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PHYSIOLOGICALLY STRUCTURED POPULATIONS WITH DIFFUSION AND DYNAMIC BOUNDARY CONDITIONS

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Abstract. We consider a linear size-structured population model with diffusion in the size-space. Individuals are recruited into the population at arbitrary sizes. We equip the model with generalized Wentzell-Robin (or dynamic) boundary conditions. This approach allows the modelling of populations in which individuals may have distinguished physiological states. We establish existence and positivity of solutions by showing that solutions are governed by a positive quasicontractive semigroup of linear operators on the biologically relevant state space. These results are obtained by establishing dissipativity of a suitably perturbed semigroup generator. We also show that solutions of the model exhibit balanced exponential growth, that is, our model admits a finite-dimensional global attractor. In case of strictly positive fertility we are able to establish that solutions in fact exhibit asynchronous exponential growth.

1. **Introduction.** A significant amount of interest has been devoted to the analysis of mathematical models arising in structured population dynamics (see e.g. [21, 27] for references). Such models often assume spatial homogeneity of the population in a given habitat and only focus on the dynamics of the population arising from differences between individuals with respect to some physiological structure. In this context, reproduction, death and growth characterize individual behavior which may be affected by competition, for example for available resources.

In a recent paper, Hadeler [18] introduced size-structured population models with diffusion in the size-space. The biological motivation is that diffusion allows for "stochastic noise" to be incorporated in the model equations in a deterministic fashion. The main question addressed in [18] is what type of boundary conditions are necessary for a biologically plausible and mathematically sound model. In this context some special cases of a general Robin boundary condition were considered. Diffusion terms have been introduced into structured population models by Waldstätter *et al.* [26], Milner and Patton [22] and Langlais and Milner [20] in the context of host-parasite models, where the parasite load is the continuous structure variable. For example, when the structuring variable represents a parasite load as

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in [26], at least one special compartment of individuals arises, namely the class of the uninfected ones. In a model where the structuring variable is continuous this state corresponds to a set of measure zero, hence it does not carry mass. The true meaning and advantage of employing Wentzell boundary conditions is that it allows this special state to carry mass.

In this paper we introduce the following linear size-structured population model

$$u_t(s,t) + (\gamma(s)u(s,t))_s$$
$$= (d(s)u_s(s,t))_s - \mu(s)u(s,t) + \int_0^m \beta(s,y)u(y,t)\,\mathrm{d}y, \quad s \in (0,m), \tag{1}$$
$$[(d(s)u_s(s,t))_s]_{s=0} - b_0 u_s(0,t) + c_0 u(0,t) = 0, \tag{2}$$
$$[(d(s)u_s(s,t))_s]_{s=m} + b_m u_s(m,t) + c_m u(m,t) = 0, \tag{3}$$

with a suitable initial condition. The function $u = u(s,t)$ denotes the density of individuals of size, or other developmental stage, s at time t. Note that, we use 0 as the minimal value of the variable of s only for mathematical convenience. It may well be replaced by an arbitrary value s_{min}. The non-local integral term in (1) represents the recruitment of individuals into the population. Individuals may have different sizes at birth and $\beta(s,y)$ denotes the rate at which individuals of size y "produce" individuals of size s. Further biologically relevant assumptions may be made on the fertility, such as $\beta(s,y) = 0$ for $s \geq y$, i.e. parents cannot have larger offspring. We also note that from this general model a single state at birth model may be deduced by formally replacing the fertility function β with an appropriate delta function, see e.g. [21]; Chapter I Section 4. μ denotes the size-specific mortality rate while γ denotes the growth rate. d stands for the size-specific diffusion coefficient, which we assume to be strictly positive. b_0 and b_m are positive numbers, while c_0 and c_m are non-negative. We will discuss special values for these constants in Equation (5) below.

Equation (1) describes the evolution of a "proper" size-structured population, in contrast to the one where it is assumed that all newborns enter the population at a minimal size. In that case, assuming that the growth rate is positive, i.e. individuals do not shrink, the linear model can be rewritten as an age-structured model, see e.g. [21]. We also refer the interested reader to [3, 7, 10] where size-structured models with distributed recruitment processes were investigated. We also note that although we refer to the structuring variable s as size, it could well represent any other physiological characteristic of individuals such as accumulated energy or biomass, volume etc. The boundary conditions (2)-(3) are the so called generalized Wentzell-Robin or dynamic boundary conditions. These "unusual" boundary conditions were investigated recently for models describing physical processes such as diffusion and wave propagation, see e.g. [11, 12, 16]. Briefly, they are used to model processes where particles reaching the boundary of a domain can be either reflected from the boundary or they can be absorbed. Hence the boundary points can carry mass. Our goal here is to introduce this rather general type of boundary condition in the context of models describing the evolution of biological populations, with particular focus on positivity and asymptotic behavior of solutions. Potential applications include cell populations with resting states at $s = 0$ and $s = m$, or models for populations structured by an infection level or parasite load [26].

