

# Structured populations: The stabilizing effect of the inflow of newborns from an external source and the net growth rate \*

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## Abstract

We investigate the effect of a positive population inflow of individuals from an external source on the dynamical behaviour of certain physiologically structured population models. We treat a size-structured model with constant inflow and nonlinear birth rate and an age-structured model with nonlinear (density dependent) inflow and linear birth rate. Analogously to the inherent net reproduction rate we introduce a net growth rate and discuss how this net growth rate can be related to our stability/instability conditions.

*Keywords:* Structured population dynamics; population inflow; stability; spectral methods; net reproduction ratio

## 1. Introduction

The following (first) nonlinear McKendrick-type age-structured model was introduced by Gurtin and MacCamy in [15].

$$\begin{aligned} p_t(a, t) + p_a(a, t) + \mu(a, P(t))p(a, t) &= 0, \\ p(0, t) &= \int_0^\infty \beta(a, P(t))p(a, t)da, \\ p(a, 0) &=: p_0(a), \quad P(t) = \int_0^\infty p(a, t)da. \end{aligned} \tag{1.1}$$

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Here the function  $p = p(a, t)$  denotes the density of individuals of age  $a$  at time  $t$ , thus,  $P(t)$  is the total population quantity at time  $t$ .  $\beta$  and  $\mu$  denote the fertility and mortality rates of individuals, respectively, and both of these vital rates depend on both age  $a$  and on the total population size  $P(t)$ .

Following the lead of [21, 22] we studied recently the linearized dynamical behaviour of (1.1) (in the case of a finite maximal age  $m$ ) and several other McKendrick-type age and size-structured population models (see [9, 10, 11, 12, 13]). After the initial steps in [9, 10], we, with T. Hagen, applied semigroup techniques to characterize the linearized dynamical behaviour of initially small perturbations of steady states via roots of an associated characteristic equation. The analytical results (see [21] or [22] for similar semigroup results in the context of other models), most importantly the positivity of the governing linear semigroup, and the special form of the characteristic function, which was first deduced in a different form than in [15] for example in the case of the age-structured model (1.1) in [14], made it possible to derive biologically meaningful conditions in terms of the net reproduction function for the stability (resp. instability) of stationary solutions. All of our stability/instability conditions were intuitively clear and naturally interpretable and were mainly given in terms of the inherent net reproduction function.

Each of the structured population models discussed in [9, 10, 11, 12, 13] (see the well-known monographs on structured population dynamics [5, 7, 16, 19, 22] and the more recent related papers [3, 4, 6], as well for further reference) describe the dynamics of a population living in a closed territory. Thus, the density of newborns (zero or minimal size individuals in the case of size-structured models) is determined by the fertility rate of sexually mature individuals. Since there is no migration, the dynamical behaviour of these type of systems is determined by the fertility, mortality and growth rates which are the main ingredients of these models and the density dependence of these vital rates makes these models nonlinear ones.

One can introduce a positive population inflow  $C$  of newborns in the boundary condition of (1.1), which represents an inflow of newborns (or minimal size individuals for size-structured models) from an external source. Then, beside the vital rates, this inflow can be naturally accounted for the dynamical behaviour of the system, as we will see later. There are several biological motivations for having a population inflow of newborns from an external source. A natural example for such an inflow is the case of migratory fish populations that lie eggs and then move on. Later on the newly hatched fish join a different fish population. Another example underscoring the relevance of this model is the case of fisheries where replenishment of newborn fish is practiced. In fact, models with population inflow have been studied intensively – we just mention the works of [1], [2] and [18] and the references therein where various aspects of related size-structured models were discussed. Recently, in [13] we addressed linear stability questions of a juvenile-adult size-structured model and we discovered and discussed very briefly the stabilizing effects of a positive constant population inflow in the case of density independent mortality and growth rates.

The goal of the present paper is to study rigorously, as far as we know for

the first time in the literature of structured population dynamics, the stabilizing effect of a population inflow in two different important cases of structured population models. First we will treat a linearized size-structured model (treated in [12] in the case of zero inflow) with nonlinear birth rate and constant inflow. In particular, the introduction of the positive constant inflow  $C$  will allow us to relax our stability conditions given in Th.5.7 in [12]. Then, we will introduce a nonlinear age-structured population model and investigate the effects of a nonlinear (density dependent) inflow on the dynamical behaviour of a this model. As an application of Th.5.7 in [17] we will establish the Principle of Linearized Stability for this new age-structured model. We will consider a linear birth rate to highlight the effect of the inflow on the linearized dynamical behaviour of the system but our results can be readily extended to more general cases of vital rates. We will omit some of the technical details, which form a significant part of our analysis, but they are rather straightforward based on [12, 13], and we don't consider them to be important to understand the new phenomena presented in this paper. Motivated by our new stability results for the age and size-structured models with inflow at the end of the paper we introduce the net growth rate function and formulate a very general conjecture.

