Stability condition for a nonlinear size-strucutred model *

Jozsef Z. Farkas†

Department of Differential Equations

Budapest University of Technology and Economics

Budapest H-1521, Hungary

Abstract

In this paper we consider a general non-linear size structured population dynamical model with size and density dependent fertility and mortality rates and with size dependent growth rate. Based on [3] we are able to deduce a characteristic function for a stationary solution of the system in a similar way. Then we establish results about the stability (resp. instability) of the stationary solutions of the system.

Keywords: Structured population dynamics,Stability

*2000 MSC: 92D25, 47D06, 35B35

†E-mail: farkas@math.bme.hu

1 Introduction

The model equation

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

$$\gamma(0)p(0,t) = \int_0^m \beta(a,P(t))p(a,t)da, \;\; t > 0, \tag{1.1}$$

with the initial condition $p(a,0) := p_0(a)$ 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 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 non-linear one. We assume a finite maximal size denoted by m and the size of any newborn is considered to be 0. We make the following general assumptions on these vital rate functions:

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

$\forall x \in [0,\infty) \;\; 0 \le \beta(a,x) \le K < \infty, \; \mu(a,x) \ge 0, \; \int_0^m \mu(a,x)da = \infty.$

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) non-linear age structured model if $\gamma \equiv 1$, (se [5],[6],[1]). This type of model can be derived from fundamental principles as a continuity equation, see e.g. [7],[4].

In [3] a characteristic equation for a stationary solution of the above mentioned age structured model is deduced which enabled us to prove stability (resp. instability) results under relatively general conditions on the vital rates β, μ.

In the present note we are going to deduce the characteristic function for a stationary solution of the more general size structured model. Then we establish sta-

bility (resp. instability) results under general and simply conditions for the vital rate functions.

2 The characteristic equation

If the model (1.1) has a stationary solution denoted by $p_1(a)$ then it has to satisfy the following equations

$$\gamma'(a)p_1(a)+\gamma(a)p_1'(a)=-\mu(a,P_1)p_1(a),\;\; P_1=\int_0^m p_1(a)da,$$

$$\gamma(0)p_1(0)=\int_0^m \beta(a,P_1)p_1(a)da \tag{2.1}$$

from which

$$p_1'(a)=\frac{-\mu(a,P_1)p_1(a)-\gamma'(a)p_1(a)}{\gamma(a)},$$

and we get the solution

$$p_1(a)=p_1(0)e^{-\int_0^a \frac{\mu(s,P_1)+\gamma'(s)}{\gamma(s)}ds}. \tag{2.2}$$

Substituting (2.2) into (2.1) we get

$$1=\frac{\int_0^m \beta(a,P_1)e^{-\int_0^a \frac{\mu(s,P_1)+\gamma'(s)}{\gamma(s)}ds}da}{\gamma(0)}=:Q(P_1) \tag{2.3}$$

what is known as the inherent net reproduction number in the age structured case ($\gamma\equiv 1$).

We can solve equation (2.3) for the single variable P_1 and from the equation

$$P_1=\int_0^m p_1(a)=p_1(0)\int_0^m e^{-\int_0^a \frac{\mu(s,P_1)+\gamma'(s)}{\gamma(s)}ds}da$$

we have the initial value $p_1(0)$.

This way we showed that for any solution P_1 of (2.3) we have exactly one stationary solution $p_1(a)$.

Now introducing the variation for an arbtitrary stationary solution $p_1(a)$

$$u(a,t) := p(a,t) - p_1(a),$$

which satisfies the following differential equation

$$u'_t(a,t) + (\gamma(a)u(a,t))'_a = p'_t(a,t) + (\gamma(a)p(a,t))'_a - (\gamma(a)p_1(a))'_a,$$

and with

$$p'_t(a,t) + (\gamma(a)p(a,t))'_a = -\mu(a,P(t))p(a,t), \;\; (\gamma(a)p_1(a))'_a = -\mu(a,P_1)P_1(a),$$

we get

$$u'_t(a,t) + (\gamma(a)u(a,t))'_a = -\mu(a,P(t))p(a,t) + \mu(a,P_1)p_1(a).$$

After linearizing the right-hand side in P we obtain

$$u'_t(a,t) + (\gamma(a)u(a,t))'_a = -\mu(a,P_1)u(a,t) - \mu'_p(a,P_1)p_1(a)\int_0^m u(a,t)da, \quad (2.4)$$

and for the initial condition

$$u(0,t) = p(0,t) - p_1(0) = \int_0^m \beta(a,P_1)u(a,t)da + \int_0^m \beta'_P(a,P_1)p_1(a)da\int_0^m u(a,t)da. \quad (2.5)$$