The first works introducing boundary conditions that involve second order derivatives for parabolic or elliptic differential operators go back to the 1950s, see the papers by Feller [13, 14] and Wentzell [24, 25]. These first studies were purely motivated from the mathematical point of view. The original question was to identify the set of all possible boundary conditions that give rise for a parabolic differential operator to generate a contraction semigroup on an appropriate state space. The abstract mathematical analysis gave a clue where physical intuition failed previously.

The boundary conditions (2)-(3) are in general form, and we shall now specify the constants b_0, b_m and c_0, c_m to give a biological explanation for the boundary conditions. Integration of Equation (1) from 0 to m yields for $U(t) = \int_0^m u(s,t)\,\mathrm{d}s$

$$\begin{aligned}\frac{d}{dt}U(t) &= \gamma(0)u(0,t) - \gamma(m)u(m,t) + d(m)u_s(m,t) - d(0)u_s(0,t)\\ &\quad + \int_0^m \int_0^m \beta(s,y)u(y,t)\,\mathrm{d}y\,\mathrm{d}s - \int_0^m \mu(s)u(s,t)\,\mathrm{d}s\\ &=: B(t) - D(t) + \gamma(0)u(0,t) - \gamma(m)u(m,t) + d(m)u_s(m,t) - d(0)u_s(0,t),\end{aligned}$$

where B and D denote the combined birth and death processes, respectively. We note that formally, by replacing the diffusion term by its counterpart from Equation (1), the boundary conditions (2)-(3) can be cast in the *dynamic form*

$$\begin{aligned}u_t(0,t) =& u(0,t)(-\gamma'(0) - \mu(0) - c_0) + u_s(0,t)(b_0 - \gamma(0)) + \int_0^m \beta(0,y)u(y,t)\,\mathrm{d}y,\\ u_t(m,t) =& u(m,t)(-\gamma'(m) - \mu(m) - c_m) + u_s(m,t)\left(-b_m - \gamma(m)\right)\\ &+ \int_0^m \beta(m,y)u(y,t)\,\mathrm{d}y.\end{aligned} \tag{4}$$

These are the governing equations for individuals of minimum and maximum sizes, respectively. It is natural to assume that in the absence of mortality and recruitment, i.e. when $B(\cdot) \equiv D(\cdot) \equiv 0$, the total population size $U(t) + u(0,t) + u(m,t)$ remains constant at every time t. Mathematically, this amounts to the condition

$$\begin{aligned}0 =& \frac{d}{dt}U(t) + u_t(0,t) + u_t(m,t)\\ =& u(0,t)\left(\gamma(0) - \gamma'(0) - c_0\right) + u(m,t)\left(-\gamma(m) - c_m - \gamma'(m)\right)\\ &+ u_s(0,t)\left(b_0 - d(0) - \gamma(0)\right) + u_s(m,t)\left(d(m) - \gamma(m) - b_m\right).\end{aligned}$$

In order to guarantee conservation of total population in the absence of birth and death processes, we make the following assumptions

$$c_0 = \gamma(0) - \gamma'(0),\ c_m = -\gamma(m) - \gamma'(m),\ b_0 = d(0) + \gamma(0),\ b_m = d(m) - \gamma(m). \tag{5}$$

We note that condition (5) together with the assumption that b is positive and c is non-negative impose a restriction on the growth rate γ.

The dynamic boundary conditions (4) can now be written as

$$\begin{aligned}u_t(0,t) &= (-\mu(0) - \gamma(0))u(0,t) + d(0)u_s(0,t) + \int_0^m \beta(0,y)u(y,t)\,\mathrm{d}y,\\ u_t(m,t) &= (\gamma(m) - \mu(m))u(m,t) - d(m)u_s(m,t) + \int_0^m \beta(m,y)u(y,t)\,\mathrm{d}y.\end{aligned} \tag{6}$$

Hence the dynamics of individuals in the two special states $s = 0$ and $s = m$ are governed by equations (6). The meaning of the governing equations (6) is intuitively clear. For example, at $s = 0$, individuals are leaving this compartment due to growth and mortality and are recruited according to the integral term, while the diffusion accounts for the flux through this state (this also yields a loss term, since the outer normal derivative is $-u_s$).

We impose the following assumptions on the model ingredients

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

In this note first we establish existence and positivity of solutions of model (1)-(3). This existence proof follows similar arguments developed in [11, 12]. The significant difference is that solutions to our model are not necessarily governed by a contraction semigroup, hence as in [8, 9] we need to rescale the semigroup to obtain the dissipativity estimate. As a result of the dissipativity calculation, we show that the resolvent operator of the semigroup generator is positive. This was not established in [12].