## 2. A size-structured model with constant inflow

In this section we consider the following size-structured model, treated previously in [12] in the case of  $C = 0$ , with a constant inflow  $C$  of newborns.

$$\begin{aligned} p_t(s, t) + (\gamma(s, P(t))p(s, t))_s + \mu(s, P(t))p(s, t) &= 0 \quad s \in [0, m], \quad t > 0, \\ p(0, t) &= C + \int_0^m \beta(s, P(t))p(s, t)ds \quad t > 0, \\ p(s, 0) &=: p_0(s) \quad s \in [0, m], \\ P(t) &= \int_0^m p(s, t)ds. \end{aligned} \tag{2.1}$$

We make the following general assumptions on the vital rate functions:

$$\mu, \beta \in C^1([0, m] \times [0, \infty)), \quad \beta \geq 0, \quad C \geq 0, \tag{2.2}$$

$$\gamma \in C^2([0, m] \times [0, \infty)), \quad \gamma > 0. \tag{2.3}$$

These assumptions suffice to make the analysis of the linearized problem work. They are, however, generally not strong enough to prove global existence results for the nonlinear problem. In addition, for practical purposes several other biologically relevant assumptions (such as  $\mu > 0$ ) will have to be imposed on these functions.

Model (2.1) is usually considered in the literature (see e.g. [2]) with a boundary condition in the form

$$\gamma(0, P(t))p(0, t) = c(t) + \int_0^m \beta(s, P(t))p(s, t)ds. \tag{2.4}$$

We prefer working with the boundary condition in form of (2.1)<sub>2</sub> (i.e. the second equation of (2.1)) because this (equivalent) boundary condition yields major simplifications in the mathematical analysis of model (2.1).

In fact, one can incorporate the growth rate  $\gamma(0, P(t))$  in the left of equation (2.4) in the right hand side of (2.1)<sub>2</sub> before introducing the inflow  $C$  in (2.1)<sub>2</sub>, i.e. the inflow is introduced in the form of a density (rather than a rate) of minimal size individuals coming from an external source.

Well-posedness of a more general size-structured model (equipped with the usual boundary condition (2.4)) was proved in [18] under some additional assumptions on the vital rates.

In [12], we determined the linearized system of (2.1) in the case of  $C = 0$  by introducing a perturbation  $w(s, t) = w - p - p_*$  for a given positive stationary solution  $p_* = p_*(s)$ . It is easy to see that the linearization of (2.1) around a positive stationary solution  $p_*$  yields the same linearized system, namely we arrive at

$$w_t(s, t) + \gamma(s, P_*) w_s(s, t) + (\gamma_s(s, P_*) + \mu(s, P_*)) w(s, t) + (\gamma_{sP}(s, P_*) p_*(s) + \mu_P(s, P_*) p_*(s) + \gamma_P(s, P_*) p_*'(s)) \bar{W}(t) = 0, \quad (2.5)$$

$$w(0, t) = \int_0^m \left( \beta(s, P_*) + \int_0^m \beta_P(\alpha, P_*) p_*(\alpha) d\alpha \right) w(s, t) ds, \quad (2.6)$$

where we have set

$$\bar{W}(t) := \int_0^m w(s, t) ds \quad \text{and} \quad P_* = \int_0^m p_*(s) ds. \quad (2.7)$$

Eqs. (2.5)–(2.6) are accompanied by the initial condition

$$w(s, 0) = w_0(s), \quad s \in [0, m]. \quad (2.8)$$

In order to determine the eigenvalues of the linearized operator one replaces  $w(s, t)$  by  $W(s)e^{\lambda t}$  in the linearized problem (2.5), (2.6). Then one may arrive at an ODE for  $W$ , which can be easily solved. Then a 2-dimensional homogeneous system for  $W(0)$  and  $\bar{W} = \int_0^m W(s) ds$  is obtained, and the characteristic equation assumes the form (see [12]):

$$1 = K(\lambda) = A_{12}(\lambda) + A_{21}(\lambda)(A_{12}(\lambda) - 1) + A_{11}(\lambda)A_{22}(\lambda), \quad (2.9)$$

where we defined

$$A_{11}(\lambda) := \int_0^m F(\lambda, \mu, \gamma, s) ds, \quad (2.10)$$

$$A_{12}(\lambda) := \int_0^m \beta(s, P_*) F(\lambda, \mu, \gamma, s) ds, \quad (2.11)$$

$$A_{21}(\lambda) := \int_0^m F(\lambda, \mu, \gamma, s) \int_0^s F^{-1}(\lambda, \mu, \gamma, r) G(\mu, \gamma, r) dr ds \quad (2.12)$$

$$A_{22}(\lambda) := \int_0^m \beta_P(s, P_*) p_*(s) ds - \int_0^m \beta(s, P_*) F(\lambda, \mu, \gamma, s) \int_0^s F^{-1}(\lambda, \mu, \gamma, r) G(\mu, \gamma, r) dr ds, \quad (2.13)$$

whith

$$F(\lambda, \mu, \gamma, s) := \exp \left\{ - \int_0^s \frac{\lambda + \gamma_s(r, P_*) + \mu(r, P_*)}{\gamma(r, P_*)} dr \right\}, \quad (2.14)$$

$$G(\mu, \gamma, r) := \frac{p_*(r)(\gamma_{sP}(r, P_*) + \mu_P(r, P_*)) + p'_*(r)\gamma_P(r, P_*)}{\gamma(r, P_*)}. \quad (2.15)$$

