$ denote the inherent net reproduction number, the number of offsprings expected to be produced by an individual in her lifetime.

If the vital rate functions $b_p(a), b_q(a), m(a, Q), n(a, P)$ are given we can solve equations (4.7) for P_*, Q_* and determine the stationary solution $(p_*(a), q_*(a))$ as in [16].

$$p_*(a) = p_*(0)\pi_p(a, Q_*), \quad q_*(a) = q_*(0)\pi_q(a, P_*)$$

where

$$p_*(0) = \frac{P_*}{\int_0^M \pi_p(a, Q_*) da}, \quad q_*(0) = \frac{Q_*}{\int_0^M \pi_q(a, P_*) da},$$

respectively.

Similarly to the case of the single species model (as in [21]) first we consider the stability of the trivial equilibrium of the system (4.1)-(4.3). The stability of the trivial equilibrium is important, for example, in case we want to raise a population from a small number of individuals.

Proposition 4.2[15] The trivial equilibrium $(0, 0)$ is asymptotically stable if $R_p(0), R_q(0) < 1$, if instead $R_p(0) > 1$ or $R_q(0) > 1$ holds then it is unstable.

Proof An easy computation shows that in the case of the trivial equilibrium our characteristic equation reduces to the following:

$$0 = \left(1 - \int_0^M e^{-\lambda a} b_p(a) \pi_p(a, 0) da\right) \left(1 - \int_0^M e^{-\lambda a} b_q(a) \pi_q(a, 0) da\right). \quad (4.8)$$

From (4.8) setting $\lambda = x + iy$ we obtain the equations

$$1 = \int_0^M e^{-xa} \cos(ya) b_p(a) \pi_p(a, 0) da, \quad 1 = \int_0^M e^{-xa} \cos(ya) b_q(a) \pi_q(a, 0) da. \quad (4.9)$$

Because $\cos(ya) \leq 1$ and $e^{-xa} \leq 1$ holds for $x \geq 0$, it is easy to see that if $\int_0^M b_p(a) \pi_p(a, 0) da = R_p(0) < 1$ and $\int_0^M b_q(a) \pi_q(a, 0) da = R_q(0) < 1$ hold, then the characteristic equation (4.4) has no roots with positive or zero real part.

On the other hand if $R_p(0) > 1$ or $R_q(0) > 1$ holds then there exists a real root $x_* > 0$ by the Intermediate Value Theorem. \square

Now suppose that there exists a stationary solution in the form $(0, \bar{q}_*(a))$ of the system (4.1)-(4.3). In this case our characteristic equation reduces to the following

$$0 = \left(1 - \int_0^M e^{-\lambda a} b_p(a) \pi_p(a, \bar{Q}_*) da\right) \left(1 - \int_0^M e^{-\lambda a} b_q(a) \pi_q(a, 0) da\right), \quad (4.10)$$

where $\bar{Q}_* = \int_0^M \bar{q}_*(a) da$.

In this case the net reproduction number of species q equals one, that is

$$1 = R_q(0) = \int_0^M b_q(a) \pi_q(a, 0) da,$$

which means $\lambda = 0$ is always a root of (4.10), thus the linearization doesn't decide the stability.

As a consequence, similarly to the proof of the Proposition we obtain that if

$R_p(\bar{Q}_*) > 1$ holds then the stationary solution $(0, \bar{q}_*(a))$ is unstable if instead

$R_p(\bar{Q}_*) < 1$ holds then every nonzero root of (4.8) must have negative real part and the linearization does not decide the stability.

Remark In this case $R_p(\bar{Q}_*)$ is not necessarily equal to 1 because the species p is not present so that its net reproduction number at the total population \bar{Q} is arbitrary.

The same argument holds for the stationary solution in the form $(\bar{p}_*(a), 0)$, of course.

In the following we treat the stability of the stationary solution $(p_*(a), q_*(a))$ when (P_*, Q_*) is lying in the interior of the positive orthant (P, Q) , and we suppose that $R'_p(Q_*), R'_q(P_*) \neq 0$.

Theorem 4.3[15] 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.

Proof We are going to show that under the condition above the characteristic equation has a positive root λ .

Simple computation shows that at $\lambda = 0$ the left-hand side of (4.4) equals

$$P_* Q_* R'_p(Q_*) R'_q(P_*). \quad (4.11)$$

Because of the condition in the Theorem (4.11) is positive and the right-hand side of (4.4) at $\lambda = 0$ equals 0.

Observe that

$$\lim_{\lambda \rightarrow \infty} (A_{14}(\lambda), A_{22}(\lambda), A_{34}(\lambda), A_{42}(\lambda), A_{11}(\lambda), A_{23}(\lambda)) = (0, 0, 0, 0, 0, 0),$$

that is for the left-hand side of (4.4) we have

$$\lim_{\lambda \rightarrow \infty} (A_{11}(\lambda)A_{34}(\lambda) + A_{14}(\lambda)A_{31}(\lambda))(A_{22}(\lambda)A_{43}(\lambda) + A_{23}(\lambda)A_{42}(\lambda)) = 0,$$

while for the right-hand side of (4.4) we find

$$\lim_{\lambda \rightarrow \infty} (A_{31}(\lambda)A_{43}(\lambda)) = 1.$$

Then by the Intermediate Value Theorem it follows that there exists a positive root λ of (4.4). \square

Remark

Note that if $\text{sign}(m'_Q) = \text{sign}(n'_P)$ then $\text{sign}(R'_p(Q_*)) = \text{sign}(R'_q(P_*))$ because

$$R'_p(Q_*) = - \int_0^M b_p(a) \pi_p(a, Q_*) \left(\int_0^a m'_Q(s, Q_*) ds \right) da,$$

and

$$R'_q(P_*) = - \int_0^M b_q(a) \pi_q(a, P_*) \left(\int_0^a n'_P(s, P_*) ds \right) da,$$

respectively. This means that in the case

$$m'_Q > 0, n'_P > 0, \text{ resp. } m'_Q < 0, n'_P < 0 \quad (4.12)$$

every stationary solution of the system is unstable, and the conditions in (4.12) mean that the model is a competitive, resp. a cooperative one.

Finally we formulate the following

Conjecture 4.4[15] In the case $\text{sign}(R'_p(Q_*)) \neq \text{sign}(R'_q(P_*))$, the case of a predator-prey model, every positive stationary solution $(p_*(a), q_*(a))$ with total population quantity (P_*, Q_*) is asymptotically stable.

5 The size structured model

In this section we treat a structured model, where a denotes the size, weight or any biologically important structuring variable of individuals (except the age) [3]. In this case a third vital rate function occurs, which measures the growth of a in time t . This generalized McKendrick model can be derived as a continuity equation similarly to the age structured model in Sect. 1.1. In our model the growth rate γ depends only on the structuring variable a , but in a more general setting it may depend on any functional of the distribution $p(a,t)$, e.g. on the total population quantity ([25],[6]).