In Section 3 we investigate the asymptotic behavior of solutions. First we establish that solutions of the model equations exhibit balanced exponential growth, in general. This is an interesting phenomenon, often observed for linear structured population models, see e.g. [8, 10]. In some sense, it is a stability result and characterizes the global asymptotic behavior of solutions to the model. Then, assuming that fertility is strictly positive, we are able to show that after a rescaling by and exponential factor solutions actually tend to a fixed size-distribution. This is shown via establishing irreducibility of the governing semigroup.

2. Existence and positivity of solutions.

In this section we are going to establish the existence of a positive quasicontractive semigroup of operators which governs the evolution of solutions of (1)-(3). For basic definitions and results used throughout this paper we refer the reader to [1, 2, 4, 6]. Let

$$\mathcal{X} = \left(L^1(0,m)\oplus\mathbb{R}^2, ||\cdot||_{\mathcal{X}}\right),$$

where for $(x,x_0,x_m)\in\mathcal{X}$ the norm is given by

$$||(x,x_0,x_m)||_{\mathcal{X}} = ||x||_{L^1} + c_1|x_0| + c_2|x_m|, \tag{7}$$

for some positive constants c_1 and c_2 that we will specify later. Then $\mathcal{X}$ is a Banach lattice. We identify a function $u\in C[0,m]$ with its restriction triple $(u|_{(0,m)}, u(0), u(m))\in\mathcal{X}$. With this identification, the set $C^2[0,m]$ is dense in $\mathcal{X}$ with respect to the $||\cdot||_{\mathcal{X}}$-norm. Let

$$\begin{aligned} D(A) = \big\{u\in C^2[0,m]\,:\,\Psi u\in L^1(0,m),\quad (d(s)u'(s))'\big|_{s=0} - b_0u'(0)+c_0u(0)=0,\\ (d(s)u'(s))'\big|_{s=m} + b_mu'(m)+c_mu(m)=0\big\},\end{aligned}$$

where

$$\Psi u(s) = (d(s)u'(s))' - (\gamma(s)u(s))' - \mu(s)u(s) + \int_0^m \beta(s,y)u(y)\,\mathrm{d}y.$$

The operator A with domain $D(A)$ is then defined by

$$Au = \begin{pmatrix} \Psi u \\ (b_0-\gamma(0))\frac{d}{ds}u\big|_{s=0} + \int_0^m\beta(0,y)u(y)\,\mathrm{d}y - \rho_0u(0) \\ (-b_m-\gamma(m))\frac{d}{ds}u\big|_{s=m} + \int_0^m\beta(m,y)u(y)\,\mathrm{d}y - \rho_mu(m)\end{pmatrix}$$

where we have set

$$\rho_0 = \mu(0)+c_0+\gamma'(0), \quad \rho_m = \mu(m)+c_m+\gamma'(m),$$

for short. We use [6, Theorem 3.15] (see also [2, Section A-II, Theorem 2.11]) which characterizes generators of contractive semigroups via dissipativity. We establish the existence of a quasicontractive semigroup for the general boundary condition (2)-(3). Recall that a strongly continuous semigroup $\{\mathcal{T}(t)\}_{t\geq 0}$ is called *quasicontractive* if $||\mathcal{T}(t)|| \leq e^{\omega t}$ for some $\omega \in \mathbb{R}$ and it is called *contractive* if the choice $\omega \leq 0$ is possible. A linear operator A with domain $D(A)$ is *dissipative*, if for all $x \in D(A)$ and $\lambda > 0$ one has $||(\lambda\mathcal{I} - A)x|| \geq \lambda||x||$.

Theorem 2.1. *Assume that*

$$c_1 = \frac{d(0)}{b_0 - \gamma(0)} > 0, \quad \text{and} \quad c_2 = \frac{d(m)}{\gamma(m) + b_m} > 0. \tag{8}$$

Then the closure of the operator A is the infinitesimal generator of a positive quasicontractive semigroup of bounded linear operators on the state space $\mathcal{X}$ (where the weights in equation (7) are chosen accordingly).