We recall the following result from [12]:

**Lemma 2.1** *Let  $p_*$  be a non-trivial, stationary solution corresponding to the population quantity  $P_*$ . Then the function  $K$  defined in Eq. (2.9) has the following properties*

$$K(0) = P_* R'(P_*) + R(P_*) \quad \text{and} \quad \lim_{\lambda \rightarrow \infty} K(\lambda) = 0, \quad (2.16)$$

the limit being taken in  $\mathbb{R}$ .

Here

$$R(P) = \int_0^m \gamma(0, P) \frac{\beta(s, P)}{\gamma(s, P)} \exp \left\{ - \int_0^s \frac{\mu(r, P)}{\gamma(r, P)} dr \right\} ds,$$

is the inherent net reproduction rate. A careful analysis of the characteristic equation (2.9) allowed us to prove the following results:

**Theorem 2.2** *The non-trivial, stationary solution  $p_*$  with corresponding population quantity  $P_*$  is linearly unstable if  $R'(P_*) > 0$ .*

**Theorem 2.3** *Let  $p_*$  be a non-trivial, stationary solution with corresponding population quantity  $P_*$ . Suppose that for  $0 \leq s \leq m$*

$$G(\mu, \gamma, s) \leq 0, \quad (2.17)$$

$$\beta(s, P_*) + \int_0^m \beta_P(\alpha, P_*) p_*(\alpha) d\alpha \geq 0, \quad (2.18)$$

$$\int_0^m p_*(s) \int_0^s G(\mu, \gamma, \alpha) d\alpha ds \geq -1. \quad (2.19)$$

Then  $p_*$  is linearly asymptotically stable if and only if  $R'(P_*) < 0$ .

Conditions (2.17), (2.18) ensure that the linearized system (2.5), (2.6) is governed by a positive semigroup, and the proof of Th.2.3 was based on Lemma 2.1 and we showed that in the case of (2.17), (2.18), (2.19) the characteristic function is monotone non-increasing for  $\lambda \geq 0$ .

Since in the case of model (2.1) we may arrive at the same linearized system (2.5), (2.6) as in the case of  $C = 0$  Lemma 2.1 holds true for a positive stationary solution  $p_*$  of (2.1).

Now, in the case of  $C > 0$  we have:

$$A_{12}(0) = \int_0^m \beta(s, P_*) F(0, \mu, \gamma, s) ds = R(P_*) = 1 - \frac{C}{p_*(0)}. \quad (2.20)$$

Making use of the previous results we can relax our stability criterion  $R'(P_*) < 0$  in the case of model (2.1) and formulate the following:

**Theorem 2.4** *Let  $p_*$  be a positive stationary solution of (2.1) with corresponding population quantity  $P_*$ . Moreover assume that (2.17), (2.18), (2.19) hold. Then, the positive stationary solution  $p_*$  is linearly asymptotically stable if*

$$p_*(0)P_*R'(P_*) < C. \quad (2.21)$$

**Proof.** In the case of (2.17), (2.18) the linearized system (2.5), (2.6) is governed by a positive semigroup (see Th.3.3 in [12]). Thus, it is enough to show that (2.9) doesn't admit a solution  $\lambda \geq 0$ . To this end, we note that, if (2.17), (2.18) and (2.19) hold, then  $K(\lambda)$  can be shown monotone non-increasing for  $\lambda \geq 0$  (see the proof of Th.5.7 in [12]). Taking into account (2.20) and applying Lemma 2.1 we obtain the result.  $\square$

**Remark 2.5** Th.2.4 shows that in case of a positive inflow we can have stability even in the case  $R'(P_*) > 0$ , if the inflow  $C$  is large enough. That is we can have stability even in the case when for sufficiently close  $P$ ,  $P > P_*$  the inherent net reproduction rate is greater than its critical value at which stationary solutions occur. This is quite remarkable on its own right and it might contradict our intuition for the first sight.

Moreover, if we assume that  $\gamma \equiv 1$ , that is (2.1) is an age-structured model, then the stability condition (2.21) can be written as

$$P_*^2 R'(P_*) < CE, \quad (2.22)$$

where

$$E := \int_0^m \pi(a, P_*) da = \int_0^m e^{-\int_0^a \mu(r, P_*) dr} da$$

is the expected lifetime of newborns.