First we deduce a characteristic function for the stationary solution $p_*(a)$ of the system, then based on the localization of the roots of this characteristic function we prove stability (resp. instability) results in the case of very general vital rate functions.

5.1 The model equation

The model equation

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

$$\gamma(0)p(0,t) = \int_0^m \beta(a,P(t))p(a,t)da, \quad t > 0, \quad (5.1)$$

with the initial condition $p(a,0) := p_0(a)$ describes the dynamics of a single species population with structuring variable a which can be considered now as the measure of an individual's size.

The mortality and the fertility functions μ, β depend on the size a and on the total population quantity

$$P(t) = \int_0^m p(a,t)da$$

at time t which makes the model a nonlinear one. We assume a finite maximal size denoted by m and the size of any newborn is considered to be 0. As usually, we make the following general assumptions on these vital rate functions:

$$\forall x \in [0, \infty) \quad \beta(.,x) \in L^1(0,m), \quad \mu(.,x) \in L^1_{loc}([0,m]),$$

$$\forall x \in [0, \infty) \quad 0 \leq \beta(a, x) \leq K < \infty, \quad \mu(a, x) \geq 0, \quad \int_0^m \mu(a, x) da = \infty.$$

The growth rate $\gamma > 0$ depends only on the size a . Moreover we assume that all the vital rate functions μ, β, γ are in C^1 class. This generalized model is equivalent to the Gurtin-MacCamy (or McKendrick) nonlinear age structured model if $\gamma \equiv 1$, (see [18],[21],[3]). It is often used to model fish, coral or tree populations where the size is a more relevant measure according to the dynamical behaviour of the system.

5.2 The characteristic equation

If the model (5.1) has a stationary solution denoted by $p_*(a)$ then it has to satisfy the following equations

$$\begin{aligned} \gamma'(a)p_*(a) + \gamma(a)p_*'(a) &= -\mu(a, P_*)p_*(a), \quad P_* = \int_0^m p_*(a) da, \\ \gamma(0)p_*(0) &= \int_0^m \beta(a, P_*)p_*(a) da. \end{aligned} \quad (5.2)$$

From (5.2) we have

$$p_*'(a) = \frac{-\mu(a, P_*)p_*(a) - \gamma'(a)p_*(a)}{\gamma(a)},$$

and we get easily the solution

$$p_*(a) = p_*(0) e^{-\int_0^a \frac{\mu(s, P_*) + \gamma'(s)}{\gamma(s)} ds}. \quad (5.3)$$

Substituting (5.3) into (5.2) we obtain

$$1 = \frac{\int_0^m \beta(a, P_*) e^{-\int_0^a \frac{\mu(s, P_*) + \gamma'(s)}{\gamma(s)} ds} da}{\gamma(0)} =: Q(P_*), \quad (5.4)$$

which quantity was known as the inherent net reproduction number in the age structured case ($\gamma \equiv 1$).

We can solve equation (5.4) for the single variable P and from the equation

$$P_* = \int_0^m p_*(a) = p_*(0) \int_0^m e^{-\int_0^a \frac{\mu(s, P_*) + \gamma'(s)}{\gamma(s)} ds} da$$

we have the initial value $p_*(0)$, and the stationary solution $p_*(a) = p_*(0) e^{-\int_0^a \frac{\mu(s, P_*) + \gamma'(s)}{\gamma(s)} ds}$.

This way we showed that for any solution P_* of (5.4) we have exactly one stationary solution $p_*(a)$.

Now introducing the variation for an arbitrary stationary solution $p_*(a)$

$$u(a, t) := p(a, t) - p_*(a),$$

$u(a, t)$ has to satisfy the following equation

$$u'_t(a, t) + (\gamma(a)u(a, t))'_a = p'_t(a, t) + (\gamma(a)p(a, t))'_a - (\gamma(a)p_*(a))'_a,$$

and with

$$p'_t(a, t) + (\gamma(a)p(a, t))'_a = -\mu(a, P(t))p(a, t), \quad (\gamma(a)p_*(a))'_a = -\mu(a, P_*)P_*(a),$$

we get

$$u'_t(a, t) + (\gamma(a)u(a, t))'_a = -\mu(a, P)p(a, t) + \mu(a, P_*)p_*(a).$$

Now expanding $\mu(a, P)$ into Taylor series in P at P_* and omitting the nonlinear terms, that is we use the approximation $\mu(a, P) \sim \mu(a, P_*) + \mu'_P(a, P_*)(P - P_*)$, we arrive at

$$u'_t(a, t) + (\gamma(a)u(a, t))'_a = -\mu(a, P_*)u(a, t) - \mu'_P(a, P_*)p_*(a) \int_0^m u(a, t) da, \quad (5.5)$$

and for the initial condition

$$u(0, t) = p(0, t) - p_*(0) = \int_0^m \beta(a, P_*)u(a, t) da + \int_0^m \beta'_P(a, P_*)p_*(a) da \int_0^m u(a, t) da. \quad (5.6)$$

Now suppose that this linearized problem has solutions of the form $u(a, t) = e^{\lambda t} U(a)$, substituting this into (5.5) and (5.6) and applying the following notation $\bar{U} = \int_0^m U(a) da$ we obtain the system

$$U'(a) = U(a) \frac{-\gamma'(a) - \mu(a, P_*) - \lambda}{\gamma(a)} - \bar{U} \frac{\mu'_P(a, P_*) p_*(a)}{\gamma(a)}, \quad (5.7)$$

$$U(0) = \int_0^m \beta(a, P_*) U(a) da + \bar{U} \int_0^m \beta'_P(a, P_*) p_*(a) da. \quad (5.8)$$

The solution of the initial problem (5.7)-(5.8) is

$$U(a) = \left(U(0) - \int_0^a \frac{\bar{U} \mu'_P(s, P_*) p_*(s)}{\gamma(s)} e^{\int_0^s \frac{\gamma'(r) + \mu(r, P_*) + \lambda}{\gamma(r)} dr} ds \right) e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*) + \lambda}{\gamma(s)} ds}. \quad (5.9)$$

Integrating (5.9) from 0 to m and using the formula $p_*(s) = p_*(0) e^{-\int_0^s \frac{\gamma'(r) + \mu(r, P_*)}{\gamma(r)} dr}$ we obtain

$$\bar{U} = A_{11}(\lambda) U(0) + A_{12}(\lambda) \bar{U},$$

whith

$$A_{11}(\lambda) = \int_0^m e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*) + \lambda}{\gamma(s)} ds} da,$$

and

$$A_{12}(\lambda) = -p_*(0) \int_0^m e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*) + \lambda}{\gamma(s)} ds} \left(\int_0^a \frac{\mu'_P(s, P_*)}{\gamma(s)} e^{\int_0^s \frac{\lambda}{\gamma(r)} dr} ds \right) da.$$