Proof. We introduce the modified operator $\widetilde{A}$ with $\beta = 0$ in the definition of A. For $\lambda > 0$ and $h \in \mathcal{X}, u \in D(\widetilde{A})$ we consider the equation

$$u - \lambda\left(\widetilde{A} - \omega\mathcal{I}\right)u = h, \quad \text{on} \quad [0, m]. \tag{9}$$

That is

$$h(s) = u(s) - \lambda\left((d(s)u'(s))' - (\gamma(s)u(s))' - \mu(s)u(s) - \omega u(s)\right), \quad s \in (0, m), \tag{10}$$

$$\lambda^{-1}h(0) = u'(0)(\gamma(0) - b_0) + u(0)\left(\lambda^{-1} + \gamma'(0) + \mu(0) + c_0 + \omega\right), \tag{11}$$

$$\lambda^{-1}h(m) = u'(m)(\gamma(m) + b_m) + u(m)\left(\lambda^{-1} + \gamma'(m) + \mu(m) + c_m + \omega\right). \tag{12}$$

Next we multiply Equation (10) by $\chi_{u^+}(s)$, where χ_{u^+} denotes the characteristic function of u^+, and integrate from 0 to m. The boundary $\partial[u > 0]$ consists of two parts, $\Gamma_1 = \partial[u > 0] \cap (0, m)$ and $\Gamma_2 = \overline{[u > 0]} \cap \{0, m\}$. The term $d(s)u'(s)$ gives negative contributions on Γ_1 since the outer normal derivative of u is negative. The term $\gamma(s)u(s)$ gives no contributions on Γ_1 since $u = 0$ there. Hence we obtain

$$\begin{aligned} ||u^+||_1 \leq & \lambda\left(\operatorname{sgn}(u^+(m))d(m)u'(m) - \operatorname{sgn}(u^+(0))d(0)u'(0)\right) \\ & - \lambda\left(\operatorname{sgn}(u^+(m))\gamma(m)u(m) - \operatorname{sgn}(u^+(0))\gamma(0)u(0)\right) \\ & - \lambda\int_0^m \chi_{u^+}(s)\mu(s)u(s)\,\mathrm{d}s - \lambda\omega||u^+||_1 + \int_0^m \chi_{u^+}(s)h(s)\,\mathrm{d}s. \end{aligned}$$

This, combined with equations (11)-(12), yields

$$\begin{aligned} & ||u^+||_1 + \operatorname{sgn}(u^+(m))u(m)\left(\frac{d(m)}{\gamma(m) + b_m}\left(1 + \lambda\left(\gamma'(m) + \mu(m) + c_m + \omega\right)\right) + \lambda\gamma(m)\right) \\ & \quad + \operatorname{sgn}(u^+(0))u(0)\left(\frac{d(0)}{b_0 - \gamma(0)}\left(1 + \lambda\left(\gamma'(0) + \mu(0) + c_0 + \omega\right)\right) - \lambda\gamma(0)\right) \\ & \leq -\lambda\int_0^m \chi_{u^+}(s)\mu(s)u(s)\,\mathrm{d}s - \lambda\omega||u^+||_1 + \int_0^m \chi_{u^+}(s)h(s)\,\mathrm{d}s \\ & \quad + \operatorname{sgn}(u^+(m))h(m)\frac{d(m)}{\gamma(m) + b_m} + \operatorname{sgn}(u^+(0))h(0)\frac{d(0)}{b_0 - \gamma(0)}. \end{aligned} \tag{13}$$

Similarly, multiplying Equation (10) by $-\chi_{u^-}(s)$ and integrating from 0 to m, we obtain

$$\begin{aligned}
&||u^-||_1 - \text{sgn}(u^-(m))u(m)\left(\frac{d(m)}{\gamma(m)+b_m}\left(1+\lambda\left(\gamma'(m)+\mu(m)+c_m+\omega\right)\right)+\lambda\gamma(m)\right) \\
&\quad - \text{sgn}(u^-(0))u(0)\left(\frac{d(0)}{b_0-\gamma(0)}\left(1+\lambda\left(\gamma'(0)+\mu(0)+c_0+\omega\right)\right)-\lambda\gamma(0)\right) \\
&\le \lambda\int_0^m \chi_{u^-}(s)\mu(s)u(s)\,\mathrm{d}s - \lambda\omega||u^-||_1 - \int_0^m \chi_{u^-}(s)h(s)\,\mathrm{d}s \\
&\quad - \text{sgn}(u^-(m))h(m)\frac{d(m)}{\gamma(m)+b_m} - \text{sgn}(u^-(0))h(0)\frac{d(0)}{b_0-\gamma(0)}.
\end{aligned} \tag{14}$$

