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On the Formulation and Analysis of General Deterministic Structured Population Models. I. Linear Theory

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Abstract

We define a linear physiologically structured population model by two rules, one for reproduction and one for "movement" and survival. We use these ingredients to give a constructive definition of next-population-state operators. For the autonomous case we define the basic reproduction ratio R_0 and the Malthusian parameter r and we compute the resolvent in terms of the Laplace transform of the ingredients. A key feature of our approach is that unbounded operators are avoided throughout. This will facilitate the treatment of nonlinear models as a next step.

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1. Introduction to physiologically structured population models

The agenda of a modeller of biological populations could look as follows:

1. Model mechanisms at the i-level (i for individual),
2. lift to p-level by bookkeeping (p for population),
3. study phenomena at the p-level.

So the aim of a modelling exercise is to investigate how mechanisms at the i-level relate to phenomena at the p-level. In step 2 deterministically inclined people, such as the majority of us, use a formal law of large numbers argument to restrict to expected values, and this is exactly what we shall do in this paper. In the theory of multi-type branching processes (see Jagers [20, 21] and the references given there) one takes the full probabilistic structure into account, which allows one to study, for example, fluctuations around the mean due to demographic stochasticity. For concrete examples of steps 1-2

we refer to METZ & DIEKMANN [25], KOOIJMAN [23], DE ROOS, DIEKMANN & METZ [26], DE ROOS [27].

The set of all conceivable i-states is called i-state space. We shall denote it by Ω (as an example, think of Ω as a subset of the positive age-size quadrant).

We shall assume that the outside world influences individuals through so-called environmental interaction variables, denoted by E and taking values in an environmental space $\mathcal{E}$ (as an example, think of $\mathcal{E}$ as $\mathbb{R}_+$ with E describing the concentration of a limiting nutrient, say in a chemostat).

The processes that have to be modelled are:

- growth (i.e. i-state development)
- survival
- reproduction (how much offspring and with what i-state at birth?)
- feedback (i.e. influence on the environmental interaction variables, such as consumption of the nutrient)

And "modelling" here means that these processes have to be described in dependence on the i-state and the environmental interaction variables (we refer to the book by KOOIJMAN [23] for a systematic exposition of the physical, chemical and biological considerations that are needed to do so). Traditionally, this is done in terms of *rates.*

The traditional version of step 2 then leads to a first order partial differential equation (pde) with, as a rule, a non-local boundary condition describing the inflow of newborn individuals along that part of the boundary of Ω where the flux points inwards. The unknown in the pde is the density function describing population size and composition (that is, for each time we have an element of $L_1(\Omega)$). The equation is the analogue of the Kolmogorov forward equation from probability theory.

Often it is advantageous, or even necessary, to describe the population size and composition with a (positive) measure on Ω (which is not necessarily absolutely continuous, i.e. for which a corresponding density function may not exist).One then uses duality theory by describing the dynamics in terms of the Kolmogorov backward equation, for a function of time with values in $C_0(\Omega)$, which is the pre-adjoint of the forward equation (see HEIJMANS [17, 18] for some nice examples).

In any case, the traditional formulation of the model at the p-level takes the form of a formal differential equation involving non-local terms. Despite strong efforts over an extended period of time, the present authors did not manage to build a qualitative theory for infinite dimensional systems describing physiologically structured populations when taking such a model formulation in terms of a would-be infinitesimal generator as their starting point (we like to add, to our defence, two remarks to this disclaimer

- even though we never reached the ultimate goal, some interesting (and even elegant, we think) mathematics resulted from our attempts, see [1, 2, 3, 4]
- one should realise that, for a given time course of the environmental variables we have a *non-autonomous* linear problem, while with feedback to the environment we are in a quasi-linear situation).

The main difficulty can actually be explained in biological terms. To keep models parameter scarce, one wants to allow for discontinuities (with respect to i-state) in the rates (think of waterfleas that start to reproduce upon reaching a critical size). Now consider a situation in which the i-state of some individual moves in Ω for an extended period of time along a line of discontinuity of, say, the rate of offspring production. Then the 'model' is *not* acceptable as a model and one should *not* expect that

existence and uniqueness of solutions at the p-level holds. Whether or not this phenomenon actually occurs in a specific model, is hidden in the rates. It is the combined, global, effect of the rates that makes the difference between the model being ill or well posed!

Mathematically we might say that it is hard to express the requirement that characteristics and surfaces of discontinuity cross transversally in verifiable abstract terms.

The aim of this paper is to present an alternative mathematical formulation of structured population models. The ingredients, that serve to describe the processes at the i-level, are not rates, but quantities at the 'global, combined' level, such as survival functions. We stress that these are actually closer to observable quantities than the rates. The advantage is that good and bad models are distinguished from one another in terms of these ingredients, that is before one starts the mathematical analysis. (If actually the model is first given in terms of rates, one has a phase in between modelling and analysis in which the new ingredients have to be computed from the rates; essentially this amounts to integration along characteristics and it is in this phase that transversality is checked.)

The corresponding p-equations, as presented in our papers [3, 4], are not *pde*, but renewal integral equations. Since the formulation does not involve unbounded operators, there are no regularity questions (if one does not differentiate, one is saved the hard technical task of finding necessary and sufficient conditions for this to be allowed; or, in other words, of turning a formal differential expression into a well-defined operator by specifying its domain of definition).
In this paper we achieve a substantial technical simplification (compared to [3, 4]) by postponing the step from i- to p-level. Here we shall perform the construction of the generation expansion (that is, the iteration of the reproduction rule to specify the expected total offspring (entire clan)) at the i-level. The step to the p-level then simply amounts to adding the contributions of all individuals. Mathematically it means that we define a semigroup of operators by means of a family of kernels (Green's function). The advantage is that standard integration theory suffices and that there is no need to go into the intricacies of abstract (Stieltjes) integration. It reduces the role of duality. In particular we are no longer obliged to consider dual evolutionary systems and this frees us from the need to make unwanted assumptions concerning the behaviour at the boundary of Ω or at infinity (see [3, 4]).

The formulation presented here overlaps considerably with that of multi-type branching processes. In essence, we simply restrict to expected behaviour. What we add, however, is the notion of i-state and, at the p-level, the evolution operators mapping the p-state at some time onto the p-state at a later time. When the environmental variables are given, the problem is linear, individuals act independently, and the extra bookkeeping only puts on some frills. But in order to treat problems that are nonlinear by feedback through the environment, the notion of 'state' (both at the i- and at the p-level) is essential, we think. It remains to investigate whether, and in what sense, the nonlinear deterministic model formulation is the limit of a stochastic model for initial population size tending to infinity (see e.g. [11]). We hope that this paper is written in such a way that our probabilistic colleagues feel invited to give it a try.

In this paper we ignore the complications of sex and pretend that mothers produce daughters without intermediary agency of males.

2. Reproduction in a fluctuating environment

Our point of view is that structured population models are nonlinear by feedback through environmental variables. So if one experimentally manipulates the environmental variables (e.g. by controlling the food availability), the feedback loop is broken and a linear (i.e. density independent) situation obtains. Alternatively one can think of the linear situation as corresponding to a thought experiment and subsequently bring the feedback back in as a second step. This approach then leads to a fixed point problem for the environmental interaction variables. We intend to deal with these fixed point problems in part II of this work.

We choose to suppress the environmental variables in our notation and instead take time t as a variable in the model ingredients. In part II we shall work, in contrast, with ingredients that depend

on the environmental variables, which in turn depend on time t.

We assume that i-states are elements of a measurable space Ω with a countably generated σ algebra. We shall frequently consider subsets of the product space $\mathbb{R}_+ \times \Omega$, where $\mathbb{R}_+$ is equipped with the σ-algebra of Borel sets. We shall often omit the adjective 'measurable' when introducing sets.

2.1. The reproduction kernel

Consider an individual which at time t has state $x \in \Omega$. Suppose at time $t+s$ this individual produces a child that has state $y \in \Omega$ at birth. Then we shall call $(s, y) \in \mathbb{R}_+ \times \Omega$ the relative *birth coordinates* of this child, where "relative" refers to the fact that we measure time from t.

The *reproduction kernel* Λ is by definition the expected number of children. More precisely we have that, for all $(t, x) \in \mathbb{R} \times \Omega$ and subsets A of $\mathbb{R}_+ \times \Omega$,

$$\Lambda(t,x)(A) \;=\; \begin{array}{l}\text{the expected number of children, with relative birth coordinates in}\\ \text{A, of an individual which at time t has state x}\end{array} \tag{2.1}$$

So for the particular case $A = [0, s) \times \omega$, for some subset ω of Ω, this is the expected number of children produced in the time interval $[t, t+s)$ with state-at-birth in ω. A structured population model requires first of all a specification of Λ. Thus we consider Λ as the first and most basic ingredient of such a model.

2.2. The generation expansion

The kernel Λ describes the *first* generation. We want to iterate the reproduction kernel to account for the fact that children get children etc. As the time component of the birth coordinates refers to the time *difference* between the reproduction event and the moment we focussed on the ancestor, we have to shift the subsets of $\mathbb{R}_+ \times \Omega$ in the time direction when we shift attention from one individual to another. It therefore pays to introduce the following notation:

$$A_{-\tau} := \{(\sigma, \xi) \in \mathbb{R}_+ \times \Omega : (\sigma + \tau, \xi) \in A\} \tag{2.2}$$

Note that when A is bounded in the time direction, $A_{-\tau} = \emptyset$ for τ sufficiently large.

We now define

$$\Lambda^k(t,x)(A) \;=\; \begin{array}{l}\text{expected number of k-th generation offspring,}\\ \text{with birth coordinates in A,}\\ \text{of an individual which at time t has state x}\end{array} \tag{2.3}$$

(and emphasize once more that the time component of the birth coordinates depends on both the ancestor whose descendants we consider and the moment at which we focussed our attention on that ancestor). Consistency requires that

$$\Lambda^{k+1}(t,x)(A) = \int_{\mathbb{R}_+ \times \Omega} \Lambda(t+\tau,\xi)(A_{-\tau})\Lambda^k(t,x)(d\tau \times d\xi) \tag{2.4}$$

and thus we can build Λ^k from Λ by iteration. We still need to formulate hypotheses on Λ which are sufficient to guarantee that this construction of later generation kernels is well defined. The next subsection and the appendix together provide the necessary mathematical background.

2.3. Kernels and the $\otimes$-product

Let $M_+(\mathbb{R}_+ \times \Omega)$ denote the set of positive measures on $\mathbb{R}_+ \times \Omega$, that is, measures defined on the product σ-algebra with values in $\bar{\mathbb{R}}_+ = [0, \infty]$.

DEFINITION 2.1. A function $\Psi : \mathbb{R} \times \Omega \to M_+(\mathbb{R}_+ \times \Omega)$ is called a *kernel* if, for any measurable set $A \subset \mathbb{R}_+ \times \Omega$ the function

$$(t,x) \to \Psi(t,x)(A)$$

from $\mathbb{R}\times\,\Omega$ to $\bar{\mathbb{R}}_+$ is measurable.

On $M_+(\mathbb{R}_+ \times \Omega)$ we define the order relation $\geq$ by:

$m_1 \geq m_2$ if and only if $m_1(A) \geq m_2(A)$ for all measurable A.

The ordered cone $M_+(\mathbb{R}_+ \times \Omega)$ inherits monotone sequential completeness from $\bar{\mathbb{R}}_+$: every monotonically increasing sequence of elements of $M_+(\mathbb{R}_+ \times \Omega)$ has a limit in $M_+(\mathbb{R}_+ \times \Omega)$.

We lift the order relation to the set of all kernels by requiring that the inequality holds for all $(t,x) \in \mathbb{R}\times\,\Omega$. Since the pointwise limit of measurable functions is measurable, the set of kernels inherits monotone sequential completeness. In particular, every series whose terms are kernels has a well-defined sum, which is a kernel.

