STRUCTURED POPULATIONS: IMMIGRATION, (BI)STABILITY AND THE NET GROWTH RATE

JÓZSEF Z. FARKAS

Abstract. We consider a class of physiologically structured population models, a first order nonlinear partial differential equation equipped with a nonlocal boundary condition, with a constant external inflow of individuals. We prove that the linearized system is governed by a quasicontraction semigroup. We also establish that linear stability of equilibrium solutions is governed by a generalized net reproduction function. In a special case of the model ingredients we discuss the nonlinear dynamics of the system when the spectral bound of the linearized operator equals zero, i.e. when linearization does not decide stability. This allows us to demonstrate, through a concrete example, how immigration might be beneficial to the population. In particular, we show that from a nonlinearly unstable positive equilibrium a linearly stable and unstable pair of equilibria bifurcates. In fact, the linearized system exhibits bistability, for a certain range of values of the external inflow, induced potentially by Allée-effect.

Keywords: Structured population dynamics; Population inflow; Bistability; Quasicontraction semigroups, Spectral methods; Net growth rate

1. Introduction

Interest in the modelling and understanding of the dynamics of biological populations is old. Classical, ordinary differential equation models assume homogeneity of individuals within population classes, and therefore involve equations for total population sizes. However, individuals in biological populations differ in their physiological characteristics. Therefore vital rates, such as those of birth, death and development, vary amongst individuals. Structured population modelling tries to account for these differences. It has played a central role in mathematical population dynamics in the past decades, being applied to amongst other systems, fish, water flea, and cell populations. The mathematical modelling of tumour growth and cancer treatment, human demography and the epidemiology of infectious diseases may also involve structured populations. The first step when modelling a population may be to consider a variable that allows one to divide the population into internally homogeneous sub-populations in order to describe the dynamics as the interaction of these groups. This structuring variable may be discrete [7] or continuous [18, 19, 24]
and may be based on age, size, stage of development or life cycle. Traditionally, (continuous) structured population models have been formulated as partial differential equations, starting with the pioneering (first nonlinear) model of Gurtin & MacCamy [17]. Following the lead of [20, 21, 24] we successfully applied the spectral theory of compact/positive operators to formulate biologically interpretable conditions for the linear stability/instability of equilibria for age and size-structured population models (see [11, 13, 14, 15]). Our method allowed us to formulate very general and elegant stability/instability conditions for scramble competition models in terms of certain associated reproduction functions. We shall note that previously, in [22], Rorres formulated linear stability/instability conditions in terms of the derivative of a net reproduction function for positive equilibrium solutions of an age-structured model in the special case when only the fertility depends on the standing population size. We shall also point out that Rorres’ analysis in [22] was not rigorous.

Although traditionally structured population models have been formulated as partial differential equations for population densities, the recent unified approach of Diekmann et al., making use of the rich theory of delay and integral equations, has been resulted in significant results. Most notably the Principle of Linearized Stability has been proven in [8, 9] for a wide class of physiologically structured population models formulated as delay equations (or abstract integral equations).

In the recent papers [12, 15] we investigated analytically the effects of the introduction of a positive influx of newborns on the linearized dynamical behaviour of age and size-structured scramble competition models. In our main result we were able to relax our linear stability conditions given previously in [11, 13] for models without inflow. Motivated by our new stability results we introduced the concept of a net growth rate and formulated a very general conjecture in [12]. One of our goals in the present work is to show that our stability results in [13] can be extended analogously in full generality to size-structured scramble competition models with (constant) inflow at birth using the recently introduced concept of the net growth rate.

In particular, in the present paper we consider the following nonlinear first order partial differential equation.

\[
\frac{d}{dt}(s, t) + \left( \frac{\beta(s, P(t))p(s, t)}{s} - \frac{\mu(s, P(t))p(s, t)}{s} \right) = -\mu(s, P(t))p(s, t), \quad t > 0, \quad s \in (0, m), \quad m < \infty.
\]

Equation (1) is equipped with the following nonlinear nonlocal boundary condition representing the influx of individuals into the population

\[
\gamma(0, P(t))p(0, t) = C + \int_0^m \beta(s, P(t))p(s, t) \, ds, \quad t > 0, \quad 0 \leq C < \infty,
\]

and is subject to the initial condition

\[
p(s, 0) =: p_0(s), \quad s \in (0, m).
\]

Here, the function \( p = p(s, t) \) denotes the density of individuals of size \( s \) at time \( t \), hence \( P(t) \) gives the total population quantity at time \( t \). \( \beta, \mu \) and \( \gamma \) denote the fertility, mortality and development rates of individuals, respectively, and all of these vital rates depend on both the structuring variable \( s \) and on the
total population size $P(t)$. We make the following general assumptions on these vital rate functions:

\[ \mu, \beta \in C^1([0, m] \times [0, \infty)), \quad \beta, \mu \geq 0, \quad \gamma \in C^2([0, m] \times [0, \infty)), \quad \gamma > 0. \]