Adding (13) and (14) yields

$$\begin{aligned}
&||u||_1 + |u(0)|\left(\frac{d(0)}{b_0-\gamma(0)}\left(1+\lambda\left(\gamma'(0)+\mu(0)+c_0+\omega\right)\right)-\lambda\gamma(0)\right) \\
&\quad + |u(m)|\left(\frac{d(m)}{\gamma(m)+b_m}\left(1+\lambda\left(\gamma'(m)+\mu(m)+c_m+\omega\right)\right)+\lambda\gamma(m)\right) \\
&\le \int_0^m \left(\chi_{u^+}(s)-\chi_{u^-}(s)\right)h(s)\,\mathrm{d}s + h(0)\frac{d(0)}{b_0-\gamma(0)}\left(\text{sgn}(u^+(0))-\text{sgn}(u^-(0))\right) \\
&\quad - \lambda\omega||u||_1 + h(m)\frac{d(m)}{\gamma(m)+b_m}\left(\text{sgn}(u^+(m))-\text{sgn}(u^-(m))\right) \\
&\quad - \lambda\int_0^m \left(\chi_{u^+}(s)-\chi_{u^-}(s)\right)\mu(s)u(s)\,\mathrm{d}s.
\end{aligned} \tag{15}$$

Assuming that condition (8) holds true the left hand side of inequality (15) can be estimated below, for $\omega \in \mathbb{R}$ large enough, by

$$||u||_1 + |u(0)|\frac{d(0)}{b_0-\gamma(0)} + |u(m)|\frac{d(m)}{\gamma(m)+b_m}.$$

Similarly, the right hand side of inequality (15) can be estimated above by

$$||h||_1 + |h(0)|\frac{d(0)}{b_0-\gamma(0)} + |h(m)|\frac{d(m)}{\gamma(m)+b_m}.$$

Hence, if condition (8) is satisfied we have the dissipativity estimate

$$||u||_{\mathcal{X}} \le ||h||_{\mathcal{X}} = \left|\left|u - \lambda\left(\widetilde{A}-\omega\mathcal{I}\right)u\right|\right|_{\mathcal{X}}$$

for the operator $\widetilde{A}-\omega\mathcal{I}$.

For the range condition we need to show that whenever h is in a dense subset of $\mathcal{X}$ then the solution u of Equation (9) belongs to the domain of A. Since we assumed that $d > 0$, i.e. we have true Wentzell boundary conditions at both endpoints of the domain, the required regularity of the solution $u \in C^2[0,m]$ and hence the range condition follows from [15, Theorem 6.31]. Thus the closure of $\widetilde{A}-\omega\mathcal{I}$ is a generator of a contractive semigroup by [6, Theorem 3.15].

Next we observe that for $h \in \mathcal{X}^+$ every term on the right hand side of Equation (14) is non-positive, while every term on the left hand side of Equation (14) is non-negative. The inequality can only hold for $h \in \mathcal{X}^+$ if $||u^-||_1 = u(0) = u(m) = 0$. This proves that the resolvent operator $R(\lambda, \widetilde{A}-\omega\mathcal{I}) = (\lambda\mathcal{I}-(\widetilde{A}-\omega\mathcal{I}))^{-1}$ is positive for λ large enough, hence the closure of $\widetilde{A}-\omega\mathcal{I}$ generates a positive semigroup. A simple perturbation result yields that the closure of $\widetilde{A}$ is a generator of a positive quasicontractive semigroup.

Finally we note that, the operator $A - \widetilde{A}$ is positive, bounded and linear, hence it generates a positive semigroup $\{\mathcal{S}(t)\}_{t\geq 0}$ which satisfies

$$||\mathcal{S}(t)|| \leq e^{tB}, \quad \text{where} \quad B = ||\beta||_\infty.$$

The proof of the Theorem is now completed on the grounds of the Trotter product formula, see e.g. [6, Corollary 5.8 Ch. 3]. □

Remark 1. Conditions (8) are clearly satisfied if only the denominators are positive. However, the notation in (8) gives immediately the norm on the state space.

Remark 2. We note that the biologically natural assumptions in (5) that guarantee conservation of the total population in the absence of mortality and recruitment imply that $c_1 = c_2 = 1$. Hence the mathematical calculations coincide with the biological intuition. It can be shown that in the absence of mortality and recruitment the operator A generates a contraction semigroup on the state space $(\mathcal{X}, ||\cdot||_\mathcal{X})$, in fact $||\mathcal{T}(t)||_\mathcal{X} = 1$ for all $t \geq 0$.

3. **Asymptotic behavior.** In this section we investigate in the framework of semigroup theory the asymptotic behavior of solutions of model (1)-(3). Since our model is a linear one, we may expect that solutions either grow or decay exponentially, unless they are at a steady state. For simple structured population models in fact it is often observed (see e.g. [5, 8, 10, 17]), that solutions grow exponentially and tend to a finite-dimensional (resp. one-dimensional) global attractor. This phenomenon is called *balanced* (resp. *asynchronous*) *exponential growth*. The rate of exponential growth is called the *Malthusian parameter* or *intrinsic growth rate*. In other words, asynchronous exponential growth means that solutions tend to a fixed size distribution (often called the stable size profile) after a suitable rescaling of the semigroup.