Substituting the solution $U(a)$ into the initial condition (5.8) we get

$$U(0) = U(0) A_{21}(\lambda) + \bar{U} A_{22}(\lambda),$$

where

$$A_{21}(\lambda) = \int_0^m \beta(a, P_*) e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*) + \lambda}{\gamma(s)} ds} da,$$

$$\begin{aligned}
 A_{22}(\lambda) &= p_*(0) \int_0^m e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*)}{\gamma(s)} ds} \beta'_P(a, P_*) da - \\
 &- p_*(0) \int_0^m e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*) + \lambda}{\gamma(s)} ds} \beta(a, P_*) \left(\int_0^a \frac{\mu'_P(s, P_*)}{\gamma(s)} e^{\int_0^s \frac{\lambda}{\gamma(r)} dr} ds \right) da.
 \end{aligned}$$

Thus, we get the same linear system as in [16] for $\bar{U}, U(0)$ but with more complicated coefficients:

$$0 = A_{11}(\lambda)U(0) + (A_{12}(\lambda) - 1)\bar{U}, \quad 0 = U(0)(A_{21}(\lambda) - 1) + \bar{U}A_{22}(\lambda). \quad (5.10)$$

The homogenous system (5.10) has a non trivial solution if and only if the following determinant is zero,

$$\begin{vmatrix}
 A_{11}(\lambda) & A_{12}(\lambda) - 1 \\
 A_{12}(\lambda) - 1 & A_{22}(\lambda)
 \end{vmatrix} = 0.$$

Thus, we may formulate the following.

Theorem 5.1[11] The stationary solution $p_*(a)$ is asymptotically stable (resp. unstable) if all the roots of the following equation have negative real part (resp. it has a root with positive real part).

$$A_{11}(\lambda)A_{22}(\lambda) - A_{12}(\lambda)A_{21}(\lambda) + A_{12}(\lambda) + A_{21}(\lambda) = 1 \quad (5.11)$$

5.3 Stability of equilibria

Next we establish our stability results.

The proof of the following result mainly follows the idea of the proof of Th.1 in [9].

Theorem 5.2[11] In the case of the following vital rates $\mu(a, P) =: \mu(a)$, $\beta(a, P)$, $\gamma(0) = 1$, the stationary solution $p_*(a)$ is asymptotically stable if $\beta'_P(\cdot, P_*) < 0$, if instead $\beta'_P(\cdot, P_*) > 0$ holds then it is unstable.

Proof

Let us introduce the following notations:

$$T(a, P_*, \lambda) := e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*) + \lambda}{\gamma(s)} ds}, \quad T(a, P_*) := e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*)}{\gamma(s)} ds},$$

and

$$T(a, P_*, \lambda) = e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*)}{\gamma(s)} ds} e^{-\lambda \int_0^a \frac{1}{\gamma(s)} ds} = T(a, P_*) e^{-\lambda \Gamma(a)},$$

where

$$\Gamma(a) = \int_0^a \frac{1}{\gamma(s)} ds.$$

If the vital rates assume the form above then the characteristic equation can be written the following way

$$\begin{aligned} K(\lambda) = 1 &= \\ &= \frac{P_*}{\int_0^m T(a, P_*) da} \int_0^m T(a, P_*) e^{-\lambda \Gamma(a)} da \int_0^m T(a, P_*) \beta'_P(a, P_*) da + \\ &\quad + \int_0^m \beta(a, P_*) T(a, P_*) e^{-\lambda \Gamma(a)} da. \end{aligned}$$

Now suppose that $\beta'_P(\cdot, P_*) > 0$ holds. Then we are going to show that the characteristic function has a positive root λ .

The following inequality is true for all $P_* > 0$

$$K(0) = P_* \int_0^m T(a, P_*) \beta'_P(a, P_*) da + \gamma(0) > 1$$

because $\gamma(0) = 1$ and $\beta'_P(\cdot, P_*) > 0$ holds.

Additionally we have

$$\lim_{\lambda \rightarrow \infty} K(\lambda) = 0,$$

and the functions μ, β, γ are nonnegative so that $K(\lambda)$ is a monotone decreasing function of λ , which shows that there exists exactly one positive λ for which $K(\lambda) = 1$.

On the other hand if $\beta'_P(\cdot, P_*) < 0$ holds, suppose that there exists a root $\lambda = x + iy$ such that $x \geq 0$.

Then

$$1 = \operatorname{Re}(K(\lambda)) = \frac{P_*}{\int_0^m T(a, P_*) da} \int_0^m T(a, P_*) e^{-x\Gamma(a)} \cos(y\Gamma(a)) da$$

$$\cdot \int_0^m T(a, P_*) \beta'_P(a, P_*) da + \int_0^m \beta(a, P_*) T(a, P_*) e^{-x\Gamma(a)} \cos(y\Gamma(a)) da.$$

For $x \geq 0$, we have $e^{-x\Gamma(a)} \leq 1$ and $\cos(y\Gamma(a)) \leq 1$ obviously, so we have

$$\begin{aligned} & \operatorname{Re}(K(\lambda)) \leq \\ & \leq \frac{P_*}{\int_0^m T(a, P_*) da} \int_0^m T(a, P_*) da \int_0^m T(a, P_*) \beta'_P(a, P_*) da + \int_0^m \beta(a, P_*) T(a, P_*) da = \\ & = P_* \int_0^m T(a, P_*) \beta'_P(a, P_*) da + \gamma(0) < 1, \end{aligned}$$

a contradiction.

That is the characteristic equation does not have a root with positive or zero real part if $\beta'_P(\cdot, P_*) < 0$ holds. \square

Remark The stability condition for the fertility function seems to be very natural in a biological sense, namely it says that if at the equilibrium the growth of the population decreases the fertility of individuals which in general decreases the number of newborns as a compensation or balancing principle, then the equilibrium is stable. In general, if the conditions for stability of equilibria arrived at by mathematical modelling of biological phenomena are intuitively obvious then the mathematical model may be relied upon perhaps by greater certainty.

The following theorem generalizes the second part of Th.5.2, that is we give a condition which implies instability of the equilibrium for general $\mu(a, P), \beta(a, P), \gamma(a)$.

Theorem 5.3[11] Suppose $\gamma(0) = 1$, then if $Q'(P_*) > 0$ holds then the stationary solution $p_*(a)$ with total population quantity P_* is unstable.