### 3. An age-structured model with nonlinear inflow and linear birth rate

In this section we introduce an age-structured McKendrick-type model with linear birth rate and with a nonlinear inflow of newborns. Namely, we consider the following model:

$$\begin{aligned}
p_t(a, t) + p_a(a, t) + \mu(a, P(t))p(a, t) &= 0 & a \in [0, m], \quad t > 0, \\
p(0, t) &= C(P(t)) + \int_0^m \beta(a)p(a, t)da & t > 0, \\
p(a, 0) &=: p_0(a) & a \in [0, m], \\
P(t) &= \int_0^m p(a, t)da, & 
\end{aligned} \tag{3.1}$$

where we make the assumptions

$$\mu \in C^2([0, m] \times [0, \infty)), \quad 0 \leq \beta \leq B < \infty, \quad 0 < C \in C^2([0, \infty)). \tag{3.2}$$

Note that, in the case of  $C \equiv 0$  (3.1) reduces to the classical Gurtin-MacCamy model (1.1) with finite maximal age  $m$  (and density independent fertility  $\beta$ ). As far as we know, this special kind of model was never considered in the literature before, because the inflow is usually introduced in the form of  $C = C(t)$ , since it is due to an external source and therefore it is assumed to be independent of the standing population. Real world problems may arise, when a density dependent inflow is more realistic. For example when one would like to use (3.1) to model a fish population at a fishery, when the quantity of fish to be replenished depends on the actual population size. Our mathematical motivation to study a density dependent inflow is to see the effects of the nonlinear inflow on the dynamical behaviour of the system.

When we solve (3.1) for a positive stationary solution  $p_*$  we arrive at the following equations:

$$\begin{aligned}
p_*(a) &= p_*(0)e^{-\int_0^a \mu(r, P_*)dr} = p_*(0)\pi(a, P_*), \\
p_*(0) &= C(P_*) + \int_0^m \beta(a)p_*(a)da = C(P_*) + p_*(0) \int_0^m \beta(a)\pi(a, P_*)da.
\end{aligned} \tag{3.3}$$

Thus, for given vital rates  $\beta, \mu$  and inflow rate  $C$  the function  $p_*$  is a positive stationary solution of (3.1) if it is determined by

$$p_*(a) = \frac{P_*\pi(a, P_*)}{\int_0^m \pi(a, P_*)da},$$

with the positive total population quantity  $P_* = \int_0^m p_*(a)da$ , which satisfies the equation

$$1 = \frac{C(P_*) \int_0^m \pi(a, P_*)da}{P_*} + R(P_*), \tag{3.4}$$

where

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

is the well-known inherent net reproduction rate. Note that  $R(P_*) < 1$  since  $C$  is positive, thus system (3.1) admits stationary solutions at lower (than 1) levels of the net reproduction rate.

Next, for a given positive stationary solution  $p_*$  we would like to determine the linearized system of (3.1). The linearization procedure is quite straightforward, (we omit here the details and refer to [12] and [13], where such a linearization procedure was carried out for similar structured models), and we may arrive at the following linear system:

$$\begin{aligned} w_t(a, t) + w_a(a, t) + \mu(a, P_*)w(a, t) + W(t)p_*(a)\mu_P(a, P_*) &= 0, \\ w(0, t) &= \int_0^m (C'(P_*) + \beta(a)) w(a, t) da, \\ W(t) &= \int_0^m w(a, t) da. \end{aligned} \quad (3.5)$$

Applying the same methods as in [12] we can readily show, in the similar way as in Th.2.1 and Th.3.1 of [12], that the linearized problem (3.5) is governed by a  $C_0$  semigroup which is eventually compact. In fact, (3.5) is a simple boundary perturbation of a special case ( $\gamma \equiv 1$ ) of system (2.3)-(2.4) in [12]. Thus, problem (3.5) is well-posed, and the spectrum of the linearized operator consists of eigenvalues of finite multiplicity only, which can be determined via zeros of a characteristic function, see [12],[13],[8],[20] for more details.

Moreover, based on Sect.3 of [12] (see Sect.3 in [21] for similar analysis, as well) it is straightforward that the linearized system (3.5) is governed by a positive semigroup if the following conditions hold:

$$\mu_P(a, P_*) \leq 0 \quad \text{and} \quad C'(P_*) + \beta(a) \geq 0 \quad \text{for} \quad a \in [0, m]. \quad (3.6)$$

The positivity of the governing linear semigroup is the key when addressing stability questions because it allows to restrict ourselves to real calculus when determining the leading zero of the characteristic function.