From the biological point of view it is natural to assume a finite maximal size $m$ which in turn helps to avoid mathematical difficulties regarding the spectral analysis of the linearized system (see e.g. [16]). $C$ represents an inflow of minimal size individuals, i.e. an inflow of individuals from an external source at birth. Note that from the modelling point of view it might be much more natural to assume that immigrants are distributed over all possible sizes. We will discuss this scenario in the last section but throughout this paper our interest is focused on the dynamical behaviour of model (1)-(3). There are several biological motivations for having a population inflow of individuals from an external source. In a discrete model the inflow might represent artificial stocking of individuals at certain life cycle stages for example in an insect population. In [23] Smith treated a nonlinear stage-structured matrix model with stocking and he applied his results to the celebrated "LPA model for the flour beetle Tribolium" to discover some interesting phenomenon due to the stocking. In the continuous setting, in which we are interested, a natural example for such an inflow is the case of migratory fish populations (such as a number of salmon species) that lie eggs and then move on to a different habitat. Later on the newly hatched fish join a different local population. Another example underscoring the relevance of this model is the case of fisheries where stocking of newborn (minimal size) fish is practiced. In this scenario we can regard the inflow $C$ as a control parameter in our system.

Model (1)-(3) was previously studied in [3] by Calsina and Saldana. They established global well-posedness and also investigated the asymptotic behaviour of solutions. In particular, they showed that under certain conditions on the vital rates (1)-(3) is governed by a strongly continuous semigroup which admits a compact global attractor. Most notably, they obtained conditions on the model ingredients which guarantee convergence of solutions to a stationary distribution when the total population tends to a constant. In contrast, our paper focuses on the local asymptotic stability of equilibrium solutions of system (1)-(3) with particular regards to the effects of the population inflow on the dynamical behaviour of the system. First, we will prove the existence of a quasicontraction semigroup describing the evolution of solutions of the linearized system. Then we will give stability/instability criterions for positive equilibrium solutions of (1)-(3). These stability results can be established following completely parallel lines of discussion contained in [13]. Then, utilizing the stability results and a “naive” approach, we will investigate the nonlinear dynamics of the model in a special case of model ingredients. In particular we will treat the case when, in the absence of inflow, the strictly dominant eigenvalue of the linearized operator is zero. We will then show, through a concrete example, that the introduction of the inflow induces bistability in the system. Our claims will be supported by numerical examples, as well.
2. Equilibrium solutions, semigroup existence and linear stability

In this section we investigate the existence and linear stability of equilibrium solutions of (1)-(3). Our discussion mainly follows similar developments in [12, 13]. We note that (1)-(3) admits the trivial solution if and only if \( C = 0 \).

When we solve (1)-(2) for a positive stationary solution \( p \) we arrive at the following equations:

\[
p_*(s) = p_*(0) \pi(s, P_*)
\]

\[
\gamma(0, P_*) p_*(0) = C + \int_0^m \beta(s, P_*) p_*(s) \, ds = C + p_*(0) \int_0^m \beta(s, P_*) \pi(s, P_*) \, ds,
\]

where

\[
\pi(s, P_*) = \exp \left\{ - \int_0^s \frac{\gamma_1(r, P_*) + \mu(r, P_*)}{\gamma(r, P_*)} \, dr \right\}.
\]

Thus, for given vital rates \( \beta, \mu, \gamma \) and inflow \( C \) the function \( p_* \) is a positive stationary solution of (1)-(3) if it is determined by

\[
p_*(s) = \frac{P_* \pi(s, P_*)}{\int_0^m \pi(s, P_*) \, ds}, \quad s \in (0, m),
\]

with the positive total population quantity

\[
P_* = \int_0^m p_*(s) \, ds,
\]

which satisfies the equation

\[
\gamma(0, P_*) P_* = C \int_0^m \pi(s, P_*) \, ds + P_* \int_0^m \beta(s, P_*) \pi(s, P_*) \, ds.
\]

Then, if for fixed \( C \in [0, \infty) \) we define the net growth rate \( Q_C \) for \( P \in (0, \infty) \) as follows:

\[
Q_C(P) = \frac{1}{\gamma(0, P)} \left( C \, P^{-1} \int_0^m \pi(s, P) \, ds + \int_0^m \beta(s, P) \pi(s, P) \, ds \right),
\]

it is easily shown that positive equilibrium solutions of (1)-(3) are in a one-to-one correspondence with positive solutions \( P_* \) of equation

\[
Q_C(P) = 1.
\]