Proof With the notations above we have

$$A_{11}(\lambda) = \int_0^m T(a, P_*, \lambda) da, \quad A_{21}(\lambda) = \int_0^m \beta(a, P_*) T(a, P_*, \lambda) da,$$

$$A_{12}(\lambda) = -\frac{P_*}{\int_0^m T(a, P_*) da} \int_0^m \left(T(a, P_*, \lambda) \int_0^a \mu'_P(s, P_*) \frac{e^{\lambda\Gamma(s)}}{\gamma(s)} ds \right) da,$$

$$A_{22}(\lambda) = \frac{P_*}{\int_0^m T(a, P_*) da} \int_0^m T(a, P_*) \beta'(a, P_*) - T(a, P_*, \lambda) \beta(a, P_*) \int_0^a \frac{\mu'_P(s, P_*)}{\gamma(s)} e^{\lambda\Gamma(s)} ds da.$$

Substituting $\lambda = 0$ into the characteristic equation (5.11) a basic calculation leads to

$$K(0) = P_* \int_0^m T(a, P_*) \beta'_P(a, P_*) da$$

$$-P_* \int_0^m T(a, P_*) \beta(a, P_*) \int_0^a \frac{\mu'_P(s, P_*)}{\gamma(s)} ds da + \int_0^m \beta(a, P_*) T(a, P_*) da.$$

Now observe that

$$P_* \int_0^m T(a, P_*) \beta'_P(a, P_*) - T(a, P_*) \beta(a, P_*) \left(\int_0^a \frac{\mu'_P(s, P_*)}{\gamma(s)} ds \right) da = P_* Q'(P_*),$$

so that we have

$$K(0) = P_* Q'(P_*) + 1 > 1.$$

Now we only have to show that $\lim_{\lambda \rightarrow \infty} K(\lambda) = 0$ which proves that there exists a real positive root λ .

For $A_{11}(\lambda), A_{21}(\lambda)$ we have $\lim_{\lambda \rightarrow \infty} A_{11}(\lambda) = \lim_{\lambda \rightarrow \infty} A_{21}(\lambda) = 0$.

For $A_{12}(\lambda)$ consider the function

$$e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*) + \lambda}{\gamma(s)} ds} \int_0^a \frac{\mu'_P(s, P_*)}{\gamma(s)} e^{\lambda \Gamma(s)} ds = e^{-\int_0^a \frac{\gamma'(s) + \mu(s, P_*)}{\gamma(s)} ds} \int_0^a \frac{\mu'_P(s, P_*)}{\gamma(s)} e^{\lambda(\Gamma(s) - \Gamma(a))} ds,$$

and we have

$\int_0^a \frac{1}{\gamma(u)} du = \Gamma(a) > \Gamma(s) = \int_0^s \frac{1}{\gamma(u)} du$ for $a > s$, which proves $\lim_{\lambda \rightarrow \infty} A_{12}(\lambda) = 0$. So does the second term of $A_{22}(\lambda)$, namely

$$\lim_{\lambda \rightarrow \infty} T(a, P_*, \lambda) \beta(a, P_*) \int_0^a \frac{\mu'_P(s, P_*)}{\gamma(s)} e^{\lambda \Gamma(s)} ds = 0.$$

That is we have

$$\lim_{\lambda \rightarrow \infty} A_{22}(\lambda) = \frac{P_*}{\int_0^m T(a, P_*) da} \int_0^m T(a, P_*) \beta'(a, P_*) da = C$$

a constant, which completes the proof. \square

Remark The condition $Q'(P_*) > 0$ gets a natural meaning for the age structured population model (the case $\gamma \equiv 1$) when $Q(P) = R(P)$ is the expected number of new-borns for an individual. Then Th.5.3 states that for sufficiently close P , $P > P_*$ the net reproduction number is greater than 1, so that the stationary solution cannot be stable. This is not a surprising behaviour again.

6 The age structured model revisited

Based on the previous section in this part we revisit our results from section 3 according to the age structured model. Because in the case of $\gamma \equiv 1$ the size structured model (5.1) reduces to the age structured model (1.19) we have as an easy consequence of Th. 5.2 the following.

Corollary 6.1 In the case of the vital rates $\mu(a, P) = m(a)$ and $\beta(a, P)$ general the stationary solution $p_*(a)$ of the age structured system (1.19) is asymptotically stable if $\beta'_P(\cdot, P_*) < 0$ holds, if instead $\beta'_P(\cdot, P_*) > 0$ holds then it is unstable.

Moreover in the case of fully general vital rates from Th.5.3 we obtain the following.

Corollary 6.2 In the case of the most general vital rate functions $\mu(a, P)$, $\beta(a, P)$ the stationary solution $p_*(a)$ of the model (1.19) with total population quantity $P_* = \int_0^m p_*(a) da$ is unstable if $R'(P_*) > 0$ holds.

At the end of section 3 we already pointed out that the conditions on the vital rates in our Th.3.1 and Th.3.2 for the stability of $p_*(a)$ implies that $R'(P_*) < 0$ holds.

We can check easily that in the case of the vital rates in Corollary 6.1 the same holds. Namely, in the case $\mu(a, P) = m(a)$ and $\beta(a, P)$ general we have

$$R'(P_*) = \int_0^m \beta'_P(a, P_*) \pi(a) da < 0,$$

in the case of a stable stationary solution $p_*(a)$.

That is all of our stability criterions imply $R'(P_*) < 0$. Comparing this with Corollary 6.2 one may guess that in the case of $R'(P_*) < 0$ the stationary solution is linearly stable, in general.

Note that this would be "the best and the most elegant" result which one may expect, because in the case of $R'(P_*) = 0$ we can see from the proof of Th.5.3 that $\lambda = 0$ is the only root of the characteristic equation with non-negative real part, so the linearization does not decide the stability.

Actually, from the very special example of Gurtin and MacCamy from Sect.1 we obtain a counterexample of this conjecture.

Recall that in the following case $\mu(a, P) = \mu(P)$ and $\beta(a, P) = e^{-\alpha a} \beta(P)$, with $\mu(P), \beta(P), \alpha \geq 0$, the stationary solution $p_*(a)$ is asymptotically stable if and only if $\mu'(P_*) > \beta'(P_*)$ holds.

In this case of vital rates we have

$$R(P) = \int_0^m \beta(P) e^{-\alpha a - a\mu(P)} da,$$

and from this we obtain

$$\begin{aligned} R'(P_*) &= \int_0^m \beta'(P_*) e^{-\alpha a - a\mu(P_*)} - \beta(P_*) a \mu'(P_*) e^{-a\mu(P_*)} da = \\ &= \int_0^m e^{-\alpha a - a\mu(P_*)} (\beta'(P_*) - \mu'(P_*) a \beta(P_*)) da. \end{aligned} \quad (6.1)$$

From (6.1) we see that it is possible in the case of $\mu'(P_*) \leq \beta'(P_*)$, when the stationary solution is unstable, that (6.1) becomes negative.

7 The non-autonomous McKendrick type equation

7.1 Preliminaries

In this section we are going to investigate the asymptotic behaviour of solutions of the following (linear non-autonomous) Gurtin-type model

$$p'_t(a,t) + p'_a(a,t) = -\mu(a,t)p(a,t), \quad 0 \leq a < m < \infty, \quad t \geq 0, \quad (7.1)$$

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

with the initial condition $p(a,0) =: p_0(a)$, which satisfies the compatibility condition

$$p_0(0) = \int_0^m \beta(a,0)p_0(a)da.$$

This model can be derived similarly to the linear McKendrick model (1.5)-(1.6).