Now suppose that the linearized problem has solutions of the form $u(t,a) = e^{\lambda t}U(a)$ substituting this into (2.4) and (2.5) and applying the following notation $\bar{U} = \int_0^m U(a)da$ we get

$$U'(a) = U(a)\frac{-\gamma'(a) - \mu(a,P_1) - \lambda}{\gamma(a)} - \bar{U}\frac{\mu'_P(a,P_1)p_1(a)}{\gamma(a)}, \tag{2.6}$$

$$U(0) = \int_0^m \beta(a,P_1)U(a)da + \bar{U}\int_0^m \beta'_P(a,P_1)p_1(a)da. \tag{2.7}$$

The solution of (2.6)-(2.7) is

$$U(a) = \left(U(0) - \int_0^a \frac{\bar{U}\mu'_P(s,P_1)p_1(s)}{\gamma(s)} e^{\int_0^s \frac{\gamma'(r)+\mu(r,P_1)+\lambda}{\gamma(r)}dr} ds\right) e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)+\lambda}{\gamma(s)}ds}. \tag{2.8}$$

Integrating (2.8) from 0 to m and using the formula $p_1(s) = p_1(0)e^{-\int_0^s \frac{\gamma'(r)+\mu(r,P_1)}{\gamma(r)}dr}$ we obtain

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

whith

$$A_{11}(\lambda) = \int_0^m e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)+\lambda}{\gamma(s)}ds} da,$$

$$A_{12}(\lambda) = -p_1(0)\int_0^m e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)+\lambda}{\gamma(s)}ds} \left(\int_0^a \frac{\mu'_P(s,P_1)}{\gamma(s)} e^{\int_0^s \frac{\lambda}{\gamma(r)}dr} ds\right) da.$$

Substituting the solution $U(a)$ into (2.7) we get

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

where

$$A_{21}(\lambda) = \int_0^m \beta(a,P_1)e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)+\lambda}{\gamma(s)}ds} da$$

$$A_{22}(\lambda) =$$

$$= p_1(0)\int_0^m \left(e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)}{\gamma(s)}ds}\beta'_P(a,P_1) - e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)+\lambda}{\gamma(s)}ds}\beta(a,P_1)\int_0^a \frac{\mu'_P(s,P_1)}{\gamma(s)}e^{\int_0^s \frac{\lambda}{\gamma(r)}dr}ds\right)da.$$

Thus, we get the same linear system as in [3] for $\bar{U}, U(0)$ but with more complicated coefficients:

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

We can formulate the following

Theorem 1 The stationary solution $p_1(a)$ 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).

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

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 [2].

Theorem 2 In the case of $\mu(a,P) = m(a)$, $\beta(a,P)$ general, $\gamma(0) = 1$, the stationary solution $p_1(a)$ is asymptotically stable if $\beta'_P(.,P_1) < 0$, if instead $\beta'_P(.,P_1) > 0$ then it is unstable.

Proof

Let us introduce the following notations:

$$T(a,P_1,\lambda) := e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)+\lambda}{\gamma(s)}ds},\ \ T(a,P_1) := e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)}{\gamma(s)}ds},$$

and

$$T(a,P_1,\lambda) = e^{-\int_0^a \frac{\gamma'(s)+\mu(s,P_1)}{\gamma(s)}ds} e^{-\lambda\int_0^a \frac{1}{\gamma(s)}ds} = T(a,P_1)e^{-\lambda\Gamma(a)},$$

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

$$K(\lambda) = 1 =$$

$$= \frac{P_1}{\int_0^m T(a,P_1)da} \int_0^m T(a,P_1)e^{-\lambda\Gamma(a)}da \int_0^m T(a,P_1)\beta'_P(a,P_1)da +$$

$$+ \int_0^m \beta(a,P_1)T(a,P_1)e^{-\lambda\Gamma(a)}da.$$

Now suppose that $\beta'_P(.,P_1) > 0$ holds. Then we are going to show that the characteristic function has a positive root λ.

The following inequality is true for all $P_1 > 0$

$$K(0) = P_1 \int_0^m T(a,P_1)\beta'_P(a,P_1)da + \gamma(0) > 1$$

because $\gamma(0) = 1$ and $\beta'_P(.,P_1) > 0$ holds.

Additionally we have

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

and the functions μ, β, γ are non-negative 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 $\beta'_P(.,P_1) < 0$ holds, suppose that there exists a root $\lambda = x + iy$ such that $x \geq 0$.

Then

$$1 = Re(K(\lambda)) = \frac{P_1}{\int_0^m T(a,P_1)da} \int_0^m T(a,P_1)e^{-x\Gamma(a)} \cos(y\Gamma(a))da \cdot$$

$$\cdot \int_0^m T(a,P_1)\beta'_P(a,P_1)da + \int_0^m \beta(a,P_1)T(a,P_1)e^{-x\Gamma(a)} \cos(y\Gamma(a))da,$$

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

$$Re(K(\lambda)) \leq$$

$$\leq \frac{P_1}{\int_0^m T(a,P_1)da} \int_0^m T(a,P_1)da \int_0^m T(a,P_1)\beta'_P(a,P_1)da + \int_0^m \beta(a,P_1)T(a,P_1)da =$$

$$= P_1 \int_0^m T(a,P_1)\beta'_P(a,P_1)da + \gamma(0) < 1,$$

a contradiction.