We shall use the notation $\Psi_n \uparrow \Psi_\infty$ whenever we have monotone convergence of kernels in the point- and setwise sense specified above.

Next we introduce more algebraic structure on the set of kernels. In the Appendix we show that for every measurable set $A \subset \mathbb{R}_+ \times \Omega$ the mapping $(t,\tau,\xi) \mapsto \Psi(t+\tau,\xi)(A_{-\tau})$ is a measurable function from $\mathbb{R}\times\,\mathbb{R}_+ \times \Omega$ to $\bar{\mathbb{R}}_+$. So the definition

$$(\Phi \otimes \Psi)(t,x)(A) = \int\limits_{\mathbb{R}_+\times\,\Omega} \Phi(t+\tau,\xi)(A_{-\tau})\Psi(t,x)(d\tau \times d\xi) \tag{2.5}$$

makes sense. In the Appendix the following collection of results is proved. (The algebraically inclined reader will recognize that the set of kernels is a semi-ring.)

THEOREM 2.2.

(i) $\Phi \otimes \Psi$ *defined by (2.5) is a kernel*
(ii) *the* $\otimes$ *product is associative:* $\Theta \otimes (\Phi \otimes \Psi) = (\Theta \otimes \Phi) \otimes \Psi$ *for all kernels* Θ, Φ, Ψ
(iii) *the* $\otimes$ *product is distributive:*

$$\begin{aligned} \Theta \otimes (\Phi + \Psi) &= \Theta \otimes \Phi + \Theta \otimes \Psi \\ (\Phi + \Psi) \otimes \Theta &= \Phi \otimes \Theta + \Psi \otimes \Theta \end{aligned}$$

for all kernels Θ, Φ, Ψ

(iv) *the* $\uparrow$ *limit and* $\otimes$ *commute:*

$$\begin{aligned} \Phi \otimes \Psi_n &\uparrow \Phi \otimes \Psi_\infty \\ \Psi_n \otimes \Phi &\uparrow \Psi_\infty \otimes \Phi \end{aligned}$$

whenever $\Psi_n \uparrow \Psi_\infty$.

It follows from this theorem that parentheses are superfluous in arbitrary finite products and, in particular, that the k^{th}-power Ψ^k of a kernel Ψ is well-defined. By monotone convergence the sum of these powers exists. Exploiting the properties (iii) and (iv) in the theorem above, one verifies that the sum is the solution of an equation, the so-called resolvent equation. We formulate this result as

THEOREM 2.3. *Let* Ψ *be a kernel. For any measurable subset* A *of* $\mathbb{R}_+ \times \Omega$ *and any* $(t,x) \in \mathbb{R}\times\,\Omega$, *the series*

$$\sum_{k=1}^{\infty} \Psi^k(t,x)(A)$$

converges in $\bar{\mathbb{R}}_+$, and the sum defines a kernel, which we denote by Ψ^c. The kernel Ψ^c is the resolvent of Ψ with respect to $\otimes$, i.e. it satisfies the resolvent equation

$$\Psi^c = \Psi + \Psi^c \otimes \Psi = \Psi + \Psi \otimes \Psi^c. \tag{2.6}$$

COROLLARY 2.4. (which explains the name "resolvent").
Let Ψ and f be given kernels. The solution of the equation

$$X = f + \Psi \otimes X$$

is given explicitly by

$$X = f + \Psi^c \otimes f.$$

where Ψ^c denotes the resolvent of Ψ.

Note that the corollary shows (a bit implicitly perhaps) that the resolvent is unique (cf. GRIPENBERG, LONDEN & STAFFANS [15]).

Before turning to the biological interpretation of the resolvent, we like to make the following side-remark. Clearly one can formulate variants in which t is restricted to a subset of $\mathbb{R}$, e.g. $[s, \infty)$ for some s. It may also happen that one has chosen Ω too large and that restriction to a subset of Ω yields a meaningful problem (see e.g. Section 2.4 below). We think such modifications are straightforward and we chose not to complicate the formulation by including them from the very beginning. However, in subsection 2.5 we need to consider certain restrictions and then the following observations are useful. Let Ω_1, Ω_2 and Ω_3 be measurable subsets of Ω and let $\Psi : \mathbb{R} \times \Omega_1 \to M_+(\mathbb{R}_+ \times \Omega_2)$ and $\Phi : \mathbb{R} \times \Omega_2 \to M_+(\mathbb{R}_+ \times \Omega_3)$ be kernels (adapt Definition 2.1 in the obvious way to make precise what "kernel" means). Then $\Phi \otimes \Psi : \mathbb{R}_+ \times \Omega_1 \to M_+(\mathbb{R}_+ \times \Omega_3)$ defined by

$$(\Phi \otimes \Psi)(t, x)(A) = \int_{\mathbb{R}_+ \times \Omega_2} \Phi(t + \tau, \xi)(A_{-\tau}) \Psi(t, x)(d\tau \times d\xi)$$

is a kernel. Wherever it contributes to clarity we shall express the domains into the notation by writing such a formula as

$$(\Phi \otimes \Psi)\Big|_{\Omega_3, \Omega_1} = \Phi\Big|_{\Omega_3, \Omega_2} \otimes \Psi\Big|_{\Omega_2, \Omega_1}.$$

Note in particular that the first index refers to the restriction $A \subset \mathbb{R}_+ \times \Omega_3$ and the second to $x \in \Omega_1$, and that the $\otimes$-product is defined whenever the middle two indices coincide.

2.4. The clan kernel and the renewal equation
Returning to the population dynamical setting, we now assume that Λ is a kernel and we shall call the sum of all generation kernels

$$\Lambda^c = \sum_{k=1}^{\infty} \Lambda^k. \tag{2.7}$$

the clan kernel.

As the members of the clan originating from an individual are either its children or members of the clan originating from one of its children, we should have

$$\Lambda^c = \Lambda + \Lambda^c \otimes \Lambda. \tag{2.8}$$

But one is just as right in noting that clan members are either children or children of clan members, i.e.

$$\Lambda^c = \Lambda + \Lambda \otimes \Lambda^c. \tag{2.9}$$

Thus we see that in our particular context both identities, that together constitute the resolvent equation (2.6), alllow for a simple and straightforward biological interpretation. This interpretation is also reflected in the name "renewal equation", that is frequently used to denote equations (2.8), (2.9) and the like (a more strict motivation for the word "renewal" derives from economic applications, having to do with the replacement of machine parts whose life time follows some distribution).

As we have seen, $\Lambda^c(t,x)(A)$ is always a well-defined element of $\overline{\mathbb{R}}_+$. But often we want and expect some form of boundedness, in particular that $\Lambda^c(t,x)(A)$ is finite for every $(t,x) \in \mathbb{R}\times\ \Omega$ and every $A \subset \mathbb{R}_+ \times \Omega$ which is bounded in the time direction. We present two results in this spirit.

Whenever there is necessarily a gap between being born and giving birth, only finitely many terms in the sum defining $\Lambda^c(t,x)(A)$ are different from zero when A is bounded in the time direction (but the number of non-zero terms increases without bound when we allow A to expand indefinitely in the time direction).

DEFINITION 2.5. We say that a measurable subset Ω_b of Ω is a *set representing the birth states*, if, for all $(t,x) \in \mathbb{R}\times\ \Omega$, $\Lambda(t,x)$ is concentrated on $\mathbb{R}_+ \times \Omega_b$ (in the sense that $\Lambda(t,x)(A) = 0$ whenever $A \cap \mathbb{R}_+ \times \Omega_b = \emptyset$).

REMARK 2.6. Of course we want to choose Ω_b as small as possible. But in general such a requirement does not translate into a workable definition (i.e. a unique characterization; for instance, when the measure is absolutely continuous on an interval you may artificially eliminate any particular point). Whenever Ω has a natural locally compact Hausdorff topology and we are dealing with regular Borel measures, we can *uniquely* define Ω_b as the smallest *closed* subset of Ω such that, for all $(t,x) \in \mathbb{R}\times\ \Omega$, $\Lambda(t,x)(\mathbb{R}_+ \times \omega) = 0$ whenever $\omega \cap \Omega_b = \emptyset$. In that case we will call Ω_b *the* set of birth states. In general, we have to live with the somewhat irritating vagueness and non-uniqueness of Definition 2.5.

DEFINITION 2.7. $x \in \Omega$ is called a juvenile state, with reproduction delay at least ε, when

$$\sup_{t\in\mathbb{R}} \Lambda(t,x)([0,\varepsilon)\times\ \Omega) = 0.$$

THEOREM 2.8. *Suppose birth states (i.e. elements of Ω_b as in Definition 2.5) are juvenile states with uniform reproduction delay ε, then the generation expansion is finite in the sense that $\Lambda^k(t,x)(A) = 0$ whenever, for some s, $A \subset [0,s)\times\ \Omega$ and $k > \frac{1}{\varepsilon}s$.*

The second type of result employs exponential estimates. We present a version in terms of integrals while noting that, under appropriate hypotheses, pointwise estimates work equally well.

The Laplace transform $\hat{\Psi}$ of a kernel Ψ is defined, for real values of z at first, by

$$\hat{\Psi}(t,x;z)(\omega) = \int\limits_{\mathbb{R}_+\times\ \omega} e^{-z\tau}\Psi(t,x)(d\tau\times\ d\xi) = \lim_{s\to\infty} \int\limits_{[0,s)\times\omega} e^{-z\tau}\Psi(t,x)(d\tau\times\ d\xi). \tag{2.10}$$

So $\hat{\Psi}$ maps $\mathbb{R}\times\ \Omega\times\ \mathbb{R}$ into $M_+(\Omega)$. We define

$$\|\Psi\|_z := \sup_{(t,x)\in\mathbb{R}\times\Omega} \hat{\Psi}(t,x;z)(\Omega). \tag{2.11}$$

A kernel Ψ is called a *Laplace kernel* if

$$\|\Psi\|_{z_0} < \infty \text{ for some } z_0 \in \mathbb{R}. \tag{2.12}$$

Note that in that case the definition (2.10) can be extended to $z \in \mathbb{C}$ with $\mathrm{Re}z > z_0$.

THEOREM 2.9. *If Φ and Ψ are kernels then*

$$\|\Phi \otimes \Psi\|_z \leq \|\Phi\|_z \|\Psi\|_z. \tag{2.13}$$

COROLLARY 2.10. *If Φ and Ψ are Laplace kernels, so are $\Phi \otimes \Psi$ and Φ^k for $k \geq 1$. Moreover*

$$\|\Phi^k\|_z \leq (\|\Phi\|_z)^k. \tag{2.14}$$

THEOREM 2.11. *Let Λ be a Laplace kernel with, for some $z_0 > 0$ and some $j \geq 1$, $\|\Lambda\|_{z_0} < \infty$ and $\|\Lambda^j\|_{z_0} < 1$. Let, for some s, $A \subset [0,s) \times \Omega$ be measurable. Then the series*

$$\Lambda^c(t,x)(A) = \sum_{k=1}^{\infty} \Lambda^k(t,x)(A)$$

converges in $\mathbb{R}$, uniformly in $t \in \mathbb{R}$ and $x \in \Omega$. Moreover, Λ^c is a Laplace kernel.

We emphasize that all information about *population* growth (or decline) is contained in Λ^c. And since Λ^c is obtained from Λ by a straightforward constructive procedure, it is possible to deduce such information directly from Λ. In section 6 we shall elaborate this for the relatively simple, but important, special case that $\Lambda(t,x)(A)$ is independent of t, which amounts to the environment being constant rather than fluctuating.

2.5. Reduction of the generation expansion

A set Ω_b representing the birth states (Definition 2.5) may be considerably smaller than Ω. In particular this is the case when age is a component of i-state, since newborns have age zero by the very definition of age.