$p(a,t)$ denotes the density of members of age a at time $t \geq 0$ and as usually, we assume finite life span denoted by m .

We believe that this linear but non-autonomous system is more useful modelling some population dynamical phenomena for example in the case of time periodic vital rate functions.

The dynamics of the system depends on the vital rates $\beta(a,t), \mu(a,t)$ for which we make the following general assumptions, as in the previous sections

$$\forall t \in [0, \infty), \forall a \in [0, m] \quad 0 \leq \beta(a,t) \leq k < \infty, \quad \mu(a,t) \geq 0, \quad (7.2)$$

$$\forall t \in [0, \infty) \quad \int_0^m \mu(a,t)da = \infty, \quad \forall t \in [0, \infty) \quad \forall a \in [0, m) \quad \mu(a,t) < \infty. \quad (7.3)$$

Later we will make other conditions on the vital rates.

Integrating along the characteristics the model (7.1) can be reduced to a Volterra integral equation that corresponds to the case $t \geq a$. Since we are investigating here the asymptotic behaviour we consider only this case $t > m \geq a$.

The ODE system of characteristics is

$$\frac{da}{d\tau} = \frac{dt}{d\tau} = 1, \quad \frac{dp}{d\tau} = -\mu(a,t)p(a,t). \quad (7.4)$$

From (7.4) we have the following formula for $p(a,t)$

$$p(a,t) = \varphi(t-a)e^{-\int_0^a \mu(s,t)ds}, \quad (7.5)$$

where φ is an arbitrary C^1 function which has to satisfy the following equation

$$p(0,t) = \int_0^m \beta(x,t)p(x,t)dx = \varphi(t), \quad (7.6)$$

and from (7.6) we obtain

$$p(a,t) = e^{-\int_0^a \mu(s,t)ds} \int_0^m \beta(x,t-a)p(x,t-a)dx, \quad (7.7)$$

thus

$$p(a,t) = p(0,t-a)\pi(a,t), \quad \text{with } \pi(a,t) = e^{-\int_0^a \mu(s,t)ds}. \quad (7.8)$$

Here $\pi(a,t)$ denotes the probability for an individual to survive the age a at time t .

Finally recall the net reproduction function

$$R(t) = \int_0^m \beta(a,t)e^{-\int_0^a \mu(s,t)ds} = \int_0^m \beta(a,t)\pi(a,t)da. \quad (7.9)$$

7.2 Extinction

In [22] Iannelli et al. studied the global boundedness of solutions of a generalized Gurtin-MacCamy system, where the vital rates depend on a weighted size of the population

$$S(t) = \int_0^m \gamma(a)p(a,t)da,$$

with $\gamma(\cdot) \geq 0$.

Under some natural condition they proved boundedness for the total population quantity $P(t) = \int_0^m p(a,t)da$.

They investigated two cases. First, the fertility function $\beta(a, S)$ is bounded by a non-increasing function $\phi(S)$ for which $\lim_{S \rightarrow \infty} \phi(S) = 0$ holds.

Secondly they proved boundedness under conditions mainly for the mortality, namely

$$\beta(a, S) \leq C\gamma(a), \quad \mu(a, S) \geq \mu_0(a) + \omega(S),$$

where γ is the weight function, C a positive constant and ω is a non-decreasing function of the weighted population size S , $\lim_{S \rightarrow \infty} \omega(S) = \infty$.

In this section we are going to apply some of the idea of their proof for the non-autonomous system. That is, first we show that under similar conditions for the fertility function the population goes to extinction. Which means in other words, that we give conditions for the stability of the trivial solution $p(a, t) \equiv 0$. This can be very important in ecological applications as we pointed out in the previous section.

Then we consider the connection between the mortality and the fertility function and establish a result in which a condition for the net reproduction number function $R(t)$ is given.

Consider the following assumptions on the fertility function $\beta(a, t)$

$$\beta(a, t) \leq \phi(t), \quad \forall t \geq 0, \quad \exists T \geq m : \phi(T) \leq \frac{1}{2m}, \quad (7.10)$$

where $\phi(t)$ is a positive non-increasing function of $t \in [0, \infty)$.

Theorem 7.1[10] Let the conditions (7.10) be satisfied. For each nonnegative initial age distribution $p(\cdot, 0) \in L^1$ we have $\int_0^m p(a, t) da = P(t) \rightarrow 0$ if $t \rightarrow \infty$.

Proof From (7.7) we have

$$p(a, t) = p(0, t - a)\pi(a, t),$$

where $\pi(a, t) \leq 1$ for all $a \in [0, m]$, $t \in [m, \infty)$.

For the density of newborns at time t we have

$$p(0, t) = \int_0^m \beta(a, t)p(a, t) da \leq \phi(t)P(t). \quad (7.11)$$

That is, we have

$$\int_0^m p(a,t)da = P(t) \leq \int_0^m p(0,t-a)da \leq \int_0^m \phi(t-a)P(t-a)da. \quad (7.12)$$

Now let $I_n := [(n-1)m, nm]$, ($n = 2, 3, \dots$) and $P_n = \max_{t \in I_n} P(t)$.

Then for $t \in I_{n+1}$ and $a \in [0, m]$ we have $(t-a) \in I_n \cup I_{n+1}$ thus, from (7.12) we obtain

$$P_{n+1} \leq \max\{P_n, P_{n+1}\} \cdot m \cdot \phi((n-1)m).$$

Let n_* be sufficiently great to have $(n_* - 1)m \geq T$. Then we have

$$P_{n_*+1} \leq \frac{\max\{P_{n_*}, P_{n_*+1}\}}{2}. \quad (7.13)$$

Then it follows that for $n \geq n_*$ we have $P_{n+1} \leq \frac{P_n}{2}$.

That is we have

$$\int_0^m p(a,t)da = P(t) \rightarrow 0, \text{ if } t \rightarrow \infty. \square$$

As we have mentioned the net reproduction rate $R(t)$ is a key parameter to decide stability of stationary solutions of the autonomous model.

Now suppose that there exists a nonnegative ϕ function and some constant $\varepsilon > 0$ such that

$$\beta(a,t) \leq \phi(t), \quad \phi(t-a) \leq (1+\varepsilon)\beta(a,t), \quad a \in [0, m], t > m. \quad (7.14)$$

Moreover suppose that there exists a finite $T \geq 0$ such that

$$R(T) \leq \frac{1}{1+\delta} \text{ for } \delta > \varepsilon, \quad (7.15)$$

and $R(t)$ is non-increasing.

Theorem 7.2[10] With the conditions (7.14)-(7.15) for each nonnegative initial age distribution $p(a,0) \in L^1$, $\int_0^m p(a,t)da = P(t) \rightarrow 0$ if $t \rightarrow \infty$.