Next we note that

\[
\frac{1}{\gamma(0, P)} \int_0^m \beta(s, P) \pi(s, P) \, ds = \int_0^m \frac{\beta(s, P)}{\gamma(s, P)} \exp \left\{ - \int_0^s \frac{\mu(r, P)}{\gamma(r, P)} \, dr \right\} \, ds
\]

\[
= \int_0^m \beta(a, P) \exp \left\{ - \int_0^a \mu(r, P) \, dr \right\} \, da
\]

by changing variables from size \( s \) to age \( a \) using the relation

\[
\frac{ds}{da} = \gamma(s(a), \).
\]
Hence the function $R$, defined by

$$R(P) = \frac{1}{\gamma(0,P)} \int_0^m \beta(s,P) \pi(s,P) \, ds = Q_0(P),$$

is the well-known inherent net reproduction function, i.e. the expected number of newborns to be produced by an individual in her lifetime when the population size is $P$. We also notice that $CP^{-1}$ is the per capita inflow and by (13) we have

$$L = \frac{1}{\gamma(0,P)} \int_0^m \pi(s,P) \, ds = \int_0^a \mu(r,P) \, dr \right\} \, da,$$

where $L$ is in turn the expected lifetime of an individual. Therefore (10) can be rewritten as

$$Q_C(P) = \int_0^m \left( C P^{-1} + \beta(a,P) \right) \exp \left\{ - \int_0^a \mu(r,P) \, dr \right\} \, da.$$

It is straightforward to verify that the rather natural assumption

$$\lim_{P \to \infty} R(P) = 0,$$

yields a sufficient condition for the existence of at least one positive solution of equation (11) and in turn for the existence of at least one positive equilibrium solution $p^*$ of (1)-(3) via formula (7).

Given a positive stationary solution $p^*$ of system (1)-(3), we introduce the perturbation $u = u(a,t)$ of $p$ by making the ansatz $p = u + p^*$. Then we are using Taylor series expansions of the vital rates to arrive at the linearised problem (see e.g. [13])

$$u_t(s,t) + \gamma(s,P^*) u_s(s,t) + (\gamma_s(s,P^*) + \mu(s,P^*)) \, u(s,t)$$

$$+ (\gamma_p(s,P^*) p^*_s(s) + \mu_p(s,P^*) p^*_s(s) + \gamma_p(s,P^*) p^*_s'(s)) \, \overline{U}(t) = 0,$$

(19)

$$u(0,t) = \int_0^m \left( \frac{\beta(s,P^*) - \gamma_p(0,P^*) p^*_s(0) + \int_0^m \beta_p(r,P^*) p^*_s(r) \, dr}{\gamma(0,P^*)} \right) u(s,t) \, ds$$

where we have set

$$\overline{U}(t) = \int_0^m u(s,t) \, ds.$$

Eqs. (18)–(19) are accompanied by the initial condition

$$u(s,0) =: u_0(s).$$

We observe that the linearised system (13)-(21) is completely equivalent (with a minor change in notations) to the one we obtained in [13] for model (1)-(3) without inflow. Hence we may invoke the results from [13] on the existence and regularity properties of the governing linear semigroup. In particular in [13] we used a perturbation result due to Desch and Schappacher to establish the existence of a governing linear semigroup. Here we give an alternative proof, which also shows that the governing semigroup is actually a quasicontractive one. We follow closely similar developments presented in [21]. To this end, we
cast the linearised system \([13]-[21]\) in the form of an abstract Cauchy problem on the state space \(\mathcal{X} = L^1(0, m)\) as follows:

\[
\frac{d}{dt} u = (\mathcal{A} + B + C) u, \quad u(0) = u_0,
\]

where

\[
\mathcal{A}u = -\gamma(\cdot, P_s) u_s \quad \text{with domain } \text{Dom}(\mathcal{A}) = \{u \in W^{1,1}(0, m) \mid u(0) = \Phi(u)\},
\]

\[
B u = - (\gamma_s(\cdot, P_s) + \mu(\cdot, P_s)) u \quad \text{on } \mathcal{X},
\]

\[
C u = - (\gamma_s p(\cdot, P_s) p_s + \mu p(\cdot, P_s) p_s + \gamma p(\cdot, P_s) p_s') \int_0^m u(s) \, ds = \rho_s(\cdot) \int_0^m u(s) \, ds \quad \text{on } \mathcal{X},
\]

\[
\Phi(u) = \int_0^m \left( \frac{\beta(s, P_s) - \gamma_P(0, P_s) p_s(0) + \int_0^m \beta_P(r, P_s) p_s(r) \, dr}{\gamma(0, P_s)} \right) u(s) \, ds \quad \text{on } \mathcal{X}.
\]

**Theorem 1.** The operator \(\mathcal{A} + B + C\) generates a strongly continuous \((C_0\) for short) quasicontraction semigroup \(\{T(t)\}_{t \geq 0}\) of bounded linear operators on \(\mathcal{X}\).