The reduced reproduction kernel Λ_b is just Λ, but with the restriction that in $\Lambda_b(t,x)(A) := \Lambda(t,x)(A)$ the domain of x is Ω_b and the domain of A consists of the measurable subsets of $\mathbb{R}_+ \times \Omega_b$. In symbols:

$$\Lambda_b = \Lambda\Big|_{\Omega_b, \Omega_b}$$

From Λ_b we build the higher generation kernels by iteration, as usual:

$$\Lambda_b^{k+1}(t,x)(A) = \int_{\mathbb{R}_+ \times \Omega_b} \Lambda_b(t+\tau,\xi)(A_{-\tau}) \Lambda_b^k(t,x)(d\tau \times d\xi) \tag{2.15}$$

with the same restriction on x and A.

The point is that we need Λ to compute the first generation for a general initial condition, but that all information concerning subsequent generations is contained in the powers of Λ_b. We formulate this precisely as

LEMMA 2.12. *For all $(t,x) \in \mathbb{R} \times \Omega$ and $A \subset \mathbb{R}_+ \times \Omega$*

$$\Lambda^{k+1}(t,x)(A) = \int_{\mathbb{R}_+ \times \Omega_b} \Lambda_b^k(t+\tau,\xi)(A_{-\tau} \cap (\mathbb{R}_+ \times \Omega_b)) \Lambda(t,x)(d\tau \times d\xi). \tag{2.16}$$

Sometimes a further reduction is possible. Suppose birth states are 'separated' from states in which reproduction is possible by a set of i-states, which we then call *renewal points.* Here 'separated' means that any individual has to pass at least one renewal point before being able to reproduce. As a concrete example consider a size structured cell population in which the minimum size of a mother is larger than the maximum size of a daughter. Then any size in between qualifies as a renewal point (see [6, 5]; note that this example demonstrates that there may be an element of choice in the definition of renewal points).

The idea is now that we may consider first passage through a renewal point as a kind of birth and base our bookkeeping of reproduction on this 'birth' process, rather than on the true birth process. When individual movement (see the next section) is continuous and deterministic, 'passage' should be taken literal, but when it is, for instance, a jump process it is more accurate to speak about first hitting a renewal point.

To describe such situations mathematically, we introduce a measurable subset Ω_r of Ω, which we call the *renewal set*, and for each $t \in \mathbb{R}$ and $x \in \Omega_b$ a measure $\pi(t,x)$ on $\mathbb{R}_+ \times \Omega_r$, which describes when and where an individual which is born at time t with birth state x will hit the set Ω_r for the first time. We assume that for any measurable $A \subset \mathbb{R}_+ \times \Omega_r$ the function $(t,x) \longmapsto \pi(t,x)(A)$ from $\mathbb{R} \times \Omega_b$ to $\mathbb{R}$ is measurable.We now require that, for each $t \in \mathbb{R}$ and $x \in \Omega_b$ and $A \subset \mathbb{R}_+ \times \Omega_b$

$$\Lambda_b(t,x)(A) = \int\limits_{\mathbb{R}_+ \times \Omega_r} \Lambda(t+\tau,\xi)(A_{-\tau})\pi(t,x)(d\tau \times d\xi). \tag{2.17}$$

Note that in (2.14) expected reproduction from birth states is expressed in expected reproduction from renewal states and expected arrival at renewal states.

We next define for $x \in \Omega_r$ and $A \subset \mathbb{R}_+ \times \Omega_r$ the reduced renewal kernel Λ_r by

$$\Lambda_r(t,x)(A) = \int\limits_{\mathbb{R}_+ \times \Omega_b} \pi(t+\tau,\xi)(A_{-\tau})\Lambda(t,x)(d\tau \times d\xi). \tag{2.18}$$

Note that Λ_r computes, for an individual with a state in Ω_r, first the true reproduction and next the hitting of Ω_r of the offspring. Or, in other words, Λ_r describes reproduction for the quasi-birth process of hitting Ω_r

The powers of Λ_r are now defined in exactly the same way as those of Λ and Λ_b. More precisely, in the computation of $\Lambda_r^k(t,x)(A)$ we restrict to $x \in \Omega_r$ and $A \subset \mathbb{R}_+ \times \Omega_r$. Of course the advantage hinges upon Ω_r being smaller than Ω_b.

We now want to express the powers of Λ_b explicitly in terms of the powers of Λ_r. As a first step we express iterated true birth kernels starting from a renewal state in powers of Λ_r and the given Λ.

LEMMA 2.13. *For any $t \in \mathbb{R}, x \in \Omega_r$ and $A \subset \mathbb{R}_+ \times \Omega_b$ the identity*

$$\Lambda^k(t,x)(A) = \int\limits_{\mathbb{R}_+ \times \Omega_r} \Lambda(t+\tau,\xi)(A_{-\tau})\Lambda_r^{k-1}(t,x)(d\tau \times d\xi) \tag{2.19}$$

holds.

PROOF. Using the notation explained at the end of subsection 2.3 we may write (2.17) as

$$\Lambda_b = \Big|_{\Omega_b,\Omega_r} \Lambda \otimes \pi \Big|_{\Omega_r,\Omega_b}$$

and (2.18) as

$$\Lambda_r = \pi\Big|_{\Omega_r,\Omega_b} \otimes \Lambda\Big|_{\Omega_b,\Omega_r}$$

and (2.19) as

$$\Lambda^k\Big|_{\Omega_b,\Omega_r} = \Lambda\Big|_{\Omega_b,\Omega_r} \otimes \Lambda_r^{k-1}\Big|_{\Omega_r,\Omega_r}.$$

We now prove the validity of this last identity by induction. Suppose it holds for k. Then

$$\Lambda^{k+1}\Big|_{\Omega_b,\Omega_r} = \Lambda_b\Big|_{\Omega_b,\Omega_b} \otimes \Lambda^k\Big|_{\Omega_b,\Omega_r} = \Lambda\Big|_{\Omega_b,\Omega_r} \otimes \pi\Big|_{\Omega_r,\Omega_b} \otimes \Lambda\Big|_{\Omega_b,\Omega_r} \otimes \Lambda_r^{k-1}\Big|_{\Omega_r,\Omega_r}$$

$$= \Lambda\Big|_{\Omega_b,\Omega_r} \otimes \Lambda_r\Big|_{\Omega_r,\Omega_r} \otimes \Lambda_r^{k-1}\Big|_{\Omega_r,\Omega_r} = \Lambda\Big|_{\Omega_b,\Omega_r} \otimes \Lambda_r^{k}\Big|_{\Omega_r,\Omega_r}$$

or, in words, it holds for $k+1$. Since the identity is trivial for $k=1$, the proof is complete. □

All that remains to be done in order to achieve our aim is to derive the higher order analogue of (2.17).

LEMMA 2.14. *For any $t \in \mathbb{R}, x \in \Omega_b$ and $A \subset \mathbb{R}_+ \times \Omega_b$ the identity*

$$\Lambda_b^k(t,x)(A) = \int\limits_{\mathbb{R}_+ \times\, \Omega_r} \Lambda^k(t+\tau,\xi)(A_{-\tau})\pi(t,x)(d\tau \times d\xi) \tag{2.20}$$

holds.

PROOF. In symbolic notation we have to prove that

$$\Lambda_b^k\Big|_{\Omega_b,\Omega_b} = \Lambda^k\Big|_{\Omega_b,\Omega_r} \otimes \pi\Big|_{\Omega_r,\Omega_b}.$$

Assume that this relation holds for k. Then

$$\Lambda_b^{k+1}\Big|_{\Omega_b,\Omega_b} = \Lambda_b\Big|_{\Omega_b,\Omega_b} \otimes \Lambda_b^k\Big|_{\Omega_b,\Omega_b} = \Lambda_b\Big|_{\Omega_b,\Omega_b} \otimes \Lambda^k\Big|_{\Omega_b,\Omega_r} \otimes \pi\Big|_{\Omega_r,\Omega_b} = \Lambda^{k+1}\Big|_{\Omega_b,\Omega_r} \otimes \pi\Big|_{\Omega_r,\Omega_b}$$

and we conclude that it holds for $k+1$. Since for $k=1$ the relation is nothing else than (2.17), the proof is complete. □

The results of this subsection are now reworded and summarised in the following

THEOREM 2.15. *(i) For $t \in \mathbb{R}$ and $x \in \Omega$ we can explicitly express Λ^c in terms of Λ and Λ_b^c:*

$$\Lambda^c(t,x)(A) = \Lambda(t,x)(A) + \int\limits_{\mathbb{R}_+ \times\, \Omega_b} \Lambda_b^c(t+\tau,\xi)(A_\tau)\Lambda(t,x)(d\tau \times d\xi) \tag{2.21}$$

(ii) If, for a suitably defined renewal set Ω_r, the kernel Λ_b allows the representation (2.17), we can explicitly express Λ_b^c in terms of Λ, π and Λ_r^c: for $t \in \mathbb{R}$ and $x \in \Omega_r$ we have that

$$\Lambda_b^c(t,x)(A) = \int\limits_{\mathbb{R}_+ \times\, \Omega_r} \Lambda^c(t+\tau,\xi)(A_{-\tau})\pi(t,x)(d\tau \times d\xi) \tag{2.22}$$

and

$$\Lambda^c(t,x)(A) = \Lambda(t,x)(A) + \int\limits_{\mathbb{R}_+ \times\, \Omega_r} \Lambda(t+\tau,\xi)(A_{-\tau})\Lambda_r^c(t,x)(d\tau \times d\xi) \tag{2.23}$$

PROOF. (i) follows from Lemma 2.12 by summing over k.
Likewise we obtain (2.23) from Lemma 2.13 by summing over k, and (2.22) from Lemma 2.14. □

3. *i*-STATE DEVELOPMENT AND SURVIVAL

So far our presentation echoes the treatment of expected behaviour in the theory of multi-type branching processes (e.g. JAGERS [21])
But now we introduce as our second ingredient

$$u(t,x;s)(\omega) \quad = \quad \begin{array}{l}\text{probability that an individual which has state } x \text{ at time } t \\ \text{is alive } s \text{ time units later and then has a state in } \omega \subset \Omega\end{array} \tag{3.1}$$

What we have in mind is that individuals follow a Markov process with death as a hidden absorbing state. But we do not need a full specification of this process. The information about i-state development in Ω (e.g. individual growth, if size is an i-state variable) and survival that is embodied in the function u with the stated interpretation, suffices for our deterministic purposes.

We emphasize that stochastic movement in Ω is allowed (such in contrast with formulations in terms of first order pde, which require movement in Ω to be described by *ode*). Stochastic movement is so easily included, at least at the formal general level, because the description in (3.1) works with finite time differences rather than with infinitesimal time differences.

The interpretation requires that u satisfies a consistency condition, the Chapman-Kolmogorov relation

$$u(t,x;s)(\omega) = \int_{\Omega} u(t+\sigma,\xi;s-\sigma)(\omega)u(t,x;\sigma)(d\xi) \tag{3.2}$$

which should hold for all $x \in \Omega, t \in \mathbb{R}, s \in \mathbb{R}_+, 0 \leq \sigma \leq s$ and $\omega \subset \Omega$. Often we shall suppress ω in identities of this kind and simply write it as

$$u(t,x;s) = \int_{\Omega} u(t+\sigma,\xi;s-\sigma)u(t,x;\sigma)(d\xi). \tag{3.3}$$

The Chapman-Kolmogorov relation expresses that i-state is a 'state' in the Markovian sense, by requiring that a rearrangement of our bookkeeping corresponding to a stop and re-start at time $t+\sigma$ in between t and $t+s$ should not lead to different results. As the same conclusion should hold when we consider reproduction, there is a second consistency relation that combines u and Λ:

$$\Lambda(t,x)(A) = \Lambda(t,x)(A \cap ([0,s)\times\Omega)) + \int_{\Omega} \Lambda(t+s,\xi)(A_{-s})u(t,x;s)(d\xi) \tag{3.4}$$

As for any A necessarily $A_s \cap ([0,s)\times\Omega) = \emptyset$ we may alternatively write this as

$$\Lambda(t,x)(A_s) = \int_{\Omega} \Lambda(t+s,\xi)(A)u(t,x;s)(d\xi). \tag{3.5}$$

This relation should hold for all $x \in \Omega, t \in \mathbb{R}, s \in \mathbb{R}_+$ and $A \subset \mathbb{R}_+ \times \Omega$.