To determine the eigenvalues of the linearized operator we follow the standard approach and substitute

$$w(a, t) = W(a)e^{\lambda t}, \quad (3.7)$$

into the linearized system (3.5). Then we may arrive at the following equations

$$\begin{aligned} W'(a) + W(a)(\lambda + \mu(a, P_*)) + \bar{W}p_*(a)\mu_P(a, P_*) &= 0, \\ W(0) &= \bar{W}C'(P_*) + \int_0^m \beta(a)W(a)da, \\ \bar{W} &= \int_0^m W(a)da. \end{aligned} \quad (3.8)$$

The solution of (3.8) is obtained easily as

$$W(a) = e^{-\lambda a} \pi(a, P_*) \left( W(0) - \bar{W} \int_0^a \frac{e^{\lambda r}}{\pi(r, P_*)} p_*(r) \mu_P(r, P_*) dr \right). \quad (3.9)$$



Next we substitute the solution (3.9) into the boundary condition (3.8)<sub>2</sub> and we integrate (3.9) from 0 to  $m$ . Then we may arrive at a 2-dimensional homogeneous system for  $W(0)$  and  $\bar{W}$ . Thus, the linearized system (3.5) admits solutions of the form (3.7) if the determinant of this homogeneous linear system is zero, that is when  $\lambda$  satisfies the following characteristic equation:

$$\begin{aligned}
1 = K(\lambda) = & \int_0^m e^{-\lambda a} \beta(a) \pi(a, P_*) da \\
& \times \left( 1 + \int_0^m e^{-\lambda a} p_*(a) \int_0^a e^{\lambda r} \mu_P(r, P_*) dr da \right) \\
& - \int_0^m e^{-\lambda a} p_*(a) \int_0^a e^{\lambda r} \mu_P(r, P_*) dr da \\
& + \int_0^m e^{-\lambda a} \pi(a, P_*) da \left( C'(P_*) - \int_0^m e^{-\lambda a} \beta(a) p_*(a) \int_0^a e^{\lambda r} \mu_P(r, P_*) dr da \right).
\end{aligned} \tag{3.10}$$

**Theorem 3.1** *The positive stationary solution  $p_*$  with total population  $P_*$  is linearly asymptotically stable if*

$$\begin{aligned}
\mu_P(\cdot, P_*) \leq 0, \quad 0 \leq C'(P_*) < (1-k) \frac{C(P_*)}{P_*} - kB, \quad \text{where } k \in (0, 1), \\
\text{and } \int_0^m p_*(a) \int_0^a (-\mu_P(r, P_*)) dr da < k < \frac{C(P_*)/P_*}{C(P_*)/P_* + B} \quad \text{holds.}
\end{aligned} \tag{3.11}$$

**Proof.** Note that, all of the positivity criterions (3.6) are satisfied by (3.11), thus it is enough to show that there is no non-negative (real) solution of (3.10). First we show that  $K(\lambda)$  is monotone non-increasing for  $\lambda \geq 0$ .

$$\begin{aligned}
K'(\lambda) = & \int_0^m a e^{-\lambda a} \beta(a) \pi(a, P_*) da \left( \int_0^m p_*(a) \int_0^a e^{-\lambda(a-r)} (-\mu_P(r, P_*)) dr da - 1 \right) \\
& + \int_0^m p_*(a) \int_0^a (a-r) e^{-\lambda(a-r)} (-\mu_P(r, P_*)) dr da \left( \int_0^m e^{-\lambda a} \beta(a) \pi(a, P_*) da - 1 \right) \\
& - C'(P_*) \int_0^m a e^{-\lambda a} \pi(a, P_*) da \\
& - \int_0^m a e^{-\lambda a} \pi(a, P_*) da \int_0^m \beta(a) p_*(a) \int_0^a e^{-\lambda(a-r)} (-\mu_P(r, P_*)) dr da \\
& - \int_0^m e^{-\lambda a} \pi(a, P_*) da \int_0^m \beta(a) p_*(a) \int_0^a (a-r) e^{-\lambda(a-r)} (-\mu_P(r, P_*)) dr da.
\end{aligned}$$

It is easy to see that all of the five terms on the right hand side of the previous equation are non-positive for  $\lambda \geq 0$  if (3.11) holds, thus  $K(\lambda)' \leq 0$  for  $\lambda \geq 0$ .

Secondly, it follows from the definition of  $R(P_*)$  and from (3.11) that

$$\int_0^m \beta(a)\pi(a, P_*)da \left( 1 + \int_0^m p_*(a) \int_0^a \mu_P(r, P_*)drda \right) - \int_0^m p_*(a) \int_0^a \mu_P(r, P_*)drda < R(P_*)(1 - k) + k.$$