**Proof.** Recall from [21] that the operator \(\mathcal{A} + B + C = D\) (which is closed and densely defined on \(\mathcal{X}\)) is \(\omega\)-dissipative for some \(\omega \in \mathbb{R}\) if

\[
(Du, u)_- \leq \omega ||u||^2
\]

for all \(u \in \text{Dom}(D)\), where the semi-inner product \((., .)_-\) (or sublinear function) on the Banach space \(\mathcal{X}\) is defined by

\[
(u, w)_- = \min_{x^* \in \mathcal{X}^*} \{ (v, x^*) : ||x^*|| = ||w||, \quad (w, x^*) = ||w||^2 \},
\]

where \((., .)\) stands for the natural pairing between elements of \(\mathcal{X}\) and its dual \(\mathcal{X}^*\) (in our case \(L^1\) and \(L^\infty\)). If we define the operator \(S : L^1 \rightarrow L^\infty\) by

\[
(S u)(s) = ||u||_1 \text{sgn } u(s) \quad \text{then } ||Su||_\infty = ||u||_1 \quad \text{and } (u, Su) = ||u||^2_1,
\]

therefore \((u, v)_- \leq (u, Su)\) if \(u \in \text{Dom}(D)\) we obtain

\[
(Du, u)_- \leq (Du, Su)
\]

\[
= -||u||_1 \int_0^m u(s) \left( \frac{d}{ds} \left[ (\gamma(s, P_s) u(s))_s + \mu(s, P_s) u(s) + \rho_s(s) \int_0^m u(s) \, ds \right] \right) |u(s)|^{-1} \, ds
\]

\[
= -||u||_1 \int_0^m \left( \frac{d}{ds} \left[ (\gamma(s, P_s) u(s))_s + \mu(s, P_s) u(s) + \rho_s(s) \int_0^m u(s) \, ds \right] \right) |u(s)|^{-1} \, ds
\]

\[
\leq -||u||_1 \int_0^m \left( \frac{d}{ds} \left[ (\gamma(s, P_s) u(s))_s + \mu(s, P_s) u(s) + \rho_s(s) \int_0^m u(s) \, ds \right] \right) ds - ||u||^2_1 \inf_{s \in [0, m]} \mu(s, P_s)
\]

\[
\leq -||u||_1 \left( ||\gamma(0, P_s) u(0) || + ||u||^2_1 \left( ||\rho_s||_1 - \inf_{s \in [0, m]} \mu(s, P_s) \right) \right)
\]

\[
\leq ||u||^2_1 \left( ||\beta(., P_s) - \gamma_P(0, P_s) p_s(0) + \int_0^m \beta_P(r, P_s) p_s(r) \, dr \right) \inf_{s \in [0, m]} \mu(s, P_s) + ||\rho_s||_1 - \inf_{s \in [0, m]} \mu(s, P_s) \right)
\]

\[
= ||u||^2_1 \omega,
\]
hence the operator \( D \) is \( \omega \)-dissipative. We observe that the equation

\[(\lambda I - A) u = g\]

for \( g \in X \) and \( \lambda > 0 \) sufficiently large has a unique solution \( u \in \text{Dom}(A) \), given by

\[u(s) = \exp\left\{ -\int_0^s \frac{\lambda}{\gamma(y, P_*)} \, dy \right\} \left( \Phi(u) + \int_0^s \exp\left\{ \int_y^s \frac{\lambda}{\gamma(x, P_*)} \, dx \right\} \frac{f(y)}{\gamma(y, P_*)} \, dy \right),\]

with

\[\Phi(u) = \left( 1 - \Phi\left( \exp\left\{ -\int_0^s \frac{\lambda}{\gamma(y, P_*)} \, dy \right\} \right) \right)^{-1} \Phi\left( \int_0^y \exp\left\{ \int_y^0 \frac{\lambda}{\gamma(x, P_*)} \, dx - \int_0^y \frac{\lambda}{\gamma(y, P_*)} \, dy \right\} \frac{f(y)}{\gamma(y, P_*)} \, dy \right).\]

The fact that \( u \in \text{Dom}(A) \) is well defined by (27), (28) follows immediately from the regularity of the functions involved and their growth behavior. Since \( B + C \) is bounded, the range condition is satisfied. The Lumer-Phillips theorem (see [25]) gives that \( D \) is a generator of a quasicontraction semigroup, which obeys

\[\|T(t)\| \leq e^{\omega t}, \quad t \geq 0.\]

\[\square\]

**Corollary 2.** The proof of Theorem 1 shows that if

\[\inf_{s \in [0,m]} \mu(s, P_*) > \left\| \beta(., P_*) - \gamma P(0, P_*) p_*(0) + \int_0^m \beta P(r, P_*) p_*(r) \, dr \right\|_\infty + \|\rho_*\|_1,\]

holds, then the growth bound \( \omega_0 \) of the semigroup is negative, hence the semigroup \( \{T(t)\}_{t \geq 0} \) is uniformly exponentially stable, see e.g. [10].