We assume that u maps $\mathbb{R}\times\Omega\times\mathbb{R}_+$ into the set $M_+(\Omega)$ of positive measures on Ω and is such that

(i) for any $\omega \subset \Omega$ the function

$$(t,x;s) \longmapsto u(t,x;s)(\omega)$$

is measurable

(ii) $u(t,x;s)(\Omega) \leq 1$, that is, $u(t,x;s)$ is a, in general defective, probability measure

(iii) the consistency conditions (3.2) and (3.4) are satisfied.

We note that (3.2) and (ii) together imply that the survival probability $s \longmapsto u(t,x;s)(\Omega)$ is a non-increasing function, as it should be. We may require as an additional condition that

$$\lim_{s\to\infty} u(t,x;s)(\Omega) = 0 \tag{3.6}$$

to express that no individual is immortal. Or, alternatively, that

$$\sup_{(t,x)\in\mathbb{R}\times\Omega} \int_0^{\infty} su(t,x;ds)(\Omega) < \infty \tag{3.7}$$

to express that life expectancy is uniformly bounded. For many submodels $u(t,x;s)(\Omega)$ will actually converge exponentially to zero as $s \to \infty$.

4. Combining i-state development, survival and reproduction

Consider one individual which at time t has state x. By $u^c(t,x;s)$ we want to describe the expected size and composition of its clan, including the individual itself. So we define:

$$u^c(t,x;s) = u(t,x;s) + \int\limits_{[0,s)\times\Omega} u(t+\tau,\xi;s-\tau)\Lambda^c(t,x)(d\tau\times d\xi) \tag{4.1}$$

What properties of u^c follow from this explicit definition? Clearly for any $\omega \subset \Omega$ the function

$$(t,x;s) \longmapsto u^c(t,x;s)(\omega)$$

from $\mathbb{R}\times\Omega\times\mathbb{R}_+$ to $\mathbb{R}$ is measurable. The estimate

$$u^c(t,x;s)(\Omega) \le 1 + \int\limits_0^s \Lambda^c(t,x)(d\tau\times\Omega)$$

readily implies that

$$u^c(t,x;s)(\Omega) \le 1 + Ke^{z_0 s}$$

whenever $\| \Lambda^c \|_{z_0} \le K$ or, in words, Λ^c is a Laplace kernel (cf. Theorem 2.11).

We now want to verify that u^c satisfies the Chapman-Kolmogorov relation. It turns out that it is convenient to prove first the analogue of (3.5).

Lemma 4.1. *Our assumptions concerning Λ and u guarantee that the identity*

$$\Lambda^c(t,x)(A_s) = \int\limits_\Omega \Lambda^c(t+s,\xi)(A)u^c(t,x;s)(d\xi) \tag{4.2}$$

holds for Λ^c defined by (2.7) and u^c defined by (4.1).

Proof. According to the renewal equation (2.9)

$$\Lambda^c(t,x)(A_s) = \Lambda(t,x)(A_s) + \int\limits_{\mathbb{R}_+\times\Omega} \Lambda(t+\tau,\xi)(A_{s-\tau})\Lambda^c(t,x)(d\tau\times d\xi).$$

We decompose $\mathbb{R}_+\times\Omega = ([0,s)\times\Omega)\cup([s,\infty)\times\Omega)$ and use (3.5) to write

$$\Lambda^c(t,x)(A_s) = \int\limits_\Omega \Lambda(t+s,\eta)(A)u(t,x;s)(d\eta)$$

$$+ \int\limits_{[0,s)\times\Omega}\int\limits_\Omega \Lambda(t+s,\eta)(A)u(t+\tau,\xi;s-\tau)(d\eta)\Lambda^c(t,x)(d\tau\times d\xi)$$

$$+ \int\limits_{[s,\infty)\times\Omega} \Lambda(t+\tau,\xi)(A_{s-\tau})\Lambda^c(t,x)(d\tau\times d\xi)$$

Using (4.1), a change in the order of integration of the second term, and the new integration variable $\sigma = \tau - s$ in the third term, we deduce that

$$\Lambda^c(t,x)(A_s) = \int\limits_\Omega \Lambda(t+s,\eta)(A)u^c(t,x;s)(d\eta)$$

$$+ \int_{\mathbb{R}_+ \times \Omega} \Lambda(t+s+\sigma,\xi)(A_{-\sigma})\Lambda^c(t,x)([s,s+d\sigma]\times d\xi).$$

Now define f by

$$f(t,x)(A) = \int_{\Omega} \Lambda(t,\eta)(A)u^c(t-s,x;s)(d\eta)$$

and X by

$$X(t,x)(A) = \Lambda^c(t-s,x)(A_s)$$

then, upon replacing t by $t-s$, we can write this identity as the renewal equation

$$X = f + \Lambda \otimes X.$$

So, by Corollary 2.4, we have

$$X = f + \Lambda^c \otimes f$$

or, written out in detail while inserting $t+s$ for t;

$$\begin{aligned}
&\Lambda^c(t,x)(A_s) = \int_{\Omega} \Lambda(t+s,\eta)(A)u^c(t,x;s)(d\eta) \\
&+ \int_{\mathbb{R}_+ \times \Omega} \Lambda^c(t+s+\tau,\xi)(A_{-\tau}) \int_{\Omega} \Lambda(t+s,\eta)(d\tau\times d\xi)u^c(t,x;s)(d\eta) \\
&= \int_{\Omega} (\Lambda(t+s,\eta)(A) + (\Lambda^c \otimes \Lambda)(t+s,\eta)(A))u^c(t,x;s)(d\eta) \\
&= \int_{\Omega} \Lambda^c(t+s,\eta)(A)u^c(t,x;s)(d\eta).
\end{aligned}$$

□

LEMMA 4.2. *Our assumptions concerning Λ and u guarantee that u^c defined by (4.1) satisfies the Chapman-Kolmogorov equation, i.e.*

$$u^c(t,x;s) = \int_{\Omega} u^c(t+\sigma,\xi;s-\sigma)u^c(t,x;\sigma)(d\xi) \tag{4.3}$$

for all $0 \le \sigma \le s$.

PROOF. According to (4.1) and (3.2)

$$\begin{aligned}
u^c(t,x;s) &= u(t,x;s) + \int_{[0,\sigma)\times\Omega} u(t+\tau,\eta;s-\tau)\Lambda^c(t,x)(d\tau\times d\eta) \\
&+ \int_{[\sigma,\infty)\times\Omega} u(t+\tau,\eta;s-\tau)\Lambda^c(t,x)(d\tau\times d\eta) \\
&= \int_{\Omega} u(t+\sigma,\xi;s-\sigma)u(t,x;\sigma)(d\xi) \\
&+ \int_{\Omega} u(t+\sigma,\xi;s-\sigma) \int_{[0,\sigma)\times\Omega} u(t+\tau,\eta;\sigma-\tau)(d\xi)\Lambda^c(t,x)(d\tau\times d\eta) \\
&+ \int_{[0,s-\sigma)\times\Omega)} u(t+\sigma+\alpha,\eta;s-\sigma-\alpha)\Lambda^c(t,x)([\sigma,\sigma+d\alpha]\times d\eta).
\end{aligned}$$

By the defining relation (4.1) the sum of the first two terms equals

$$\int_{\Omega} u(t+\sigma,\xi;s-\sigma)u^c(t,x;\sigma)(d\xi)$$

while by Lemma 4.1 the last term can be rewritten as

$$\int_{[0,s-\sigma)\times\Omega} u(t+\sigma+\alpha,\eta;s-\sigma-\alpha)\int_{\Omega}\Lambda^c(t+\sigma,\xi)(d\alpha\times d\eta)u^c(t,x;\sigma)(d\xi).$$

Combining these steps we find that

$$u^c(t,x;s) = \int_{\Omega}[u(t+\sigma,\xi;s-\sigma)+ \int_{[0,s-\sigma)\times\Omega} u(t+\sigma+\alpha,\eta;s-\sigma-\alpha)\Lambda^c(t+\sigma,\xi)(d\alpha\times d\eta)]u^c(t,x;\sigma)(d\xi).$$

Using definition (4.1) once more we finally arrive at

$$u^c(t,x;s) = \int_{\Omega} u^c(t+\sigma,\xi;s-\sigma)u^c(t,x;\sigma)(d\xi). \qquad \square$$

Let us summarise the situation. We have introduced two ingredients Λ and u that together fully specify a linear, time-dependent, structured population model. From these we have defined, by a constructive procedure, u^c such that $u^c(t,x;s)$ is the measure on Ω that describes at time $t+s$ the expected size and composition of the population descending from one individual at time t having state x. This interpretation demands that u^c satisfies the Chapman-Kolmogorov equation. We have verified that the construction procedure at the i-level guarantees that the Chapman-Kolmogorov equation indeed holds and we are ready to take up the bookkeeping at the p-level. As we will see, this now simply amounts to adding contributions.

5. The population level

Let $M(\Omega)$ denote the linear space of measures on the i-state space Ω and $M_+(\Omega)$ the subset of positive measures. The generic element is denoted by m. We now define linear operators mapping $M(\Omega)$ into itself and leaving $M_+(\Omega)$ invariant. Reproduction operators are denoted by V and next-state operators by U. Such operators carry an index i which can take the values 1 and c. When the index equals 1 we often suppress it in the notation (in fact we have done so consistently in the foregoing).

Definition 5.1.

$$(V^i(t+\tau,\tau)m)(\omega) := \int_{\Omega}\Lambda^i(\tau,x)([0,t)\times\omega)m(dx) \tag{5.1}$$

$$(U^i(t+\tau,\tau)m)(\omega) := \int_{\Omega} u^i(\tau,\xi;t)(\omega)m(d\xi) \tag{5.2}$$

The Chapman-Kolmogorov equations (3.2) and (4.3) and the consistency conditions (3.3) and (4.2) have as an immediate

Corollary 5.2. For $0\le\sigma\le s$

$$U^i(t+s,t) = U^i(t+s,t+\sigma)U^i(t+\sigma,t) \tag{5.3}$$

and

$$V^i(t+s,t) = V^i(t+\sigma,t) + V^i(t+s,t+\sigma)U^i(t+\sigma,t) \tag{5.4}$$

The identity (5.3) can be summarised in words by saying that U^i forms a (forward) evolutionary system while, in the terminology of DIEKMANN, GYLLENBERG and THIEME [4, 3], (5.4) expresses that V^i is a cumulative output family for the evolutionary system U^i.

Symbolically, we can lift the renewal equations (2.8) and (2.9) and the definition (4.1) to the p-level as well and write

$$V^c(t+s,t) = V(t+s,t) + \int_t^{t+s} V(t+s,\sigma)V^c(d\sigma,t) \tag{5.5}$$

$$V^c(t+s,t) = V(t+s,t) + \int_t^{t+s} V^c(t+s,\sigma)V(d\sigma,t) \tag{5.6}$$

$$U^c(t+s,t) = U(t+s,t) + \int_t^{t+s} U(t+s,\sigma)V^c(d\sigma,t) \tag{5.7}$$

In earlier work, we have taken such abstract equations and identities as our starting point, putting quite some energy in the precise underpinning of the abstract Stieltjes integral. Now we tend to view them as a kind of shorthand notation: in order to give them a precise meaning (in particular the integrals), we have to apply both sides to a measure m and then 'insert' a set $\omega \subset \Omega$. The key point is that the operators are defined in terms of kernels which satisfy certain identities!