That means that the characteristic equation does not have a root with positive or zero real part if $\beta'_P(.,P_1) < 0$ holds. □

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 can be relied upon perhaps by greaten certainty.

The following theorem generalizes the first part of Th.2., that is we give a condition which implies instability of the equilibrium for general $\mu(a,P),\beta(a,P),\gamma(a)$.

Theorem 3 Suppose $\gamma(0)=1$, then if $Q'(P_1)>0$ holds then the stationary solution $p_1(a)$ with total population quantity P_1 is unstable.

Proof With the notations above we have

$$A_{11}(\lambda)=\int_0^m T(a,P_1,\lambda)da,\ \ A_{21}(\lambda)=\int_0^m \beta(a,P_1)T(a,P_1,\lambda)da,$$

$$A_{12}(\lambda)=-\frac{P_1}{\int_0^m T(a,P_1)da}\int_0^m\left(T(a,P_1,\lambda)\int_0^a \mu_P'(s,P_1)\frac{e^{\lambda\Gamma(s)}}{\gamma(s)}ds\right)da,$$

$$A_{22}(\lambda)=\frac{P_1}{\int_0^m T(a,P_1)da}\int_0^m T(a,P_1)\beta'(a,P_1)-T(a,P_1,\lambda)\beta(a,P_1)\int_0^a\frac{\mu_P'(s,P_1)}{\gamma(s)}e^{\lambda\Gamma(s)}dsda.$$

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

$$K(0)=P_1\int_0^m T(a,P_1)\beta_P'(a,P_1)-T(a,P_1)\beta(a,P_1)\int_0^a\frac{\mu_P'(s,P_1)}{\gamma(s)}dsda+\int_0^m\beta(a,P_1)T(a,P_1)da$$

and observe that the first term on the right hand side is $P_1Q'(P_1)$ so that we have

$$K(0)=P_1Q'(P_1)+1>1.$$

Now we only have to prove that $\lim_{\lambda\to\infty}K(\lambda)=0$ which proves that there exists a real positive root λ. For $A_{11}(\lambda),A_{21}(\lambda)$ we have $\lim_{\lambda\to\infty}A_{11}(\lambda)=\lim_{\lambda\to\infty}A_{21}(\lambda)=0$. For $A_{12}(\lambda)$ consider the function

$$e^{-\int_0^a\frac{\gamma'(s)+\mu(s,P_1)+\lambda}{\gamma(s)}}\int_0^a\frac{\mu_P'(s,P_1)}{\gamma(s)}e^{\lambda\Gamma(s)}=e^{-\int_0^a\frac{\gamma'(s)+\mu(s,P_1)}{\gamma(s)}}\int_0^a\frac{\mu_P'(s,P_1)}{\gamma(s)}e^{\lambda(\Gamma(s)-\Gamma(a))}$$

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 $\lim_{\lambda\to\infty} A_{12}(\lambda) = 0$. So does the second term of $A_{22}(\lambda)$, namely

$$\lim_{\lambda\to\infty} T(a,P_1,\lambda)\beta(a,P_1)\int_0^a \frac{\mu_P'(s,P_1)}{\gamma(s)}e^{\lambda\Gamma(s)}ds = 0.$$

That is we have

$$\lim_{\lambda\to\infty} A_{22}(\lambda) = \frac{P_1}{\int_0^m T(a,P_1)da}\int_0^m T(a,P_1)\beta'(a,P_1)da = C$$

a constant, which completes the proof. □

Remark The condition $Q'(P_1) > 0$ 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 newborns for an individual. Then Th.3. states that for sufficiently close P, $P > P_1$ the net reproduction number is greater than 1, so that the stationary solution cannot be stable. This is not a surprising behaviour again.

At the moment the problem, that whether for $R'(P_1) < 0$ (or even in general in the case of a size structured model for $Q'(P_1) < 0$), the stationary solution is stable, seems to be open.

Acknowledgements The author is thankful to Professor Miklós Farkas.

References

[1] Cushing, J.M.: *An Introduction to Structured Population Dynamics,* SIAM, Philadelphia, PA (1998)

[2] Farkas, J.Z.: Stability conditions for the non-linear McKendrick equations, *Applied Mathematics and Computations* **156** (2004), 771-777

[3] Farkas, M.: On the stability of stationary age distributions, *Applied Mathematics and Computation* **131** (2002), 107-123

[4] Farkas, M.: *Dynamical Models in Biology,* Academic Press (2001)

[5] Gurtin, M.E.; MacCamy, R.C.: Non-linear age-dependent populations dynamics, *Arch. Rat. Mech. Anal.* **54** (1974), 281-300

[6] Iannelli, M.: *Mathematical Theory of Age-Structured Population Dynamics*, Giardini Editori, Pisa (1994)

[7] Metz, J.A.J.; Diekmann, O.: *The Dynamics of Physiologically Structured Populations*, Lecture Notes in Biomath. 68, Springer-Verlag, Berlin, 1986