Proof

We have again

$$p(a, t) = p(0, t - a)\pi(a, t), \quad t \in [m, \infty)$$

and in the same way as in the proof of Th.1 we obtain

$$P(t) \leq \int_0^m \phi(t - a)P(t - a)\pi(a, t)da$$

From the conditions (7.14)-(7.15) we obtain

$$P(t) \leq \int_0^m (1 + \varepsilon)\beta(a, t)\pi(a, t)P(t - a)da, \quad (7.16)$$

and with the same $I_n := [(n - 1)m, nm]$, ($n = 2, 3, \dots$) and $P_n := \max_{t \in I_n} P(t)$, if $t \in I_{n+1}$, $a \in [0, m]$, $(t - a) \in I_n \cup I_{n+1}$ thus we obtain

$$P_{n+1} \leq \max\{P_n, P_{n+1}\}(1 + \varepsilon) \int_0^m \beta(a, t)\pi(a, t)da, \quad (7.17)$$

and because $\int_0^m \beta(a, t)\pi(a, t)da = R(t) \leq \frac{1}{1+\delta}$ for $t \geq T$, for sufficiently large n_* we have for $n \geq n_*$

$$P_{n_*+1} \leq \frac{1 + \varepsilon}{1 + \delta} \max\{P_{n_*}, P_{n_*+1}\}, \quad (7.18)$$

from where follows that $P_{n+1} \leq P_n \frac{1+\varepsilon}{1+\delta} < P_n$, for $n \geq n_*$.

That is $P(t) \rightarrow 0$ if $t \rightarrow \infty$. \square

Remarks The conditions in Th.7.2 for the fertility function are quite technical. The condition for $R(t)$ is the essential one. Roughly speaking it means that if there exists some finite $T \geq 0$ such that $R(t)$ is bounded by some $\frac{1}{1+\delta} < 1$ for $t \geq T$ then the population goes to extinction. In other words if the expected number of newborns at time t is less than 1 for $t \geq T$ then the total population quantity tends to zero, of course.

7.3 Bounded survival

In the previous section we established conditions for the vital rates which guarantee the extinction of the population. One may expect that if there exists some finite T such that for $t \geq T$ the inherent net reproduction number $R(t)$ is lower than 1, in other

words, the number of per capita offspring is below 1 then the total population quantity decreases and the population goes to extinction.

In this section we are going to formulate conditions for the boundedness of solutions which guarantee the survival of the population at the same time. The conditions are also in close relation with the net reproduction rate R as we will see.

Integrating both sides of the equation in (7.1) from 0 to m we have

$$\begin{aligned}\dot{P}(t) &= - \int_0^m \mu(a,t)p(a,t)da - \int_0^m p'_a(a,t)da = p(0,t) - \int_0^m \mu(a,t)p(a,t)da = \\ &= \int_0^m \beta(a,t)p(a,t)da - \int_0^m \mu(a,t)p(a,t)da.\end{aligned}\quad (7.19)$$

The solution of the ODE (7.19) obtained easily

$$P(t) = \int_0^t \int_0^m (p(a,s)\beta(a,s) - p(a,s)\mu(a,s))dads + P(0), \quad (7.20)$$

and we have

$$\overline{\lim}_{t \rightarrow \infty} P(t) \leq \int_0^\infty \int_0^m (p(a,s)\beta(a,s) - p(a,s)\mu(a,s))dads + P(0). \quad (7.21)$$

Thus the question is when does the function

$$F(s) = \int_0^m (p(a,s)\beta(a,s) - p(a,s)\mu(a,s))da \quad (7.22)$$

belong to $L^1_{[0,\infty)}$.

From (7.4) we have $p(a,s) = p(0,s-a)\pi(a,s)$ for $s \geq a$, that is we have

$$F(s) = \int_0^m p(0,s-a)(\beta(a,s)\pi(a,s) - \mu(a,s)\pi(a,s))da \quad (7.23)$$

for $s \geq m$, and clearly $\int_0^m F(s)ds < \infty$ holds.

If the density of newborns $p(0,t)$ is finite for every t then there exists a function C which is also bounded, such that $p(0,s-a) \leq C(s)p(0,s)$ for every $a \in [0,m]$, $s \geq a$.

That is, we have

$$F(s) \leq p(0,s)C(s) \left| \int_0^m \beta(a,s)\pi(a,s)da - \int_0^m \mu(a,s)\pi(a,s)da \right|. \quad (7.24)$$

Now observe that $\int_0^m \beta(a,s)\pi(a,s)da = R(s)$ by definition and $\int_0^m \mu(a,s)\pi(a,s)da = 1$ because $\mu(a,s)\pi(a,s)da$ is the probability for an individual to survive the age a and then die in $[a, a + da]$.

That is, we have

$$\overline{\lim}_{t \rightarrow \infty} P(t) \leq \int_0^\infty p(0,s)C(s)|R(s) - 1|ds + P(0). \quad (7.25)$$

Note that if the net reproduction number R is bounded by some $M < \infty$ for every s , then the density of newborns $p(0,s)$ and the function C is bounded for every s , too.

For example, if $0 \leq (R(s) - 1) \leq \frac{1}{s^{1+\alpha}}$ for some $\alpha > 0$, then the improper integral in (7.25) is convergent. This means that the total population is bounded simultaneously

$$0 < P(0) \leq P(t) \leq \int_0^\infty p(0,s)C(s)|R(s) - 1|ds + P(0) < \infty.$$

Example Consider the following special vital rate functions with maximal life span $m = 100$

$$\beta(a,t) = b(a)f(t) = \frac{a^4}{C}(100-a)^2 1.11^{-a} \left(1 + \frac{1}{t^2+1}\right), \quad \mu(a) = \frac{1}{100-a},$$

with $C = \int_0^{100} a^4(100-a)^2 1.11^{-a} \pi(a) da \sim 0,4045064485 \cdot 10^{10}$.