In this section we show that solutions of our model exhibit the same asymptotic behavior. This question can be addressed effectively in the framework of semigroup theory (see [2, 4, 6]). Briefly, to establish balanced exponential growth, one needs to show that the growth bound of the semigroup is governed by a leading eigenvalue of finite (algebraic) multiplicity of its generator, and there exists a spectral gap, i.e. the leading eigenvalue is isolated in the spectrum. Our first result will assure this latter condition. Moreover, if it is also possible to establish that the semigroup is irreducible then one has that the algebraic multiplicity of the spectral bound equals one (with a corresponding positive eigenvector) and the semigroup exhibits asynchronous exponential growth.

Lemma 3.1. *The spectrum of A can contain only isolated eigenvalues of finite algebraic multiplicity.*

Proof. We show that the resolvent operator $R(\lambda, A)$ is compact. Since $\widetilde{A}$ is a bounded perturbation of A it is enough to show that $R(\lambda, \widetilde{A})$ is compact. This follows however, from the regularity of the solution of the resolvent Equation (9) and noting that $C^2[0,m] \subset W^{1,1}(0,m) \oplus \mathbb{R}^2$ which is compactly embedded in $L^1(0,m) \oplus \mathbb{R}^2$ by the Rellich-Kondrachov Theorem [1, Theorem 6.3, Part I]. The claim follows on the ground of [6, Proposition II.4.25]. □

Next we recall some necessary basic notions from linear semigroup theory, see e.g. [2, 4, 6]. A strongly continuous semigroup $\{\mathcal{S}(t)\}_{t\geq 0}$ on a Banach space $\mathcal{Y}$ with generator $\mathcal{O}$ and *spectral bound*

$$s\left(\mathcal{O}\right)=\sup\left\{\,\mathrm{Re}(\lambda)\;:\;\lambda\in\sigma\left(\mathcal{O}\right)\,\right\}$$

is said to exhibit *balanced exponential growth* if there exists a projection Π on $\mathcal{Y}$ such that

$$\lim_{t\to\infty}\|e^{-s(\mathcal{O})t}\,\mathcal{S}(t)-\Pi\|=0.$$

If the projection P is of rank one then the semigroup has *asynchronous exponential growth.* Moreover, the *growth bound* ω_0 is the infimum of all real numbers ω such that there exists a constant $M\geq 1$ with $||\mathcal{S}(t)||\leq Me^{\omega t}$. We also recall (see e.g. [2, C-III Definition 3.1]) that a positive semigroup $\{\mathcal{S}(t)\}_{t\geq 0}$ on a Banach lattice $\mathcal{Y}$ is called *irreducible* if there is no $\mathcal{S}(t)$ invariant closed ideal of $\mathcal{Y}$ except the trivial ones, $\{0\}$ and $\mathcal{Y}$.

Theorem 3.2. *Model (1)-(3) admits a finite dimensional global attractor.*

Proof. We have shown in Theorem 2.1 that solutions of our model are governed by a positive semigroup. Derndinger's Theorem (see e.g. [6, Theorem VI.1.15]) implies that the spectral bound of the generator equals to the growth bound of the semigroup, i.e. $s(A)=\omega_0$. Lemma 3.1 implies that the spectral bound $s(A)$ is an eigenvalue of finite algebraic (hence geometric) multiplicity unless the spectrum is empty. If the spectrum of A is empty we have by definition $\omega_0=-\infty$ and every solution tends to zero. Otherwise we have for the semigroup $\{\mathcal{T}(t)\}_{t\geq 0}$ generated by the closure of A

$$\lim_{t\to\infty}\left|\left|e^{-s(A)t}\mathcal{T}(t)-\Pi\right|\right|=0,\tag{16}$$

where Π is the projection onto the finite dimensional eigenspace corresponding to the eigenvalue $s(A)$. □

Recall that a subspace $I\subset\mathcal{Z}$ of a Banach lattice $\mathcal{Z}$ is an *ideal* iff $f\in I$ and $|g|\leq|f|$ implies that $g\in I$. The following useful result is from [2, C-III, Proposition 3.3].

Proposition 3.3. *Let B be the generator of a positive semigroup $\mathcal{U}(t)$ on the Banach lattice $\mathcal{Z}$ and K a bounded positive operator. Let $\mathcal{V}(t)$ be the semigroup generated by $B+K$. For a closed ideal $I\subset\mathcal{Z}$ the following assertions are equivalent:*
(i) I is $\mathcal{V}$-invariant,
(ii) I is invariant under both $\mathcal{U}$ and K.

We introduce the recruitment operator $K=A-\widetilde{A}$.