6. GROWTH OR DECLINE IN A CONSTANT ENVIRONMENT?

In the case of a constant environment both $\Lambda(t,x)$ and $u(t,x;s)$ are independent of t. It then follows that the same is true for $\Lambda^c(t,x), u^c(t,x;s), V^i(t+s,t)$ and $U^i(t+s,t)$. In particular the one-parameter family of operators

$$T^i(s) := U^i(t+s,t) \tag{6.1}$$

forms a semigroup with

$$W^i(s) := V^i(t+s,t) \tag{6.2}$$

as a corresponding cumulative output family.

In a constant environment the time of birth does not matter and we can, if we like, study the population from a *generation* perspective. Let the measure m on Ω describe the size of a generation and its distribution with respect to state at birth. Then $W(\infty)m$ defined by

$$(W(\infty)m)(\omega) = \int_\Omega \Lambda(x)(\mathbb{R}_+ \times \omega)m(dx) \tag{6.3}$$

contains exactly that same information concerning the next generation and consequently we shall call $W(\infty)$ the next generation operator (note: here and in the following we suppress t in the notation for Λ; our choice to work with relative time for the time component of the birth coordinates, instead of absolute time, was actually motivated by the wish to achieve such a straightforward reduction in the notation for the case of a constant environment).

When $\sup_{x\in\Omega} \Lambda(x)(\mathbb{R}_+ \times \Omega)$ is bounded, $W(\infty)$ is a bounded linear operator on $M(\Omega)$, equipped with the total variation norm.

The *basic reproduction ratio* R_0 is by definition the spectral radius of $W(\infty)$.

In most cases of interest positivity arguments guarantee that R_0 is an eigenvalue (usually called the *dominant* eigenvalue). An irreducibility assumption is needed to accomplish that R_0 is the only positive eigenvalue and that it is simple. When further conditions bring about that the rest of the spectrum is contained in a circle with radius *strictly* less than R_0, it is clear that iteration of $W(\infty)$ leads to a *stable distribution* for the state-at-birth (viz., the eigenvector corresponding to R_0 normalized such that the measure of Ω equals one), while the population size changes in the long run with a factor R_0 from generation to generation. We therefore identify R_0 with the generation growth rate.

In order to characterise the population growth rate in real time we consider the Laplace-Stieltjes transform

$$(d\hat{W}(z)m)(\omega) = \int_{\mathbb{R}_+ \times \Omega} e^{-z\tau}\Lambda(x)(d\tau \times \omega)m(dx). \tag{6.4}$$

Note that $d\hat{W}(z)$ adds offspring, while discounting for the reproduction delay by weighing a newborn with $e^{-z\tau}$ when the time interval between the birth of mother and daughter equals τ. This interpretation suggests, as FISCHER [13] made clear in the context of the Euler-Lotka characteristic equation for age-dependent population growth, that the population growth rate r in real time is determined by the condition that $d\hat{W}(r)$ should have dominant eigenvalue 1. When $R_0 > 1$ the equation

$$\text{spectral radius } d\hat{W}(z) = 1 \tag{6.5}$$

has a unique solution $z = r$ on the real line and necessarily $r > 0$. When $R_0 < 1$ the existence of a real solution of (6.5) is not guaranteed, as the integral in (6.4) may grow insufficiently when we approach the abscissa of convergence. But additional conditions (see JAGERS [22], SHURENKOV [28]) are known that guarantee the existence of r also in this case, and then necessarily $r < 0$. We note that r is often called the Malthusian parameter.

The eigenvector of $d\hat{W}(r)$ corresponding to the eigenvalue one describes the *stable distribution* for the state-at-birth when we sample newborns at a particular moment in time (which is different indeed from sampling newborns that belong to a specific generation).

In summary, and with reference to the end of section 2, we conclude that, under suitable conditions, both the generation growth rate R_0 and the Malthusian parameter r are well-defined once Λ is specified and that $r > 0$ if and only if $R_0 > 1$. To prove that r is indeed the growth rate of the semigroup $T^c(s)$ defined by (6.1) one can employ Laplace transforms. We shall deal with this method in the next section . It requires conditions which are somewhat stronger than needed and it is worth the effort to consult SHURENKOV [29, 30] and THIEME [31], for general results covering both the lattice and the non-lattice case (see FELLER [12] for these notions and for the main ideas in the simplest context).

The borderline case $R_0 = 1$ is of special interest, as it leads to a steady state. For (abstract) differential equations $\frac{dy}{dt} = Ay$ one can spot steady states by solving $Ay = 0$; in particular one can characterize steady states directly in terms of the given ingredient A, without paying any attention to (the construction of) the semigroup of solution operators generated by A. The aim of the rest of this section is to expose explicitly the corresponding result for the setting of the non-local ingredients Λ and u. For the linear situation the question is perhaps a bit academic, as steady states will be the exception rather than the rule. But in the nonlinear theory of part II the result will play a prominent role. Moreover, in the next section we shall give a very natural extension by expressing the resolvent in terms of Laplace(-Stieltjes) transforms of the ingredients.

When individuals are immortal, a steady state may exist at the generation level, but the total extant population will keep growing. In order to exclude such a degenerate situation we require for the rest of this section that

$$\sup_{x\in\Omega} \int_0^\infty u(x;\tau)(\Omega)d\tau < \infty \tag{6.6}$$

i.e. life expectancy is bounded, uniformly with respect to the state-at-birth.

THEOREM 6.1. *i) Assume that*

$$W(\infty)b = b \tag{6.7}$$

then m defined by

$$m = \int_0^\infty T(\tau)bd\tau = \int_0^\infty \int_\Omega u(\xi;\tau)b(d\xi)d\tau \tag{6.8}$$

is a steady state of $T^c(t)$, i.e.

$$T^c(t)m = m \quad \text{for all } t \geq 0 \tag{6.9}$$

ii) Conversely, let m be a steady state of $T^c(t)$ then b defined by

$$b = \frac{1}{t}W^c(t)m \tag{6.10}$$

does not depend on t and satisfies (6.7).

PROOF. To give a precise meaning to the integrals and identities that follow, one should insert an arbitrary set $\omega \subset \Omega$ to obtain $\mathbb{R}$-valued functions of t.
i) Assume (6.7) and define m by (6.8) (note that m is well-defined, since we assumed (6.6)). Then

$$W(t)m = W(t)\int_0^\infty T(\tau)bd\tau = \int_0^\infty W(t)T(\tau)bd\tau.$$

So by (5.4) we find

$$\begin{aligned} W(t)m &= \int_0^\infty [W(t+\tau) - W(\tau)]bd\tau \\ &= \int_0^\infty [W(t+\tau) - W(\infty)]bd\tau + \int_0^\infty [W(\infty) - W(\tau)]bd\tau \\ &= \int_t^\infty [W(\tau) - W(\infty)]bd\tau + \int_0^\infty [W(\infty) - W(\tau)]bd\tau \\ &= \int_0^t [W(\infty) - W(\tau)]bd\tau = tb - \int_0^t W(\tau)bd\tau. \end{aligned}$$

The autonomous version of (5.6) reads

$$W^c(t) = W(t) + \int_0^t W^c(t-\sigma)W(d\sigma). \tag{6.11}$$

Applying both sides to m and using the expression for $W(t)m$ we find

$$W^c(t)m = tb - \int_0^t W(\tau)bd\tau + \int_0^t W^c(\sigma)bd\sigma - \int_0^t W^c(t-\sigma)W(\sigma)bd\sigma.$$

If, on the other hand, we integrate over time, we obtain

$$\int_0^t W^c(\tau)d\tau = \int_0^t W(\tau)d\tau + \int_0^t W^c(t-\sigma)W(\sigma)d\sigma.$$

Combining these two identities we see that necessarily

$$W^c(t)m = tb.$$

The autonomous version of (5.7) reads

$$T^c(t) = T(t) + \int_0^t T(t-\tau)W^c(d\tau). \tag{6.12}$$

Applying both sides to m we deduce that

$$\begin{aligned} T^c(t)m &= T(t)m + \int_0^t T(t-\tau)bd\tau = \int_0^t T(\tau)bd\tau + \int_t^\infty T(\tau)bd\tau \\ &= \int_0^\infty T(\tau)bd\tau = m. \end{aligned}$$

ii) Assume (6.9). Then

$$W^c(t+s)m - W^c(s)m = W^c(t)T^c(s)m = W^c(t)m.$$

It follows that for rational t

$$W^c(t)m = tW^c(1)m.$$

But if we evaluate for a set $\omega \subset \Omega$ we obtain a non-decreasing real-valued function and a sandwich argument makes clear that the identity necessarily holds for all t.

Define

$$b = W^c(1)m.$$

Then

$$\begin{aligned} b &= \frac{1}{t}W^c(t)m = \frac{1}{t}W(t)m + \frac{1}{t}\int_0^t W(t-\tau)W^c(d\tau)m \\ &= \frac{1}{t}W(t)m + \frac{1}{t}\int_0^t W(\sigma)bd\sigma. \end{aligned}$$

For $t \to \infty$ the right hand side converges to $W(\infty)b$ and we conclude that necessarily

$$b = W(\infty)b.$$

□

The biological interpretation of Theorem 6.1 is that steady states for the generation process and for the real time process are in one to one correspondence. For the generation process, we have to compute the eigenvector of eigenvalue 1 for the operator $W(\infty)$ defined directly in terms of Λ. Next we can use the operators $T(t)$, defined directly in terms of u, to compute the real time steady state m from the generation steady state b. So the i) part of Theorem 6.1 delineates a constructive procedure for determining the steady states directly from the ingredients that specify the model, while the ii) part makes sure that we cannot possibly miss a steady state in this manner.

7. The resolvent

A steady state exists when $z = 0$ is a singularity of the resolvent of the generator. In this section we extend our interest to singularities in general. More precisely, we shall employ the Laplace transform to derive a product representation for the resolvent, which exemplifies the perturbation approach. A key point is that the factors are directly expressed in terms of Laplace transforms of the ingredients.

Recalling that

$$(T^i(t)m)(\omega) = \int_\Omega u^i(x;t)(\omega)m(dx) \tag{7.1}$$

and

$$(W^i(t)m)(\omega) = \int_\Omega \Lambda^i(x)([0,t)\times\omega)m(dx) \tag{7.2}$$

we define the Laplace transform of T and the Laplace-Stieltjes transform of W by the explicit formulas

$$(\hat{T}^i(z)m)(\omega) = \int_{\mathbb{R}_+\times\,\Omega} e^{-zt}u^i(x;t)(\omega)dtm(dx). \tag{7.3}$$

$$(d\hat{W}^i(z)m)(\omega) = \int_{\mathbb{R}_+\times\,\Omega} e^{-zt}\Lambda^i(x)(dt\times\omega)m(dx) \tag{7.4}$$

Throughout this section we assume that Λ is a Laplace kernel, so that (7.4) makes sense for Re z sufficiently large (cf. Theorem 2.11). According to the estimates from the beginning of Section 4, the definition (7.3) with $i = c$ then makes sense as well for Re z large. Actually, as we show now, one can express $\hat{T}^c$ in terms of $\hat{T}$ and $d\hat{W}$.

Theorem 7.1. *For* Rez *sufficiently large the identity*

$$\hat{T}^c(z) = \hat{T}(z)(I - d\hat{W}(z))^{-1} \tag{7.5}$$

holds.