**Theorem 3.** Let \( p_* \) be a non-trivial stationary solution with corresponding population quantity \( P_* \). If

\[Q'_C(P_*) > 0\]

then \( p_* \) is linearly unstable. (Note that \( Q'_C \) stands for the derivative of the function \( Q_C \) with respect to \( P \).) On the other hand, suppose that for \( 0 \leq s \leq m \)

\[\rho_*(s) \leq 0,\]

\[\beta(s, P_*) - \gamma P(0, P_*) p_*(0) + \int_0^m \beta P(r, P_*) p_*(r) \, dr \geq 0,\]

\[\int_0^m p_*(s) \int_0^s \left( \frac{\gamma P(r, P_*) + \mu P(r, P_*)}{\gamma(r, P_*)} - \frac{\gamma P(r, P_*) (\gamma_*(r, P_*) + \mu(r, P_*))}{\gamma^2(r, P_*)} \right) \, dr \, ds \geq -1\]

hold. Then, \( p_* \) is linearly asymptotically stable if

\[Q'_C(P_*) < 0.\]
We omit the proof of the above theorem since it can be obtained by following the developments in [13] with minor modifications.

3. Nonlinear dynamics and bistability

In [13] our aim was to formulate linear stability/instability conditions for the model (1)-(3) in the absence of inflow. Therefore, the case $R'(P_*) = Q'_0(P_*) = 0$ was left completely untreated. In this case, zero is an eigenvalue of the linearized operator (see [13]). If conditions (31)-(33) also hold true, then zero is in fact a strictly dominant eigenvalue, hence linearisation does not decide stability. The goal of the present section is to consider this interesting and rather difficult case. To our knowledge there are a very few results in the literature (see [6]) which treat the case when the spectral bound of the linearized operator equals zero. We point out that our discussion will be less rigorous and some of the details need to be elaborated. For basic concepts and results used throughout this chapter we refer the reader to [2, 5, 10].

For the rest of the section we assume that conditions (31)-(33) hold true. We invoke from [13] that the semigroup $\{T(t)\}_{t \geq 0}$ generated by the operator $A + B + C$ is eventually compact. It follows that $\sigma(A + B + C)$, the spectrum of the linearized operator $A + B + C$, consists of isolated eigenvalues of finite (algebraic) multiplicity (see e.g. [10]). Therefore we may split the spectrum $\sigma(A + B + C)$ into the union of two disjoint closed subsets as follows:

$$\sigma(A + B + C) = \{0\} \cup \left( \sigma(A + B + C) \setminus \{0\} \right).$$

Moreover, $X$ splits into the direct sum of two $\{T(t)\}_{t \geq 0}$-invariant closed subspaces: $Y$ and $Z$. In fact, there exists a spectral decomposition of $X$ with respect to (35). This is because the set $\{0\}$ in (35) is trivially bounded, see e.g. [2]. Note that, in general, the set $\sigma(A + B + C) \setminus \{0\}$ is non-empty, hence the spectral decomposition is not trivial, but the formulation of precise conditions is left for future work. Moreover, we may determine the subspace $Y$ explicitly. Straightforward calculations show that the eigenvalue equation

$$(A + B + C)U = 0$$

subject to

$$U(0) = \int_0^m \left( \frac{\beta(s, P_*) - \gamma P(0, P_*) p_*(0) + \int_0^m \beta P(r, P_*) p_*(r) dr}{\gamma(0, P_*)} \right) U(s) ds,$$

has a one-dimensional solution space spanned by the function

$$F(s) \left( \frac{1 + \int_0^m F(s) \int_0^s \frac{G(r)}{F(r)} dr ds}{\int_0^m F(s) ds} - \int_0^s \frac{G(r)}{F(r)} dr \right) \in L^1(0, m),$$

where

$$F(s) = \exp \left\{ -\int_0^s \frac{\gamma s P(r, P_*) p_*(r) + \mu P(r, P_*) p_*(r)}{\gamma(r, P_*)} dr \right\}, \quad s \in [0, m],$$

and

$$G(r) = \gamma s P(r, P_*) p_*(r) + \mu P(r, P_*) p_*(r) + \gamma P(r, P_*) p_*(r), \quad r \in [0, m].$$
When we look to obtain solutions of the following system:

\[(44)\]

\[
\frac{d}{dt}U = AU,
\]

\[
U(0) = \frac{1}{\gamma(0)} \left( \int_0^m \beta(s, P_*) U(s) \, ds + U^2 \int_0^m \beta_{PP}(s, P_*) p_*(s) \, ds \right),
\]