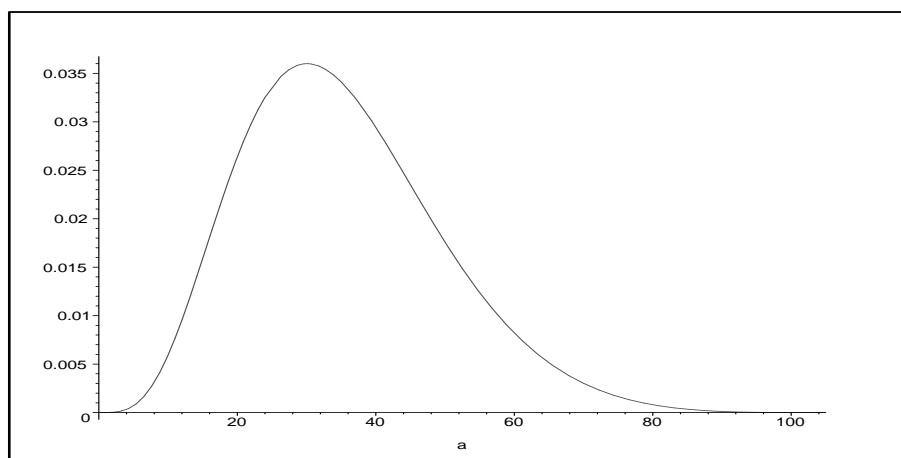


Fig.1. $b(a) = \frac{a^4}{C}(100 - a)^2 1.11^{-a}$

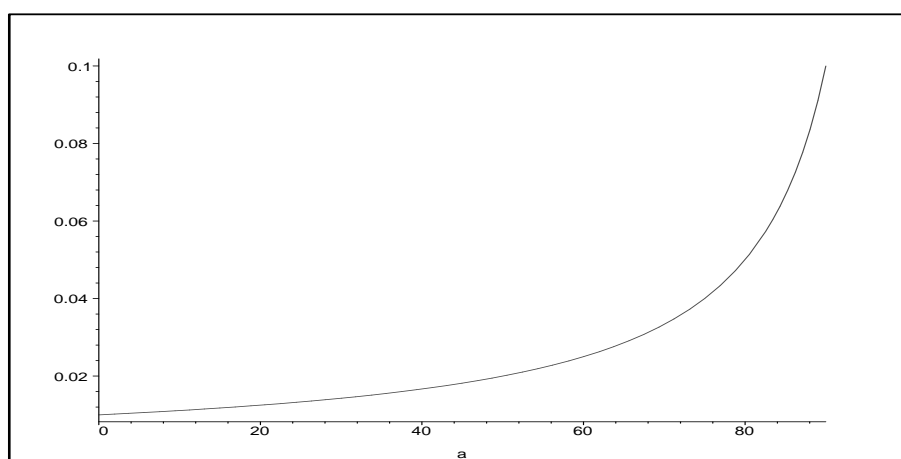


Fig.2. $\mu(a) = \frac{1}{100 - a}$

It is easy to show that these functions satisfy the conditions (7.2)-(7.3).

With $\pi(a) = 1 - \frac{a}{100}$

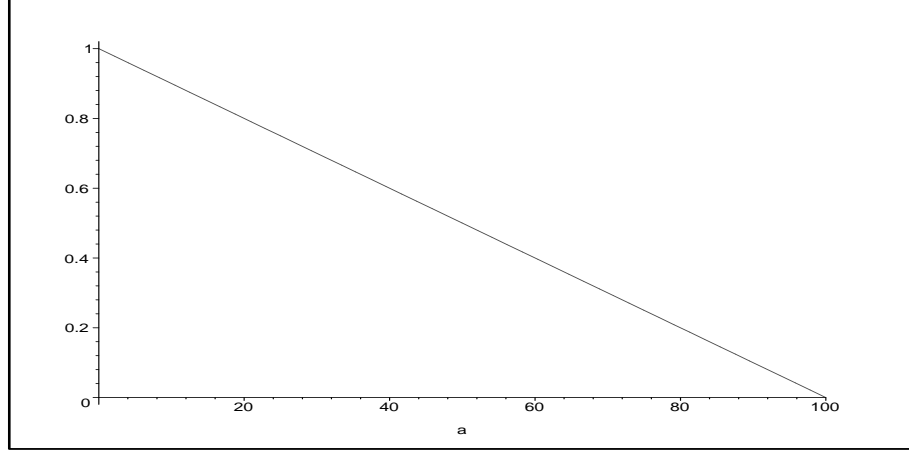


Fig.3. $\pi(a) = 1 - \frac{a}{100}$

we arrive at

$$R(t) = \int_0^{100} \frac{a^4}{C} (100-a)^2 1.11^{-a} \left(1 + \frac{1}{t^2+1}\right) \left(1 - \frac{a}{100}\right) da = 1 + \frac{1}{1+t^2}$$

Thus $R(t) \geq 1$ for $t \geq 0$, which means that P is a non-decreasing function of time t , and $R(t) \rightarrow 1$ in a sufficient order.

From (7.25)

$$\lim_{t \rightarrow \infty} P(t) \leq \int_0^{\infty} \frac{p(0,s)C(s)}{1+s^2} ds + P(0), \quad (7.26)$$

that is, for any given initial age distribution $p_0(a)$ which satisfies the compatibility condition

$$p_0(0) = \int_0^{100} 2p_0(a) \frac{a^4}{C} (100-a)^2 1.11^{-a} da$$

the solution $p(a,t) \rightarrow p_*(a)$ if $t \rightarrow \infty$ with some non-trivial age distribution $p_*(a)$ in the following L^1 norm:

$$|p(\cdot, t)|_{L^1} := \int_0^m |p(a, t)| da. \quad (7.27)$$

Remarks The example above is a very special one but shows the essential role of the net reproduction function $R(t)$. Thus the general problem namely the formulation of necessary or sufficient conditions for the convergence to a non-trivial age distribution seems to be still open. We are working now on the important special case in which the vital rates are periodic functions of time.

8 Bifurcations of equilibria

In this section we consider a one parameter class of systems and investigate how equilibria arise by varying a biologically important parameter. We apply our Th.3.1 to determine the stability of the equilibria.

Recall the following theorem from [21] which characterises the stability of the trivial equilibrium of the age structured system (1.19).

Theorem 8.1(M. Iannelli[21]) If $R(0) < 1$ then the trivial equilibrium $p_1(a) \equiv 0$ is asymptotically stable, if instead $R(0) > 1$ then it is unstable.

In section 3 we have proved results about the stability of stationary solutions of the age structured model. One of them characterizes the stability in a case when the vital rates assume a special form, namely

$$\mu(a, P(t)) =: \mu(a), \beta(a, P(t)) = b(a)f(P(t)), \quad (8.1)$$

a factorization property for β .

Now consider a family of systems with the following vital rates

$$\mu(a, P) = \mu(a), \beta_c(a, P) = b(a)f_c(P), f_c(P) = \frac{1}{P+1} + cP$$

with bifurcation parameter $c > 0, \mu, \beta_c \in C^1$.

Setting $K = \int_0^m b(a)\pi(a)da$, we get the following equation

$$Kf_c(P) - 1 = \frac{cKP^2 + cKP + 1}{P+1} - 1 = 0$$

for the population quantity P .

Observe that now $R(0) = K$ holds.

From the equation

$$cKP^2 + (cK - 1)P + K - 1 = 0$$

we get the solutions

$$P_1^{1,2} = \frac{(1 - cK) \pm \sqrt{c^2K^2 - 4cK^2 + 2cK + 1}}{2cK}, \quad (8.2)$$

and we search for a positive equilibrium.

8.1 The case $K > 1$

In (8.2)

$$c^2 K^2 - 4cK^2 + 2cK + 1 > 0,$$

holds if

$$0 < c < 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$$

or

$$c > 2 - \frac{1}{K} + 2\sqrt{1 - \frac{1}{K}}.$$

First consider the interval $0 < c < 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$, and because of $\frac{1}{K} > 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$ now $1 - cK > 0$ holds. The inequality $1 - cK > \sqrt{c^2 K^2 - 4cK^2 + 2cK + 1}$ shows that in this interval of parameter value c there exist exactly two nontrivial equilibria.