Proof. Taking Laplace transforms of the renewal equation (6.11) we find

$$I + d\hat{W}^c(z) = (I - d\hat{W}(z))^{-1}$$

The identity (6.12) likewise transforms into

$$\hat{T}^c(z) = \hat{T}(z)(I + d\hat{W}^c(z))$$

and by combining the two we obtain (7.5) (which appears as (1.16) in [3]). □

In general $\hat{T}(z)$ will be analytic in some (relatively large, i.e. extending quite far to the left) right half plane, and so will be $d\hat{W}(z)$. The representation (7.5) therefore demonstrates that $z \in \mathbb{C}$ for which $I - d\hat{W}(z)$ is non-invertible are of paramount importance when studying asymptotic behaviour and the related decomposition of the state space $M(\Omega)$.

In the construction of $(I - d\hat{W}(z))^{-1}$ one can make certain reductions, just as in the construction of the generation expansion discussed in subsection 2.5 (and for the same biological reasons). Recalling the Definition 2.5 of a set representing the birth states, we first of all note that the decomposition

$$\Omega = \Omega_b \cup (\Omega\backslash\Omega_b)$$

induces a direct sum decomposition

$$M(\Omega) = M(\Omega_b) \oplus M(\Omega \backslash \Omega_b) \tag{7.6}$$

with corresponding projection operator on $M(\Omega_b)$

$$(Pm)(\omega) = m(\omega \cap \Omega_b). \tag{7.7}$$

The fact that the range of $d\hat{W}(z)$ is contained in $M(\Omega_b)$ motivates the following elementary auxiliary result.

LEMMA 7.2. *Let X be a Banach space and P a projection operator on X such that, with $Y = \mathcal{R}(P)$ and $Z = \mathcal{R}(I-P)$,*

$$X = Y \oplus Z.$$

Let K be a linear operator on X with $\mathcal{R}(K) \subset Y$. Then $I-K$ is invertible if and only if $(I-K)|_Y$ is invertible and

$$(I-K)^{-1} = (I-K)|_Y^{-1}(P + K(I-P)) + I - P \tag{7.8}$$

COROLLARY 7.3. *Define $d\hat{W}_b(z) : M(\Omega_b) \to M(\Omega_b)$ by*

$$(d\hat{W}_b(z)m)(\omega) = \int\limits_{\mathbb{R}_+ \times \Omega_b} e^{-zt}\Lambda_b(x)(dt \times \omega)m(dx). \tag{7.9}$$

Then $I - d\hat{W}(z)$ is invertible if and only if $I - d\hat{W}_b(z)$ is invertible. Moreover, the formula (7.8) allows the us to compute the residue of $(I - d\hat{W}(z))^{-1}$ in a pole from the Laurent expansion of $(I - d\hat{W}_b(z))^{-1}$ and the Taylor expansion of $d\hat{W}(z)$.

When only finitely many states at birth are possible, i.e. Ω_b is finite, the condition amounts to the invertibility of a matrix and by taking the determinant we find a characteristic equation. As we now explain, the same is possible when there are only finitely many states at birth in a stochastic sense. By this we mean that $\Lambda_b(x)$ is the sum of finitely many product measures, i.e.

$$\Lambda_b(x)(A) = \sum_{i=1}^{n} (\beta_i(x) \times \gamma_i)(A) \tag{7.10}$$

or, in more detail, that for any $t \geq 0$ and $\omega \subset \Omega_b$

$$\Lambda_b(x)([0,t) \times \omega) = \sum_{i=1}^{n} \beta_i(x)([0,t))\gamma_i(\omega). \tag{7.11}$$

In words one could say that the range of $\Lambda_b(x)$ is spanned by finitely many product measures on $\mathbb{R}_+ \times \Omega_b$, with the second factors the same for all x. As a consequence, the range of $d\hat{W}_b(z)$ is, for all allowable z, spanned by finitely many measures on Ω_b, viz. the $\{\gamma_i\}$.

THEOREM 7.4. *Assume that Λ_b allows the representation (7.11). Then $I - d\hat{W}(z)$ is invertible if and only if*

$$\det \Delta(z) \neq 0 \tag{7.12}$$

where $\Delta(z)$ is the $n \times n$-matrix with entries

$$\Delta(z)_{ij} = \int\limits_{\mathbb{R}_+ \times \Omega_b} e^{-zt}\beta_i(x)(dt)\gamma_j(dx). \tag{7.13}$$

PROOF. Combination of (7.9) and (7.11) yields that

$$(d\hat{W}_b(z)m)(\omega) = \sum_{i=1}^{n} \int_{\mathbb{R}_+ \times \Omega_b} e^{-zt}\beta_i(x)(dt)m(dx)\gamma_i(\omega)$$

from which we deduce that indeed the range of $d\hat{W}_b(z)$ is spanned by $\{\gamma_i\}$. The conclusion now follows from Corollary 7.3 and another application of Lemma 7.2. □

REMARK. A minor further simplification is possible when $\beta_i(x)([0,t)) = c_i(x)b_i([0,t))$, since then we can compute $\Delta(z)$ from the product representation

$$\Delta(z)_{ij} = \int_{\Omega_b} c_i(x)\gamma_j(dx) \int_0^\infty e^{-zt} b_i(dt).$$

The key point in Theorem 7.4 is the finite dimensionality of the range of $d\hat{W}_b(z)$. We now expose another situation in which that is the case (and refer to [5] for a concrete example). Assume we can identify a renewal set Ω_r and measures $\pi(x)$ such that (2.17), which we here repeat for the autonomous case as

$$\Lambda_b(x)(A) = \int_{\mathbb{R}_+ \times \Omega_r} \Lambda(\xi)(A_{-\tau})\pi(x)(d\tau \times d\xi), \tag{7.14}$$

holds. Next, assume that Ω_r is finite, say

$$\Omega_r = \{\xi_1, \xi_2, \ldots, \xi_n\}.$$

Then

$$\Lambda_b(x)(A) = \sum_{i=1}^{n} \int_{\mathbb{R}_+} \Lambda(\xi_i)(A_{-\tau})\pi_i(x)(d\tau) \tag{7.15}$$

and consequently

$$(d\hat{W}_b(z)m)(\omega) = \sum_{i=1}^{n} \int_{\mathbb{R}_+} e^{-z\sigma}\Lambda(\xi_i)(d\sigma \times \omega) \int_{\mathbb{R}_+ \times \Omega_b} e^{-z\tau}\pi_i(x)(d\tau)m(dx).$$

So now the range of $d\hat{W}_b(z)$ is spanned by measures γ_i defined by

$$\gamma_i(z;\omega) = \int_{\mathbb{R}_+} e^{-z\sigma}\Lambda(\xi_i)(d\sigma \times \omega).$$

Note in particular that the range has fixed dimension but a z-dependent basis!

THEOREM 7.5. *Assume that Λ_b allows the representation (7.15). Then $I - d\hat{W}(z)$ is invertible if and only if*

$$\det \Delta(z) \neq 0$$

where $\Delta(z)$ is the $n \times n$-matrix with entries

$$\Delta(z)_{ij} = \int_{\mathbb{R}_+ \times \Omega_b} e^{-z\tau}\pi_i(x)(d\tau) \int_{\mathbb{R}_+} e^{-z\sigma}\Lambda(\xi_j)(d\sigma \times dx) \tag{7.16}$$

Suppose λ is a zero of $\det \Delta(z)$. We should be able to define, by residue calculus, a spectral projection operator P_λ. We conjecture that the dimension of $P_\lambda M(\Omega)$ equals the multiplicity of λ as a zero of $\det \Delta(z)$. On $P_\lambda M(\Omega)$ the action of $T^c(t)$ is described by an ode. The Jordan structure should follow from the structure of the Jordan chains of Δ, just as in the case of delay equations (cf. Section IV. 4 of [7]. We intend to elaborate these issues in a joint publication with S.M. Verduyn Lunel.

When (7.14) holds, but Ω_r is not finite, an infinite-dimensional variation on the same theme arises. In that case it is natural to decompose the Laplace-Stieltjes transform of W_b into two factors. For this purpose we define $L(z) : M(\Omega_b) \to M(\Omega_r)$ and $K(z) : M(\Omega_r) \to M(\Omega_b)$ by, respectively,

$$(L(z)m)(\omega) = \int_{\mathbb{R}_+ \times \Omega_b} e^{-zt}\pi(x)(dt \times \omega)m(dx) \tag{7.17}$$

and

$$(K(z)m)(\omega) = \int_{\mathbb{R}_+ \times \Omega_r} e^{-zt}\Lambda(x)(dt \times \omega)m(dx). \tag{7.18}$$

LEMMA 7.6. (i) $d\hat{W}_b(z) = K(z)L(z)$

ii) *Define* Λ_r by (cf. (2.18))

$$\Lambda_r(x)(A) = \int_{\mathbb{R}_+ \times \Omega_b} \pi(\xi)(A_{-\tau})\Lambda(x)(d\tau \times d\xi) \tag{7.19}$$

where $x \in \Omega_r$ *and* $A \subset \mathbb{R}_+ \times \Omega_r$. *Next define* $d\hat{W}_r(z)$ *by*

$$(d\hat{W}_r(z)m)(\omega) = \int_{\mathbb{R}_+ \times \Omega_r} e^{-zt}\Lambda_r(x)(dt \times \omega)m(dx). \tag{7.20}$$

Then

$$d\hat{W}_r(z) = L(z)K(z).$$

Essentially this lemma is just the familiar result that convolution becomes a product under the Laplace transform. The proof consists of writing everything out in detail and applying Fubini's theorem, and we omit it.

Let us first assume that $L(z)$ is surjective and that

$$M(\Omega_b) = Y \oplus Z$$

with $\mathcal{R}(K(z)) = Y$ and $L(z) : Y \to M(\Omega_r)$ injective. Lemma 7.2 implies that $I - K(z)L(z)$ is invertible if and only if $(I - K(z)L(z))|_Y$ is invertible. The latter condition, in turn, is equivalent to the invertibility of $I - L(z)K(z)$.

One can relate the invertibility of $I - K(z)L(z)$ to that of $I - L(z)K(z)$ under more general conditions involving, in particular, a decomposition of $M(\Omega_r)$ as well. We refrain from a further elaboration, the main point being anyhow that one can exploit the idea of renewal points to discover structure in the construction of the resolvent (see e.g. [5]).

The resolvent representation (7.5) is the key step for proving results concerning asymptotic large time behaviour. We first recall a fact which is rather hidden in the notation: (7.5) is a statement about the Laplace transforms of a collection of $\mathbb{R}$-valued functions obtained by applying the semigroup to a particular measure and evaluating for a particular subset of Ω. Hence we can apply Tauberian theorems from classical analysis (see in particular WIDDER [32]) to deduce the asymptotic behaviour for $t \to \infty$ from the behaviour of the Laplace transform for z near r (cf. (6.5)), while exploiting positivity. Thus one can show that, when all other singularities satisfy the strict inequality $\mathrm{Re}\ z < r$, asymptotically for $t \to \infty$ balanced exponential growth obtains:

$$(T^c(t)m)(\omega) \sim C(m)e^{rt}\phi(\omega),\ t \to \infty,$$

where ϕ is the eigenvector of $d\hat{W}(r)$ corresponding to the eigenvalue 1 and C is a constant depending on m. When Ω is equipped with a locally compact Hausdorff topology one can reformulate this as convergence of

$$e^{-rt}(T^c(t)m - C(m)\phi)$$

with respect to the weak * topology. We refrain from a detailed elaboration of such inferences while noting that, alternatively, one can refer to SHURENKOV [29, 30], JAGERS [21] or THIEME [31] (in preparation) for formulations of such results appropriate for the present generality. We emphasize that Shurenkov and Jagers also deal with the much more subtle "lattice" case, characterized by the presence of a discrete additive subgroup of singularities on the line $\mathrm{Re}z = r$ (also see [5] for a concrete example of this phenomenon, elaborated in full detail).