which is \((A + B + C)\)-invariant, is the centre eigenspace. We note that the set \(\sigma(A + B + C) \setminus \{0\}\) is contained in the half plane \(H_\delta = \{ z \in \mathbb{C} : \text{Re}(z) < \delta \}\) for some \(\delta < 0\). This, and the existence of the spectral decomposition implies that the semigroup \(\{S(t)\}_{t \geq 0}\), which is the restriction of \(\{T(t)\}_{t \geq 0}\) to \(Z\) is uniformly exponentially stable (see e.g. \([2]\)). There exists a centre manifold (see e.g. \([5]\)), but it cannot be determined explicitly since the eigenvalues of \(A + B + C\) (and in turn the corresponding eigenspaces) are not explicitly available (except the zero eigenvalue).

In the rest of the section we restrict our attention to the special case of vital rates:

\[(42)\]

\[
\mu = \mu(s), \quad \gamma = \gamma(s), \quad \beta = \beta(s, P), \quad s \in [0, m], \quad P \in [0, \infty),
\]

and we further assume that

\[(43)\]

\[
R'(P_*) = \int_0^m \beta p(s, P_*) \exp \left\{ - \int_0^s \frac{\gamma(s) + \mu(r)}{\gamma(r)} \, dr \right\} \, ds = 0,
\]

\[
R''(P_*) = \int_0^m \beta_{PP}(s, P_*) \exp \left\{ - \int_0^s \frac{\gamma(s) + \mu(r)}{\gamma(r)} \, dr \right\} \, ds \neq 0.
\]

In this scenario, equation \((41)\) is linear, and the only nonlinearity arises in the boundary condition \((42)\). Since linearisation does not decide stability we take into account the quadratic term when using Taylor series expansion for the fertility function \(\beta\). We obtain the nonlinear problem:

\[
\frac{d}{dt}U = AU,
\]

\[
U(0) = \frac{1}{\gamma(0)} \left( \int_0^m \beta(s, P_*) U(s) \, ds + U^2 \int_0^m \beta_{PP}(s, P_*) p_*(s) \, ds \right),
\]

When we look to obtain solutions of the following system:

\[(45)\]

\[
AU = \varepsilon, \quad \varepsilon \in \mathbb{R},
\]

\[
U(0) = \frac{1}{\gamma(0)} \left( \int_0^m \beta(s, P_*) U(s) \, ds + U^2 \int_0^m \beta_{PP}(s, P_*) p_*(s) \, ds \right),
\]

we arrive at

\[(46)\]

\[
0 = \varepsilon \int_0^m \beta(s, P_*) F(s) \int_0^s \frac{1}{F(r)} \, dr \, ds + U^2 \int_0^m \beta_{PP}(s, P_*) p_*(s) \, ds,
\]

an equation for \(\overline{U}\). Existence of a (real) solution of \((46)\) is shown to be necessary and sufficient for the existence of a non-trivial solution of \((45)\). This shows that \((45)\) admits solutions only for \(\varepsilon > 0\) or for \(\varepsilon < 0\) depending on the sign of \(R''(P_*)\). This means that the flow generated by the linear operator \(A\) together
with the nonlinear boundary operator in (44) is monotone in a neighbourhood
of $U \equiv 0$, which in turn implies that the equilibrium $p_*$ is unstable.

This claim will be confirmed numerically in case of an example. When we
make the following choice of vital rates:

$$\mu \equiv 1, \quad \gamma \equiv 1, \quad \beta = \frac{P^2 e^{-P} s e^{-s} + 0.5 P^2 e^{-P}}{3e^{-2} - 2e^{-8} - 13e^{-14}} \quad s \in [0, 6],$$

system (1)-(3) admits for $C = 0$ a unique positive equilibrium solution

$$p_*(s) = \frac{2e^{-s}}{1 - e^{-6}}, \quad s \in [0, 6],$$

with total population size $P_* = 2$. It is straightforward to confirm that con-
ditions (31)-(33) hold true and $Q_0'(P_*) = R'_0(P_*) = 0$, $Q_0''(P_*) = R''_0(P_*) < 0$
since $\beta_{PP}(s, P_*) < 0$ holds for $s \in [0, 6]$. For $C = 0$ we have $Q_0(0) = 0 < 1$
which implies that the trivial equilibrium is locally asymptotically stable (see
e.g. [13]). The positive equilibrium $p_*$ given by (48) is nonlinearly unstable.