At the parameter value $c = 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$ we have $c^2 K^2 - 4cK^2 + 2cK + 1 = 0$ and $1 - cK > 0$ so at this value of c there exists only one positive equilibrium with total population quantity $P_1 = \frac{1 - K + K\sqrt{1 - \frac{1}{K}}}{2K - 1 - 2K\sqrt{1 - \frac{1}{K}}}$.

For $2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}} < c < 2 - \frac{1}{K} + 2\sqrt{1 - \frac{1}{K}}$ there aren't any positive equilibria, and this holds for $c > 2 - \frac{1}{K} + 2\sqrt{1 - \frac{1}{K}}$ because $1 - cK < 0$ and $cK - 1 > \sqrt{c^2 K^2 - 4cK^2 + 2cK + 1}$.

Now we are going to determine the stability of the equilibria.

First consider the positive equilibrium at the parameter value $c = 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$ with total population quantity $P_1 = \frac{1 - cK}{2cK} = \frac{1 - K + K\sqrt{1 - \frac{1}{K}}}{2K - 1 + 2K\sqrt{1 - \frac{1}{K}}}$.

We have

$$f'_c(P) = c - \frac{1}{P^2 + 2P + 1},$$

and a simple calculation leads to

$$f'_c(P_1) = 0.$$

It is easy to show that for $P > P_1$ we have $f'_c(P) > 0$ and for $P < P_1$ we get $f'_c(P) < 0$. Applying Theorem 3.1 we get that one of the positive equilibria is asymptotically stable and the other one is unstable at the parameter interval $0 < c < 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$. The trivial equilibrium is unstable by Theorem 8.1 because $R(0) = K > 1$. As a summary we have the following

Theorem 8.2 (*Saddle-node bifurcation*) For $c > 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$ there is no positive equilibrium, for $c_0 = 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$ we have one positive equilibrium. For $c < c_0$ there are two curves of positive equilibria in a neighbourhood of

$$(P, c) = \left(\frac{1 - K + K\sqrt{1 - \frac{1}{K}}}{2K - 1 - 2K\sqrt{1 - \frac{1}{K}}}, c_0 \right).$$

The upper equilibria are unstable and the lower equilibria are asymptotically stable.

8.2 The case $K < 1$

Now $c^2K^2 - 4cK^2 + 2cK + 1 > 0$ for every $c > 0$. If $0 < c < \frac{1}{K}$ then $1 - cK > 0$ and because of $1 - cK < \sqrt{c^2K^2 - 4cK^2 + 2cK + 1}$ we get one positive nontrivial equilibrium with total population quantity

$$P_1 = \frac{1 - cK + \sqrt{c^2K^2 - 4cK^2 + 2cK + 1}}{2cK}.$$

For $c \geq \frac{1}{K}$ we have $1 - cK \leq 0$ and $1 - cK + \sqrt{c^2K^2 - 4cK^2 + 2cK + 1} \leq 0$ so there aren't any positive equilibria.

The positive equilibrium above tends to zero if c tends to $\frac{1}{K}$ and tends to infinity if c tends to 0. For this positive equilibrium

$$f'_c(P_1) = c - \frac{1}{P_1^2 + 2P_1 + 1} > 0$$

so it is unstable.

The trivial equilibrium is asymptotically stable because $R(0) = K < 1$.

Theorem 8.3 (*Transcritical bifurcation*) There are no positive equilibria for $c \geq \frac{1}{K}$ and for $c < \frac{1}{K}$ there is a curve of equilibria which are unstable and the trivial equilibrium is stable.

8.3 The case $K=1$

Now we have

$$P_1^{1,2} = \frac{(1-c) \pm \sqrt{c^2 - 2c + 1}}{2c}$$

from which we obtain $P_1^1 = 0$ and there exists a nontrivial equilibrium for $c < 1$, namely $P_1^2 = \frac{1}{c} - 1$.

For this positive equilibrium P_1^2 we have

$$f'_c(P^2) = c - \frac{1}{\left(\frac{1-c}{c}\right)^2 + 2\frac{1-c}{c} + 1} = c - c^2 > 0,$$

which means that this positive equilibrium P^2 is unstable.

For the trivial equilibrium P_1^1 we have $R(0) = K = 1$, but $f'_c(0) = c - 1$ means that for small P we have $R(P) > 1$ if $c > 1$ and $R(P) < 1$ for $c < 1$. This means that the trivial equilibrium is stable for $c < 1$ and it is unstable for $c > 1$.

Theorem 8.4 (*Transcritical bifurcation*) For $c \geq 1$ we have only the trivial equilibrium, for $c < 1$ a curve of positive unstable equilibria emerges.

8.4 Discussion

In the present section we have considered the well-known age-structured model of Gurtin and MacCamy (1.19), in a special case when the mortality of the individuals is only age-dependent and the fertility function is separable in the variables a of age and P of total population quantity. In that case Th.3.1 shows the stability of the positive equilibrium, while the stability of the trivial equilibrium depends on the constant

$$K = \int_0^m b(a)e^{-\int_0^a m(s)ds} da = R(0)$$

in Th.8.1. We showed that a degenerate transcritical bifurcation occurs, that is for, $K \leq 1$, a curve of positive unstable equilibria bifurcates from the trivial one at the critical parameter value $c_0 = \frac{1}{K}$ and as c tends to 0 the total population quantity at the equilibrium tends to the infinity. For $K > 1$ we have showed that a saddle-node bifurcation occurs at the critical parameter value $c_0 = 2 - \frac{1}{K} - 2\sqrt{1 - \frac{1}{K}}$. For $c < c_0$ two curves of positive equilibria appear from which one contains unstable equilibrium points with total population quantity tending to infinity, and the other curve consists of positive stable equilibrium points.

9 Conclusions

In this dissertation we mainly investigated the stability of structured population dynamical models. Our main tool the characteristic equation, deduced in [16] for the age-structured model and deduced in [11] for the more general size-structured model similarly, enabled us to prove stability results under very general conditions on the vital rate functions. Although our techniques are not new, as we believe, the results which we obtained and their biological interpretation show a significant step toward the understanding of long-time behaviour of such structured models.

As we mentioned earlier there is a good number of interesting open problems, which may describe the directions of the future work. One of the most interesting is the case of a size-structured model with density dependent growth rate, on which other researchers are working heavily as we know. Based on section 5 we strongly believe that in this more general case the linearization procedure can be handled and stability results can be proven with similar methods.

Recently O. Diekmann et al. working with modern functional analytical tools [8],[7],[6] formulate successfully a very general theory for these types of deterministic structured population models. The advantage of their work is the generality, to handle a wide class of models at the same time.

Based on the good number of positive feedback and interest of other researchers working in a similar field we believe that our attempts may represent a reasonable direction of research.

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