Using Hölder's inequality

$$\left\| \beta(a)p_*(a) \int_0^a (-\mu_P(r, P_*))dr \right\|_{L^1(0,m)} \leq \|\beta(a)\|_{L^\infty(0,m)} \left\| p_*(a) \int_0^a (-\mu_P(r, P_*))dr \right\|_{L^1(0,m)}$$

we have

$$\int_0^m \pi(a, P_*)da \left( C'(P_*) - \int_0^m \beta(a)p_*(a) \int_0^a \mu_P(r, P_*)drda \right) \leq \frac{P_*}{p_*(0)} (C'(P_*) + kB),$$

and making use of  $p_*(0) = \frac{C(P_*)}{1-R(P_*)}$  and the condition

$$C'(P_*) < (1 - k) \frac{C(P_*)}{P_*} - kB,$$

we have  $K(0) < 1$ , and the result follows. □

**Remark 3.2** Notice that, if there is no inflow, that is  $C \equiv 0$ , and moreover  $\mu_P(\cdot, P_*) < 0$  holds (which implies  $R'(P_*) > 0$  in the present case) then every positive stationary solution  $p_*$  is unstable by Th.2.2. On the other hand, now we can have stability even in the case of  $R'(P_*) > 0$  and  $C'(P_*) > 0$ , as well.

#### 4. Principle of linearized stability for model (3.1)

In the remarkable paper [17] the author proved the Principle of Linearized Stability (which establishes the rigorous link between the dynamical behaviour of a linearized system and the original nonlinear system) for a very general nonlinear evolution equation of the form

$$\frac{d}{dt}u(t) + Au(t) = 0, \quad t \geq 0,$$

where  $A$  is a quasi- $m$ -accretive operator. He applied his result to the following very general nonlinear age-structured problem:

$$\begin{aligned} u_t(a, t) + u_a(a, t) &= G(u(t, \cdot))(a), & t \geq 0, a \geq 0, \\ u(0, t) &= F(u(t, \cdot)), & t \geq 0, \end{aligned} \quad (4.1)$$

where  $F$  and  $G$  are some continuously Fréchet differentiable operators.

When, for given  $C$ ,  $\beta$  and  $\mu$ , we define:

$$\begin{aligned} K : L^1(0, m) &\rightarrow [0, \infty) \text{ by } K\phi = \int_0^m \phi(a) da, \\ \text{and } F : L^1(0, m) &\rightarrow \mathbb{R}, \quad G : L^1(0, m) \rightarrow L^1(0, m) \\ \text{as } F(\phi) &= C(K\phi) + \int_0^m \beta(a)\phi(a) da, \quad \phi \in L^1(0, m), \\ \text{and } G(\phi)(a) &= -\mu(a, K\phi)\phi(a), \text{ a.e. } 0 < a \leq m, \quad \phi \in L^1(0, m), \end{aligned} \quad (4.2)$$

model (3.1) can be cast in the form of (4.1).

Then, if  $C \in C^2(\mathbb{R})$  and  $\beta \in L^\infty([0, m])$  (i.e.  $\beta$  is bounded) the above defined  $F$  is shown to be continuously Frèchet differentiable in the following sense (see Sect. 5 in [17]).

For any  $\phi \in L^1(0, m)$ , there exists an operator  $DF(\phi) \in \mathcal{L}(L^1, \mathbb{R})$  such that

$$F(\phi + h) = F(\phi) + DF(\phi)h + o_F(h), \quad h \in L^1(0, m),$$

where  $o_F : L^1(0, m) \rightarrow \mathbb{R}$ ,  $|o_F(h)| \leq b_F(r)\|h\|_{L^1}$  for  $\|h\|_{L^1} \leq r$ , and  $b_F : [0, \infty) \rightarrow [0, \infty)$  is a continuous increasing function satisfying  $b_F(0) = 0$ , and there exists an increasing function  $d_F(r) : [0, \infty) \rightarrow [0, \infty)$  such that

$$\|DF(\phi) - DF(\psi)\|_{\mathcal{L}(L^1; \mathbb{R})} \leq d_F(r)\|\phi - \psi\|_{L^1},$$

for  $\|\phi\|_{L^1} \leq r$  and  $\|\psi\|_{L^1} \leq r$ , where  $\|\cdot\|_{\mathcal{L}(L^1; \mathbb{R})}$  stands for the usual operator norm.

Now  $C$  can be written as

$$C(x + h) = C(x) + hC'(x) + h^2 \int_0^m (1 - \theta)C''(x + \theta h)d\theta.$$

Then

$$DF(\phi)h = C'(K\phi)Kh + \int_0^m \beta(a)h(a) da,$$

and

$$o_F(h) = (Kh)^2 \int_0^1 (1 - \theta)C''(K\phi + \theta Kh)d\theta.$$

It is easy to see that  $DF(\phi) : L^1(0, m) \rightarrow \mathbb{R}$  is bounded and linear. If we let

$$b_F(r) = \max_{\xi \in [0, \|\phi\|_{L^1} + r]} |C''(\xi)| r,$$

then  $b_F$  is continuous, increasing,  $b_F(0) = 0$  and

$$o_F(h) \leq b_F(r)\|h\|_{L^1}.$$

Furthermore, we have

$$\|DF(\phi) - DF(\psi)\|_{\mathcal{L}(L^1; \mathbb{R})} \leq d_F(r)\|\phi - \psi\|_{L^1},$$

if  $\|\phi\|_{L^1} \leq r$ ,  $\|\psi\|_{L^1} \leq r$  with

$$d_F(r) = \max_{\xi \in [0, r]} |C''(\xi)|,$$

which is continuous and increasing.