When we introduce the inflow, at $C = 0$ a pair of equilibria, denoted by $p^1_*$
and $p^2_*$, bifurcates from the positive equilibrium $p_*$. We may assume that

$$P^1_* = \int_0^m p^1_*(s) \, ds < P^2_* = \int_0^m p^2_*(s) \, ds.$$

Then, it is easily shown that $Q'_C(P^2_*) < 0$ holds, and conditions (31)-(33)
are satisfied. Hence the equilibrium $p^2_*$ is linearly stable while $p^1_*$, for which
$Q'_C(P^1_*) > 0$ holds, is linearly unstable by Theorem 3. The third positive
equilibrium, which is “connected” to the trivial one, satisfies also the stability
conditions of Theorem 3 hence it remains locally asymptotically stable. The
system is bistable for $C \in (0, C_*)$ for some $C_*>0$. This bistability is induced
potentially by an Allée-type effect. When $C$ reaches the critical value $C_*$ the
system undergoes another bifurcation. This is illustrated in Figure 1.

In Figure 2, we present the results of some numerical simulations. We
used the hier-community program which solves equations (1)-(3) using a finite
Structured Populations: Immigration, (Bi)Stability and the Net Growth Rate

difference scheme approximation, see [1]. It is developed by A. S. Ackleh and his collaborators and it is available at the author’s web page.

Figure 2. In the first column we plotted the evolution of the solution and its integral starting with the initial condition \( p_0(x) = \frac{1.9e^{-x}}{1 - e^{-6}} \), and the graph of the net reproduction rate \( R \), respectively. (Here \( x \) replaces the structuring variable \( s \).) In the second column we plotted again the evolution of the solution and its integral starting with the initial population distribution \( p_0(x) = \frac{0.7e^{-0.4x}}{1 - e^{-6}} \), and the graph of net growth rate \( Q \), in the case of \( C = 0.2 \).

4. Concluding remarks

As we noted earlier, introduction of an external inflow only at birth may seem rather artificial and less satisfying from the modelling point of view. It may be much more natural to assume that immigrants are distributed over all possible sizes. In the following we propose a model which incorporates migration of individuals at all possible sizes.

Assume that we would like to study the dynamics of a population living on two distinct patches, where resources over the two patches may be different but we assume that the population is homogeneous in space over each of the
patches. Let us consider the following set of model equations:

\[
p_i(s, t) + \left( \gamma(s, P(t))p(s, t) \right)_s = -\mu(s, P(t))p(s, t) + C_1(s, E_1(s, t), E_2(s, t)) - C_2(s, E_1(s, t), E_2(s, t)),
\]

\[
\gamma(0, P(t))p(0, t) = \int_0^m \beta(s, P(t))p(s, t) \, ds, \quad P(t) = \int_0^m p(s, t) \, ds,
\]

\[
p(s, 0) =: p_0(s), \quad E_1(s, t) = \int_0^s \alpha_1(y)p(y, t) \, dy + \int_s^m \alpha_2(y)p(y, t) \, dy,
\]

\[
q_i(s, t) + \left( \tilde{\gamma}(s, Q(t))q(s, t) \right)_s = -\bar{\mu}(s, Q(t))q(s, t) - C_1(s, E_1(s, t), E_2(s, t)) + C_2(s, E_1(s, t), E_2(s, t)),
\]

\[
\tilde{\gamma}(0, Q(t))q(0, t) = \int_0^m \bar{\beta}(s, Q(t))q(s, t) \, ds, \quad Q(t) = \int_0^m q(s, t) \, ds,
\]

(50) \quad q(s, 0) =: q_0(s), \quad E_2(s, t) = \int_0^s \alpha_3(y)q(y, t) \, dy + \int_s^m \alpha_4(y)q(y, t) \, dy,

where

(51) \quad \gamma, \tilde{\gamma} > 0, \quad \mu, \beta, \bar{\mu}, \bar{\beta}, C_1, C_2, \alpha_i \geq 0, \quad i = 1..4, \quad m < \infty.

We assume that individuals living on the two patches have different vital rates due to different environmental conditions and that there is scramble competition between individuals on each of the patches e.g. for available resources, which influences their fertility, mortality and growth rates. Individuals can move between patches at any stage in their life and movement between patches is assumed to be instantaneous. \(C_1\) represents the inflow of individuals into patch one from patch two while \(C_2\) the outflow from patch one into patch two. The probability of movement from patch one to patch two and vica-versa of individuals of size \(s\) at time \(t\) depends in general on the sum of the weighted population sizes, denoted by \(E_1\) and \(E_2\), of “smaller” and “bigger” individuals present at time \(t\) on each of the patches. Note that it would be natural to assume that \(C_1\) depends only on \(E_2\) and \(C_2\) on \(E_1\) since individuals on patch one probably do not have any information about environmental conditions on patch two and vica-versa. The general form of \(C_1\) and \(C_2\) is intended to allow to describe different scenarios of competition effects which influence the migration of individuals. For example the case \(\alpha_1 \equiv \alpha_2, \alpha_3 \equiv \alpha_4\) represents scramble competition, while the case \(\alpha_1 \equiv \alpha_3 \equiv 0\) represents effects of size related hierarchy in migration.