8. EXAMPLES

To make the examples easily accessible we have chosen to formulate them for the autonomous (i.e. time independent) situation. The non-autonomous situation requires a more elaborate notation, but is otherwise identical. To underline this we have indicated for one particular example, viz. 8.3, how the extension proceeds.

8.1. Age

When age qualifies as i-state, we have $\Omega = \mathbb{R}_+ = [0, \infty)$ and $\Omega_b = \{0\}$. We write

$$\Lambda_b(0)([0, s) \times \omega) = L(s)\delta_0(\omega)$$

where $L(s)$ is the expected number of children produced before reaching (dead or alive) age s, and δ_0 is the Dirac measure concentrated in $a = 0$. When incorporating grandchildren etc. we similarly have

$$\Lambda_b^c([0, s) \times \omega) = R(s)\delta_0(\omega)$$

where R and L are related by the reduced renewal equation

$$R(s) = L(s) + \int_{[0,s)} L(s - \tau)R(d\tau) = L(s) + \int_{[0,s)} R(s - \tau)L(d\tau)$$

or, equivalently, by the generation expansion

$$R = \sum_{k=1}^{\infty} L^{k\otimes}.$$

Note that $R_0 = L(\infty)$ and that r is the real root of the equation

$$\int_{\mathbb{R}_+} e^{-r\tau}L(d\tau) = 1.$$

In order to describe the age composition of the extant population we need as a second ingredient the survival probability $\mathcal{F}(a)$. From L and $\mathcal{F}$ we can compute the expected number $L_a(s)$ of children produced by an a year old individual before reaching age $a + s$ as

$$L_a(s) = \frac{L(a + s) - L(a)}{\mathcal{F}(a)}.$$

The corresponding quantity with all generations included is given explicitly by

$$Q_a(s) = L_a(s) + \int_{[0,s)} R(s-\tau)L_a(d\tau)$$

(it is here that we exploit that all newborns have age zero and that, accordingly, we only have an equation for $Q_0 = R$). Clearly

$$u^c(a;s) = u(a;s) + \int_{[0,s)} \delta_{s-\tau}\mathcal{F}(s-\tau)Q_a(d\tau)$$

where

$$u(a;s) = \frac{\mathcal{F}(a+s)}{\mathcal{F}(a)}\delta_{a+s}.$$

And just for completeness we note that

$$\Lambda(a)([0,s)\times\omega) = L_a(s)\delta_0(\omega),$$

and

$$\Lambda^c(a)([0,s)\times\omega) = Q_a(s)\delta_0(\omega).$$

8.2. Age plus state-at-birth

Assume that $\Omega = \mathbb{R}_+ \times Y$, where the first component corresponds to age and the second, essentially, to state-at-birth, in the sense that it is constant during life. Then $u((0,y);s)$ is necessarily concentrated in (s,y) and so we can define a survival function $\mathcal{F}(y)(s)$ by

$$u((0,y);s) = \delta_{(s,y)}\mathcal{F}(y)(s)$$

while, conversely, given such a family of survival functions we can define u by

$$u((a,y);s) = \delta_{(a+s,y)}\frac{\mathcal{F}(y)(a+s)}{\mathcal{F}(y)(a)}.$$

Likewise we can use the consistency condition (3.4) to express $\Lambda((a,y))$ in terms of $\Lambda((0,y))$ and $\mathcal{F}(y)(a)$. Note that $\Omega_b = \{0\}\times Y$.

In order to express conveniently that $\Lambda((0,y))$ is concentrated in $\mathbb{R}_+ \times \{0\}\times Y$ we introduce

$$J : \{0\}\times Y \to Y \quad , \quad J(0,y) = y.$$

With a slight abuse of notation we use the same symbol J to denote the induced mapping from $\mathbb{R}_+ \times \{0\}\times Y$ into $\mathbb{R}_+ \times Y$ defined by $J(s,(0,y)) = (s,y)$.

Let, for $y \in Y$ and $\tilde{A} \subset \mathbb{R}_+ \times Y$, $\tilde{\Lambda}(y)(\tilde{A})$ be the expected number of children with birth coordinates in $J^{-1}\tilde{A}$, of an individual with state-at-birth y.

We then require that

$$\Lambda((0,y))(A) = \tilde{\Lambda}(y)(J(A\cap(\mathbb{R}_+\times\{0\}\times Y)))$$

and

$$\Lambda((a,y))(A) = \frac{\Lambda((0,y))(A_a)}{\mathcal{F}(y)(a)}.$$

We conclude that the model is fully specified by the collection of survival functions $\mathcal{F}(y)$ and the collection of positive measures $\tilde{\Lambda}(y)$.

How special is the assumption that $\Omega = \mathbb{R}_+ \times Y$? For a constant environment and general i-state, one can always define, for all possible birth states y, the survival functions $\mathcal{F}(y)$ and the reproduction

kernel $\tilde{\Lambda}(y)$. So for all individuals born after the time at which we pose an initial condition, we can equivalently work with the combination of state-at-birth and age. In particular, the salient aspects of the asymptotic behaviour can be discussed in those terms. As far as the initial condition is concerned, things are a bit more delicate. When movement is deterministic (i.e. described by an ode), we can reconstruct the birth state from the present state and work with state-at-birth throughout. In general, that is impossible.

We shall now illustrate these remarks with a concrete example.

8.3. Age and birth position in space

Let $Y \subset \mathbb{R}^n$ denote a spatial region. To describe dispersal from the position at birth, we introduce a family of measures $w(a,y)$ on Y such that, for any subset $D \subset Y$, the number $w(a,y)(D)$ gives the probability that an individual born at position $y \in Y$ is alive at age a and then is situated in D. As a second ingredient we introduce the rate $\beta(a,x)$ of giving birth while having age a and being at position x.

For the survival probability we have

$$\mathcal{F}(y)(s) = w(s,y)(Y).$$

For $\tilde{A} \subset \mathbb{R}_+ \times Y$ of the form $\tilde{A} = [0,a) \times D$ the production of children in $\tilde{A}$ is described by

$$\tilde{\Lambda}(y)(\tilde{A}) = \int_0^a \int_D \beta(\alpha,x) w(\alpha,y)(dx) d\alpha$$

and subsequently the definition of $\tilde{\Lambda}(y)$ is extended to arbitrary measurable $\tilde{A}$ by approximation.

As a next step in our top down approach we may define the measures $w(a,y)$ by fundamental solutions of a diffusion equation (i.e. Green's function). So let

$$w(a,y)(D) = \int_D v(y;a,x)dx$$

where v satisfies

$$\frac{\partial v}{\partial a} = \frac{\partial}{\partial x}(c(a,x)\frac{\partial v}{\partial x}) - \mu(a,x)v$$

$$v(y;0,x) = \delta_y$$

and no-flux boundary conditions whenever D has a boundary (or zero Dirichlet boundary conditions when reaching the boundary is a deadly affair; on unbounded domains the behaviour at infinity is controled by the requirements that $v \geq 0$ and $\int_Y v(y;a,x)dx \leq 1$.

Whenever $c(a,x) \geq \epsilon > 0$ for all $(a,x) \in \mathbb{R}_+ \times D$, we can refer to FRIEDMAN [14] or LADYSHENSKAYA & URALTSJEVA [24] for the existence and uniqueness of the solution v. But actually we have in mind situations where dispersal stops at the end of a juvenile period, so where $c(a,x) = 0$ for large a. When $c(a,x) = e(a)d(x)$ one can use the transformation $\alpha = \alpha(a) = \int_0^a e(\sigma)d\sigma$ to deduce from the standard result the existence and uniqueness of v up to the age at which movement stops, after which one only has to solve an ode. For general c one probably has to approximate with positive c and pass to the limit (most likely one needs some smoothness for the zero-level set $\{(a,x) : c(a,x) = 0\}$). We thank J.C. van Duijn (personal communication [10]) for these suggestions.

Of course it may also be appropriate to assume that movement only starts after some phase of maturation has been completed (e.g., an immobile egg stage). In that case we just take $w(a,y) = \delta_y$ for small a and start using the representation by a density function v that satisfies the diffusion equation only after the immobile stage has ended.

To handle population level initial conditions in terms of current position, rather than position at birth, we use the solution of the diffusion equation with a Dirac measure as an initial condition at an arbitrary age.

It is straightforward to adapt the formalism to the time-dependent situation in which the diffusion coefficient c, the death rate μ and the birth rate β are functions of t, a and x. The family of functions v then carries birth time t as an extra index (in addition to birth position y) and is defined by

$$\frac{\partial v}{\partial a} = \frac{\partial}{\partial x}\left(c(t+a,a,x)\frac{\partial v}{\partial x}\right) - \mu(t+a,a,x)v, \quad v(t,x;0,x) = \delta_y.$$

Likewise the (reduced) reproduction kernel is given by

$$\tilde{\Lambda}(t,y)([0,a)\times D) = \int_0^a \int_D \beta(t+\alpha,\alpha,x)v(t,x;\alpha,x)dxd\alpha.$$

The present example demonstrates, we hope, how stochastic movement in i-state space is incorporated and how one can build ingredients at the high level, with which we started, from submodels for movement, death and reproduction that involve in their turn ingredients that are often rates. Admittedly the matter of the existence and uniqueness of a fundamental solution for diffusion equations, with diffusion coefficients that are dependent on time (which amounts to the same thing as age) and are allowed to become zero, is not an entirely trivial matter and our analysis here has been somewhat superficial. But once the fundamental solution is there, our general results yield strong conclusions about population behaviour.

8.4. Size, with individual differences in growth rate

As a concrete example, think of plants that reproduce by dispersing seeds. Depending on the quality of the site in which the seed lands, the resulting plant may grow slower or faster. We assume that all seeds are equal and that site quality $\xi \in \Omega$ follows a distribution γ (which in no way depends explicitly on spatial position; in other words, γ describes the homogeneous fine structure of the landscape). We ignore crowding.

Let the size z of a plant grow, in a site of quality ξ, according to

$$\begin{cases} \dfrac{dz}{da} = g(z,\xi) \\ z(0;\xi) = z_b \end{cases}$$

We denote the solution by $z(a;\xi)$. Let a plant of size z in a site of quality ξ have a probability $\mu(z,\xi)$ per unit of time of dying. Let a plant of size z in a site of quality ξ produce seeds with probability $\beta(z,\xi)$ per unit of time. These seeds are instantaneously distributed over the sites. Then

$$\Lambda(\xi)([0,t)\times\omega) = \int_0^t \beta(z(a;\xi),\xi)\, e^{-\int_0^a \mu(z(\alpha;\xi),\xi)d\alpha} da\gamma(\omega)$$

So Λ has one-dimensional range spanned by γ and explicitly we have that

$$R_0 = \int_\Omega \int_0^\infty \beta(z(a;\xi),\xi)\, e^{-\int_0^a \mu(z(\alpha;\xi),\xi)d\alpha} da\gamma(d\xi).$$

8.5. Size and age, with fixed or variable birth size

Let $g(a,z), \mu(a,z)$ and $\beta(a,z)$ denote, respectively, the growth-, death- and reproduction rate of an individual with age a and size z. We define functions $z(a;z_b), \mathcal{F}(a;z_b)$ and $L(a;z_b)$ by

$$\begin{cases} \dfrac{dz}{da} = g(a,z) \\ z(0) = z_b \end{cases}$$

$$\mathcal{F}(a;z_b) = \exp\left(-\int_0^a \mu(\alpha, z(\alpha;z_b))d\alpha\right)$$

$$L(a;z_b) = \int_0^a \beta(\alpha, z(\alpha;z_b))\mathcal{F}(\alpha;z_b)d\alpha.$$

When the distribution of z_b is given by a measure γ which does not depend on the age and/or size of the mother, we are still in the one-dimensional situation and R_0 can easily be computed explicitly. When γ does depend on the age or size of the mother, our formalism tells us how to compute the operator whose dominant eigenvalue is R_0. We don't elaborate this step, but hope this somewhat incomplete example illustrates once more that our high level "ingredients" are easily expressed, often somewhat implicitly as solutions of nonlinear ode are involved, in terms of lower level ingredients such as individual growth-, death- and reproduction rates.