For the Frèchet differentiability of  $G$  (in the similar sense as in the case of  $F$  above), suppose that  $\mu \in L^\infty((0, m) \times \mathbb{R})$  and the mapping  $\xi \mapsto \mu(a, \xi)$  is a  $C^2$ -function for *a.e.*  $a \in (0, m)$  and its first and second order partial derivatives with respect to  $\xi$  denoted by  $\mu'(a, \xi)$  and  $\mu''(a, \xi)$ , respectively, are bounded on  $(0, m) \times \mathbb{R}$ . Then  $G$  can be shown to be continuously Frèchet differentiable. In particular, we have

$$[DG(\phi)h](a) = -\mu'(a, K\phi)\phi(a)Kh - \mu(a, K\phi)h(a),$$

and

$$[o_G(h)](a) = -\mu'(a, K\phi)h(a)Kh - (Kh)^2(\phi(a) + h(a)) \int_0^1 (1-\theta)\mu''(a, K\phi + \theta Kh)d\theta.$$

It is shown  $DG(\phi) : L^1(0, m) \rightarrow L^1(0, m)$ , bounded linear and

$$\|o_G(h)\|_{L^1} \leq b_G(r)\|h\|_{L^1},$$

if  $\|h\|_{L^1} \leq r$  with

$$b_G(r) = r(\|\mu'\|_{L^\infty} + \|\mu''\|_{L^\infty}),$$

which is continuous, increasing and  $b_G(0) = 0$ . Finally, with

$$d_G(r) = \|\mu'\|_{L^\infty} + r\|\mu''\|_{L^\infty},$$

which is continuous and increasing, we have

$$\|DG(\phi) - DG(\psi)\|_{\mathcal{L}(L^1; L^1)} \leq d_G(r)\|\phi - \psi\|_{L^1},$$

if  $\|\phi\|_{L^1} \leq r$ ,  $\|\psi\|_{L^1} \leq r$ , where  $\|\cdot\|_{\mathcal{L}(L^1; L^1)} = \sup_{\|h\|_{L^1} \leq 1} \|\cdot h\|_{L^1}$ , is the usual operator norm again.

Thus, if  $C \in C^2(\mathbb{R})$  and  $\beta$  is bounded, then, as showed above,  $F$  and  $G$  defined in (4.2) are continuously Frèchet differentiable in the sense as in Sect. 5 in [17] thus, Th.5.7 in [17] applies for model (3.1). That is,  $p_*$  is an asymptotically stable positive equilibrium of the nonlinear system (3.1) if the conditions of (3.11) of Th.3.1 are satisfied.

## 5. Heuristic remarks regarding the stability of structured population models and the net growth rate

We found in [12] that in case of the size-structured model (2.1) (with no inflow taking place, i.e.  $C = 0$ ) the inherent net reproduction function has to be defined as

$$R(P) = \int_0^m \beta(s, P) \exp \left\{ - \int_0^s \frac{\gamma_s(r, P) + \mu(r, P)}{\gamma(r, P)} dr \right\} ds \quad (5.1)$$

and it plays a key role in the stability analysis of this basic size-structured model.

In particular, positive equilibrium (or stationary) solutions of the model are in a one-to-one correspondence with positive solutions of equation

$$R(P) = 1, \quad (5.2)$$

that is if  $P_* \in \mathbb{R}^+$  is such that  $R(P_*) = 1$  then

$$p_*(s) = \frac{P_* \exp \left\{ - \int_0^s \frac{\gamma_s(r, P) + \mu(r, P)}{\gamma(r, P)} dr \right\}}{\int_0^m \exp \left\{ - \int_0^s \frac{\gamma_s(r, P) + \mu(r, P)}{\gamma(r, P)} dr \right\}} \quad (5.3)$$

determines a stationary solution of the model uniquely.

Regarding the stability of stationary solutions of the basic size-structured system we were able to prove that  $R'(P_*) > 0$  implies instability of the stationary solution  $p_*$ , in general (Th.2.2). Moreover, in the case when the linearized system is governed by a positive semigroup we were able to prove, under some minor additional assumption, that the stationary solution  $p_*$  with corresponding total population  $P_*$  is linearly asymptotically stable if and only if  $R'(P_*) < 0$  (Th.2.3). We claim that the condition

$$R'(P_*) < 0 \quad (5.4)$$

implies asymptotic stability of the stationary solution  $p_*$  in general in case of the basic size-structured model treated in [12]. Note that, a similar condition characterizes the local asymptotic stability of the trivial steady state, namely  $p_* \equiv 0$  is stable if  $R(0) < 1$  and unstable if  $R(0) > 1$  (see e.g. Prop.3.3 in [16]).