In [4] existence and uniqueness results for a very general model of physiologically structured populations, which incorporates recruitment of individuals into the population at all possible sizes, were established. However, in the model treated in [4] it was assumed that recruitment of individuals into the population is due to birth only. This assumption also results in a zero influx of individuals through the boundary, namely at \(s = 0\). The analysis of system [5] may be a subject of future investigations.

Acknowledgment
The author was supported by the EPSRC grant EP/F025599/1 and by a Royal Society Conference Grant 2007/R4.

REFERENCES

[1] A. S. Ackleh, K. Deng, and S. Hu, A quasilinear hierarchical size-structured model: well-posedness and approximation, *Appl. Math. Optim.* **51** (2005), 35–59.

[2] W. Arendt, A. Grabosch, G. Greiner, U. Groh, H. P. Lotz, U. Moustakas, R. Nagel, F. Neubrander and U. Schlotterbeck, *One-parameter semigroups of positive operators*, Springer-Verlag, Berling, (1986).

[3] Á. Calsina and J. Saldana, A model of physiologically structured population dynamics with a nonlinear individual growth rate, *J. Math. Biology* **33** (1995), 335–364.

[4] Á. Calsina and J. Saldana, Basic theory for a class of models of hierarchically structured population dynamics with distributed states in the recruitment, *Math. Models Methods Appl. Sci.* **16** (2006), 1695-1722.

[5] J. Carr, *Applications of centre manifold theory*, Springer-Verlag, New York-Berlin, (1981).

[6] C. B. Clemons, S. I. Hariharan and D. D. Quinn Amplitude equations for time-dependent solutions of the McKendrick equations *SIAM J. Appl. Math.* **62** (2001), 684-705.

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

[8] O. Diekmann and M. Gyllenberg, *Abstract delay equations inspired by population dynamics*, in “Functional Analysis and Evolution Equations” (Eds. H. Amann, W. Arendt, M. Hieber, F. Neubrander, S. Nicaise and J. von Below), Birkhäuser, (2007), 187–200.

[9] O. Diekmann, Ph. Getto and M. Gyllenberg, Stability and bifurcation analysis of Volterra functional equations in the light of suns and stars, *SIAM J. Math. Anal.* **39** (2007), 1023–1069.

[10] K.-J. Engel and R. Nagel, *One-Parameter Semigroups for Linear Evolution Equations*, Springer, New York 2000.

[11] J. Z. Farkas, On the linearized stability of age-structured multispecies populations, *J. Appl. Math.* (2006), Article ID 60643.

[12] J. Z. Farkas, Structured populations: The stabilizing effect of the inflow of newborns from an external source and the net growth rate, *Appl. Math. Comput.* **199** (2008), 547-558.

[13] J. Z. Farkas and T. Hagen, Stability and regularity results for a size-structured population model, *J. Math. Anal. Appl.* **328** (2007), 119-136.

[14] J. Z. Farkas and T. Hagen, Stability and positivity results for a generalized size-structured *Daphnia* model with inflow, *Appl. Anal.* **86** (2007), 1087-1103.

[15] J. Z. Farkas and T. Hagen, Asymptotic behaviour of size-structured populations via juvenile-adult interaction, *Discrete Cont. Dyn. Syst. Ser. B* **9** (2008), 249-266.

[16] J. Z. Farkas and T. Hagen, Asymptotic analysis of a size-structured cannibalism model with infinite dimensional environmental feedback, submitted.

[17] M. E. Gurtin and R. C. MacCamy, Non-linear age-dependent population dynamics, *Arch. Rat. Mech. Anal.* **54** (1974), 281–300.

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

[19] J. A. J. Metz and O. Diekmann, *The Dynamics of Physiologically Structured Populations*, Springer, Berlin, 1986.

[20] J. Prüff, Equilibrium solutions of age-specific population dynamics of several species, *J. Math. Biol.* **11** (1981), 65–84.

[21] J. Prüff, Stability analysis for equilibria in age-specific population dynamics, *Nonlin. Anal. TMA* **7** (1983), 1291–1313.

[22] C. Rorres, Local stability of a population with density-dependent fertility, *Theoret. Population Biol.* **16** (1979), 283-300.

[23] H. L. Smith, The discrete dynamics of monotonically decomposable maps, *J. Math. Biol.* **53** (2006), 747-758.
[24] G. F. Webb, *Theory of Nonlinear Age-Dependent Population Dynamics*, Marcel Dekker, New York, (1985).

[25] K. Yosida, *Functional analysis*, Springer, Berlin, 1995.

Department of Computing Science and Mathematics, University of Stirling, Stirling, FK9 4LA, UK

E-mail address: jzf@maths.stir.ac.uk