Theorem 3.4. *Assume that (8) holds true and $\beta>0$. Then the semigroup generated by the closure of A exhibits asynchronous exponential growth.*

Proof. Our goal is to apply Proposition 3.3 for the operator $\widetilde{A}$, whose closure is the generator of a positive semigroup as shown in Theorem 2.1 and to K, which is clearly positive and bounded. Every closed ideal I of $\mathcal{X}$ can be written as $I_1\oplus I_2\oplus I_3$, where I_1 is a closed ideal in the Banach lattice $L^1(0,m)$ and I_2,I_3 are closed ideals in $\mathbb{R}$. Note that, $\mathbb{R}$ admits only two ideals, i.e. $\{0\}$ or $\mathbb{R}$ itself. Next we observe that non-trivial closed ideals in $L^1(0,m)$ can be characterized via closed subsets G of positive measure of $(0,m)$. That is, the subspace J is a closed ideal of $L^1(0,m)$ if it contains the functions $f\in L^1(0,m)$ vanishing on G. Next we show that no non-trivial closed ideal $I = I_1 \oplus I_2 \oplus I_3$ is invariant under K or under the semigroup generated by $\widetilde{A}$. If $I_1 \neq \{0\}$ then the condition $\beta > 0$ guarantees that $Ku(s) = \int_0^m \beta(s,y)u(y)\,\mathrm{d}y > 0$, for every $s \in (0,m)$ for any $u \in I_1$, i.e. the image Ku does not vanish anywhere, hence by the previous characterization we must have $I_1 = L^1(0,m)$. Moreover, in this case $\beta > 0$ implies that we must have $I_2 = I_3 = \mathbb{R}$, since $\int_0^m \beta(0,y)u(y)\,\mathrm{d}y > 0$ and $\int_0^m \beta(m,y)u(y)\,\mathrm{d}y > 0$ for any $u \not\equiv 0$. On the other hand, if $I_1 = \{0\}$ then we have $D(\widetilde{A}) \cap I = \{0\}$, hence the restriction of $\widetilde{A}$ to $\mathbb{R} \oplus \mathbb{R}$ (or even to $\mathbb{R}$) does not generate a semigroup. This means that I cannot be invariant under the semigroup generated by $\widetilde{A}$. That is we have by Proposition 3.3 that the semigroup generated by A has no non-trivial closed invariant ideal. Therefore it is irreducible, and solutions exhibit asynchronous exponential growth, see e.g. [4]. □

The previous result completely characterizes the asymptotic behavior of solutions to the population model. That is, solutions behave asymptotically as $e^{rt}u_*(s)$ independently of the initial condition, where r is the so called Malthusian parameter, and u_* is often referred to as the final size distribution.

4. **Concluding remarks.**

In this note we introduced a linear structured population model with diffusion in the size space. Introduction of a diffusion is natural in the biological context [18], since unlike in age-structured models, individuals that have the same size initially, may disperse as time progresses. In other words, diffusion amounts to adding noise in a deterministic fashion. We equipped our model with generalized Wentzell-Robin boundary conditions. We showed that the model is governed by a positive quasicontractive semigroup on the biologically relevant state space. Furthermore we have characterized the asymptotic behavior of solutions via balanced exponential growth of the governing semigroup. We also established that solutions exhibit asynchronous exponential growth if the function β is strictly positive. An important biological consequence of asynchronous exponential growth is population stabilization in the sense that the proportion of the population in any subset of the structure space converges to a limiting value as time evolves, independently of the initial state of the population. The question of irreducibility of the semigroup generated by the Laplace operator with mixed Robin boundary conditions on a L^p-space (for $1 < p < \infty$) was addressed in the recent work by Haller-Dintelmann *et al.* [19]. It is expected that a similar result holds if generalized Wentzell-Robin boundary conditions are imposed. This is a topic of ongoing research.

In our model we have taken the view that individuals may be recruited into the population at different sizes. This appears to be the natural choice in the context of general physiologically structured population models, as opposed to age-structured models, where every individual is born at the same age zero. It is interesting to investigate whether a mathematically sound "limiting relationship" exists between models with infinite states at birth and one state at birth. This will be addressed in future work.

The power of generalized Wentzell boundary conditions in the context of population models is to allow the boundary states to carry mass. This is especially interesting in the L^p context as the boundary is a set of measure zero and therefore seems to play no role in an integral term. Interestingly, sinks on the boundary can cause ill-posedness in space dimensions ≥ 2 as Vazquez and Vitillaro [23] have shown.