Although at the moment we are not able to prove this claim all of the numerical simulations carried out with the use of the hier-community program, which is available for free download at <http://www.uclouvain.be/~asa5773/>, developed by Prof. Azmy S. Ackleh and his two former students Joel Derouen and Shuhua Hu at the Department of Mathematics of the University of Louisiana at Lafayette, support our claim.

Computer simulations also indicate, that if we slightly modify the vital rates in the way that the value  $R'(P_*)$  (for a certain stationary population size  $P_*$ ) increases but remains negative (obviously we will have different stationary solutions i.e. different solutions of (5.2)) then we experience that the speed of the convergence to the stationary solution decreases and we need to require a higher number of time steps in the simulation, as well. On the other hand,  $R'(P_*) \ll 0$  indicates faster convergence and larger basin of attraction, too. These phenomena indicate also that there should be a relation between not just

the sign of  $R'(P_*)$  but also between the magnitude of  $R'(P_*)$  and the magnitude of the spectral bound of the linearized operator, as well.

In [2] the authors proved that the dynamics of the basic size-structured system is in fact determined at the total population level (see Th.8 in [2]). Let us assume for a moment that the dynamics of the total population can be characterized by an ODE of the form

$$\frac{d}{dt}P = N(P), \quad (5.5)$$

with some "smooth enough" function  $N$ . Then we can rewrite (5.5) in the form

$$\frac{d}{dt}P = (R(P) - 1) \frac{N(P)}{R(P) - 1} =: M(P)(R(P) - 1), \quad (5.6)$$

as long as we can assure that  $M$  defined in (5.6) is bounded over  $\mathbb{R}^+$ . Now if we linearize the right hand side of (5.6) around  $P_*$  we arrive at

$$(R(P_*) - 1)M(P_*) + [(R(P_*) - 1)M'(P_*) + R'(P_*)M(P_*)] [P - P_*] + \text{h.o.t.} \quad (5.7)$$

It should be intuitively clear that  $M \geq 0$  since the total population is increasing if  $R > 1$  and it is decreasing if  $R < 1$  thus  $\text{sign}(N(P)) = \text{sign}(R(P) - 1)$ . The first two terms on the right hand side of (5.7) equal zero, thus the sign of  $R'(P_*)$  determines the local asymptotic stability of the stationary solution  $P_*$  since the higher order terms may be omitted.

At the moment we are unable to give a rigorous proof for our claim, but the main idea can be illustrated in more detail in case of the following simple example. In the case of age independent vital rates (and infinite maximal age  $m$ ), i.e.

$$\beta(s, P) := \beta(P) > 0, \quad \mu(s, P) = \mu(P) > 0, \quad \gamma(s, P) \equiv 1, \quad s \in [0, \infty) \quad (5.8)$$

with some positive and bounded functions  $\beta$  and  $\mu$  it can be readily shown that equation (5.5) takes the form

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

and

$$R(P) = \frac{\beta(P)}{\mu(P)},$$

that is (5.6) takes the form

$$\frac{d}{dt}P = (R(P) - 1)P\mu(P),$$

i.e. the total population is increasing if and only if  $R(P) > 1$  and the positive stationary solution  $p_*$  which corresponds to the total population  $P_*$  is asymptotically stable if  $R'(P_*) < 0$ .

One may notice that the conditions in (3.11) imply surprisingly that  $R'(P_*) \geq 0$ , i.e. it looks like that our claim proves to be false in case of model (3.1) and in general in case of models with inflow. Matter of fact this is not the case, we just need to look at the "right" function i.e. we just need to introduce the concept of the net growth rate. In case of model (3.1) we define the net growth rate  $\tilde{R}$  as follows:

$$\tilde{R}(P) := \frac{C(P) \int_0^m \pi(a, P) da}{P} + R(P), \quad (5.9)$$

where  $R(P)$  is the inherent net reproduction rate as in (5.1). Our motivation is clear: solutions of equation  $\tilde{R}(P) = 1$  are in a one-to-one correspondence with positive stationary solutions of model (3.1).

We claim that for a given positive stationary solution  $p_*$  with total population size  $P_*$  condition  $\tilde{R}(P_*) > 0$  implies instability while  $\tilde{R}(P_*) < 0$  implies the local asymptotic stability of the stationary solution  $p_*$ .

Let us finally consider the special case of age-independent vital rates and density dependent inflow with infinite life span, (i.e.  $a \in [0, \infty)$ )

$$\beta = \beta(P) > 0, \quad \mu = \mu(P) > 0, \quad C = C(P) > 0. \quad (5.10)$$

Then the dynamics at the total population level can be described as

$$\frac{d}{dt}P = C(P) + P(\beta(P) - \mu(P)), \quad (5.11)$$

which can be cast in the form

$$\frac{d}{dt}P = (\tilde{R}(P) - 1)P\mu(P). \quad (5.12)$$

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