In the future we will extend our model to incorporate interaction variables, to allow competition. Then model (1)-(3) becomes a nonlinear one, and the mathematical analysis will become more difficult. To our knowledge, positivity results are rather rare in the literature for nonlinear models. In [11] it was shown that the nonlinear semigroup generator satisfies the positive minimum principle, hence the semigroup is positive. This however, does not apply to population models, as the positive cone of the natural state space L^1 has empty interior, hence the positive minimum principle does not apply. It will be also interesting to consider more general models with a finite number of structuring variables, such as age-size structured models. Then the domain will be a cube $[0,1]^n$ and the prescription of appropriate boundary conditions will be much more involved.

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REFERENCES

[1] R. A. Adams and J. J. F. Fournier, "Sobolev Spaces," 2nd edition, Elsevier/Academic Press, Amsterdam, Boston, 2003.

[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, Berlin, 1986.

[3] À. Calsina and J. Saldaña, *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.

[4] Ph. Clément, H. J. A. M. Heijmans, S. Angenent, C. J. van Duijn and B. de Pagter, "One-Parameter Semigroups," North–Holland, Amsterdam 1987.

[5] J. Dyson, R. Villella-Bressan and G. F. Webb, *Asynchronous exponential growth in an age structured population of proliferating and quiescent cells*, Math. Biosci., **177&178** (2002), 73–83.

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

[7] J. Z. Farkas, D. Green and P. Hinow, *Semigroup analysis of structured parasite populations*, Math. Model. Nat. Phenom., **5** (2010), 94–114, arXiv:0812.1363.

[8] J. Z. Farkas and T. Hagen, *Asymptotic analysis of a size-structured cannibalism model with infinite dimensional environmental feedback*, Commun. Pure Appl. Anal., **8** (2009), 1825–1839, arXiv:0812.1369.

[9] J. Z. Farkas and T. Hagen, *Hierarchical size-structured populations: The linearized semigroup approach*, Dyn. Contin. Discrete Impuls. Syst. Ser. A Math. Anal., **17** (2010), 639–657, arXiv:0812.1367.

[10] J. Z. Farkas and P. Hinow, *On a size-structured two-phase population model with infinite states-at-birth*, Positivity, **14** (2010), 501–514, arXiv:0903.1649.

[11] A. Favini, G. R. Goldstein, J. A. Goldstein and S. Romanelli, *C_0-semigroups generated by second order differential operators with general Wentzell boundary conditions*, Proc. Amer. Math. Soc., **128** (2000), 1981–1989.

[12] A. Favini, G. R. Goldstein, J. A. Goldstein and S. Romanelli, *The heat equation with generalized Wentzell boundary condition*, J. Evol. Equ., **2** (2002), 1–19.

[13] W. Feller, *The parabolic differential equations and the associated semi-groups of transformations*, Ann. of Math., **55** (1952), 468–519.

[14] W. Feller, *Diffusion processes in one dimension*, Trans. Amer. Math. Soc., **77** (1954), 1–31.

[15] D. Gilbarg and N. Trudinger, "Elliptic Partial Differential Equations of Second Order," Springer-Verlag, Berlin, 1983.

[16] G. R. Goldstein, *Derivation and physical interpretation of general boundary conditions*, Adv. Differential Equations, **11** (2006), 457–480.

[17] M. Gyllenberg and G. F. Webb, *Asynchronous exponential growth of semigroups of nonlinear operators*, J. Math. Anal. Appl., **167** (1992), 443–467.

[18] K. P. Hadeler, *Structured populations with diffusion in state space*, Math. Biosci. Eng., **7** (2010), 37–49.

[19] R. Haller-Dintelmann, M. Hieber and J. Rehberg *Irreducibility and mixed boundary conditions*, Positivity, **12** (2008), 83–91.

[20] M. Langlais and F. A. Milner, *Existence and uniqueness of solutions for a diffusion model of host-parasite dynamics*, J. Math. Anal. Appl., **279** (2003), 463–474.

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

[22] F. A. Milner and C. A. Patton, *A diffusion model for host–parasite interaction*, J. Comput. Appl. Math., **154** (2003), 273–302.

[23] J. L. Vazquez and E. Vitillaro, *Heat equation with dynamical boundary conditions of reactive type*, Comm. Partial Differential Equations, **33** (2008), 561–612.

[24] A. D. Ventcel, *Semigroups of operators that correspond to a generalized differential operator of second order (Russian)*, Dokl. Akad. Nauk SSSR (N.S.), **111** (1956), 269–272.

[25] A. D. Ventcel, *On boundary conditions for multi-dimensional diffusion processes*, Theor. Probability Appl., **4** (1959), 164–177.

[26] R. Waldstätter, K. P. Hadeler and G. Greiner, *A Lotka-McKendrick model for a population structured by the level of parasitic infection*, SIAM J. Math. Anal., **19** (1988), 1108–1118.

[27] G. F. Webb, "Theory of Nonlinear Age-Dependent Population Dynamics," Marcel Dekker, New York, 1985.

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