8.6. Size structured cell populations
When the smallest size of a mother is larger than the largest size of a daughter, there exists a size interval that a cell necessarily has to transverse in between the fission event in which it is created and the fission event in which it produces two daughters. Any size in this interval qualifies as a renewal point. Thus the problem becomes one dimensional. We refer once more to [5] and the references given there for a detailed elaboration, paying also attention to the lattice case in which the asymptotic behaviour is *not* balanced exponential growth but rather a merry-go-round.

When the smallest size of a mother is only larger than 2^{-k} times the largest size of a daughter for some $k \geq 1$, one can define a renewal set consisting of $k+1$ points and use this to reduce the description of the dynamics to a system of $k+1$ coupled linear renewal equations. See [19, 6].

8.7. Discrete i-state space
Let $\Omega = \{1, 2, \ldots, n\}$. Let us assume that an individuals state is following a continuous time Markov chain with transition matrix M. Let Θ_i denote the i-th unit vector in $\mathbb{R}^n$, i.e. $(\Theta_i)_j = \delta_{ij}$. Then

$$u(i;t) = e^{tM}\Theta_i.$$

Let the reproduction matrix B be composed of the rates at which individuals with state j produce offspring with state-at-birth i. Then

$$\Lambda(i;t) = \int_0^t Be^{\tau M}\Theta_i d\tau.$$

Whenever $B_{ij} = \beta_j\pi_i$, for two n-vectors β and π, we have once more a one-dimensional situation:

$$\Lambda(i;t) = (\int_0^t \beta \cdot e^{\tau M}\Theta_i d\tau)\pi.$$

So the range of Λ is then spanned by π and

$$R_0 = -\beta \cdot M^{-1}\pi$$

while r is the real root of the equation

$$\beta \cdot (zI - M)^{-1}\pi = 1.$$

Such models arise, for instance, when studying the initial spread of a sexually transmitted disease when transmission is restricted to partnerships that remain in existence for an extended period of time (see e.g. [8]).

8.8. Epidemic spread

By re-interpreting "reproduction" as the "transmission of an infective agent to another host," all of the theory of this paper extends to the initial phase of the spreading of an infective agent in a susceptible host population. Several more-or-less concrete examples are to be found in [9]. There it is always assumed that the reproduction measure Λ is absolutely continuous, that is, Λ can be represented by a density function (which is the product of the host distribution and the function A in [9]).

Appendix

In this appendix we gather a number of auxiliary results (and their proofs) that show that the $\otimes$-product is well-defined and that it has the properties listed in Theorem 2.2.

Lemma A1. *Let Ψ be a kernel. Then for any measurable $A \subset \mathbf{R}_+ \times \Omega$ the functions*

$$(t, \tau, \xi) \mapsto \Psi(t, \xi)(A_{-\tau})$$

and

$$(t, \tau, \xi) \mapsto \Psi(t + \tau, \xi)(A_{-\tau})$$

are measurable.

Proof. Obviously the second statement follows from the first. In order to show the first statement, let B be a measurable subset of Ω.

Step 1: For fixed (t, τ, ξ) the function

$$(a, b) \mapsto \Psi(t, \xi)\big([a, b) \times B\big)$$

is left-continuous in a and left-continuous in b.

Proof: This follows from the fact that $\Psi(t, \xi)$ is a measure.

Step 2: The mapping

$$(t, \xi, a, b) \mapsto \Psi(t, \xi)\big([a, b) \times B\big)$$

is measurable.

It is sufficient to show that, for any $c \geq 0$, the set

$$S = \Big\{(t, \xi, a, b); \quad a \leq b,\ \Psi(t, \xi)\big([a, b) \times B\big) \geq c\Big\}$$

is a measurable set.

Proof: By Step 1, we have that

$$S = \Big\{(t, \xi, a, b); \quad a \leq b, \lim_{q \nearrow a, s \nearrow b, q, s \in \mathbf{Q}} \Psi(t, \xi)\big([q, s) \times B\big) \geq c\Big\}.$$

Hence

$$S = \Big\{\ (t, \xi, a, b); \quad a \leq b,\ \forall n \in \mathbf{N}\ \exists q, s :\ q \leq a, s \leq b,\ q, s \in \mathbf{Q},$$

$$\forall r, t,\ r \in [q, a] \cap \mathbf{Q}, t \in [s, b] \cap \mathbf{Q} :\ \Psi(t, \xi)\big([r, t) \times B\big) \geq c - 1/n\Big\}.$$

Thus

$$S = \bigcap\nolimits_{n \in \mathbf{N}} \Big\{\ (t, \xi, a, b); \quad a \leq b,\ \exists q, s :\ q \leq a, s \leq b,\ q, s \in \mathbf{Q},$$

$$\forall r, t,\ r \in [q, a] \cap \mathbf{Q}, t \in [s, b] \cap \mathbf{Q} :\ \Psi(t, \xi)\big([r, t) \times B\big) \geq c - 1/n\Big\}.$$

Hence

$$S = \bigcap_{n\in\mathbf{N}} \quad \bigcup_{q,s\in\mathbf{Q}} \Big\{ (t,\xi,a,b); \quad a\le b, q\le a, s\le b,$$

$$\forall r\in[q,a]\cap\mathbf{Q}, t\in[s,b]\cap\mathbf{Q}: \ \Psi(t,\xi)\big([r,t)\times B\big) \ge c-1/n\Big\}.$$

Thus

$$S = \bigcap_{n\in\mathbf{N}} \quad \bigcup_{q,s\in\mathbf{Q}} \quad \bigcap_{r,t\in\mathbf{Q}, r\ge q, t\ge s}$$

$$\Big\{(t,\xi,a,b); \quad a\le b, r\in[0,a], t\in[0,b]: \ \Psi(t,\xi)\big([r,t)\times B\big)\ge c-1/n\Big\}.$$

Hence

$$S = \bigcap_{n\in\mathbf{N}} \quad \bigcup_{q,s\in\mathbf{Q}} \quad \bigcap_{r,t\in\mathbf{Q}, r\ge q, t\ge s}$$

$$\Big\{(t,\xi,a,b); \quad a\le b, a\ge r, b\ge t: \ \Psi(t,\xi)\big([r,t)\times B\big)\ge c-1/n\Big\}.$$

Thus

$$S = \bigcap_{n\in\mathbf{N}} \quad \bigcup_{q,s\in\mathbf{Q}} \quad \bigcap_{r,t\in\mathbf{Q}, r\ge q, t\ge s}$$

$$\Big\{(t,\xi); \quad \Psi(t,\xi)\big([r,t)\times B\big)\ge c-1/n\Big\} \times \Big\{(a,b); r\le a\le b, b\ge t\Big\}.$$

The sets

$$\Big\{(t,\xi); \quad \Psi(t,\xi)\big([r,t)\times B\big)\ge c-1/n\Big\}$$

are measurable because Ψ is a kernel (Definition 2.1). Hence the product sets

$$\Big\{(t,\xi); \ \Psi(t,\xi)\big([r,t)\times B\big)\ge c-1/n\Big\}\times\Big\{(a,b); \ r\le a\le b, b\ge t\Big\}$$

are measurable. Then S is measurable because the countable unions and intersections of measurable sets are measurable again.

Step 3: For fixed $a\le b$, the mapping

$$(t,\xi,\tau) \quad\longmapsto\quad \Psi(t,\xi)\big(([a-\tau,b-\tau)\cap[0,\infty))\times B\big)$$

is measurable.

Proof: This follows from Step 2 and the fact that the composition of measurable functions is measurable again.

Step 4: For any Borel set J in $\mathbf{R}_+$ the mapping

$$(t,\xi,\tau) \quad\longmapsto\quad \Psi(t,\xi)\big(((J-\tau)\cap[0,\infty))\times B\big) = \Psi(t,\xi)((J\times B)_{-\tau})$$

is measurable.

Proof: The collection of sets J with this property is a σ-algebra which, by step 3, contains all intervals of the form $[a,b)$ and hence contains all Borel sets in $\mathbf{R}_+$.

Step 5: For any measurable set A in $\mathbf{R}_+ \times \Omega$ the function

$$(t, \tau, \xi) \mapsto \Psi(t, \xi)(A_{-\tau})$$

is measurable.

Proof: The collection of sets A in $\mathbf{R}_+ \times \Omega$ with this property is a σ-algebra which, by step 4, contains all rectangle sets $J \times B$ and thus all sets in the product σ-algebra. This finishes the proof. □

Lemma A2. *If Φ and Ψ are kernels, so is $\Phi \otimes \Psi$ defined by (2.5), i.e.*

$$(\Phi \otimes \Psi)(t, x)(A) = \int\limits_{\mathbf{R}_+ \times \Omega} \Phi(t + \tau, \xi)(A_{-\tau}) \Psi(t, x)(d\tau \times d\xi)$$

Proof. Obviously $\Phi \otimes \Psi$ is measure-valued. By Lemma A.1, the function

$$(t, \tau, \xi) \mapsto \Phi(t + \tau, \xi)(A_{-\tau})$$

is measurable and non-negative. Hence it can be pointwise approximated by a non-decreasing sequence of functions of the form

$$\sum_{j=1}^{n} \alpha_j \chi_{C_j}$$

with measurable subsets C_j of $\mathbf{R} \times \mathbf{R}_+ \times \Omega$ and χ_{C_j} denoting the characteristic or indicator function of C_j ([33], Theorem 11.35). Hence it is sufficient to show that

$$\int\limits_{\mathbf{R}_+ \times \Omega} \chi_C(t, \tau, \xi) \Psi(t, x)(d\tau \times d\xi)$$

is measurable in (t, x) for measurable subsets C of $\mathbf{R} \times \mathbf{R}_+ \times \Omega$. See [33], Corollary 11.14. Apparently the collection of subsets C with this property form a σ-algebra. Thus it is sufficient to show this property for rectangle sets $C = C_1 \times C_2$ with C_1 being a measurable subset of $\mathbf{R}$ and C_2 a measurable subset of $\mathbf{R}_+ \times \Omega$. Now

$$\int\limits_{\mathbf{R}_+ \times \Omega} \chi_{C_1 \times C_2}(t, \tau, \xi) \Psi(t, x)(d\tau \times d\xi) = \chi_{C_1}(t) \Psi(t, x)(C_2).$$

This is a measurable function of (t, x) because Ψ is a kernel (Definition 2.1). □

Lemma A3. *Let Φ and Ψ be kernels and let $f : \mathbf{R}_+ \times \Omega \to \bar{\mathbf{R}}_+$ be measurable. Then*

$$\int\limits_{\mathbf{R}_+ \times \Omega} f(\rho, \zeta)\ (\phi \otimes \psi)(t, x)(d\rho \times d\zeta)$$

$$= \int\limits_{\mathbf{R}_+ \times \Omega} \left(\int\limits_{\mathbf{R}_+ \times \Omega} f(\rho + \tau, \zeta) \phi(t + \tau, \xi)(d\rho \times d\zeta) \right) \psi(t, x)(d\tau \times d\xi).$$

and this integral defines a non-negative measurable function of (t, x).

Proof: We rewrite

$$\Phi(t+\tau,\xi)(A_{-\tau}) = \int\limits_{\mathbf{R}_+\times\Omega} \chi_{A_{-\tau}}(\rho,\zeta)\Phi(t+\tau,\xi)(d\rho\times d\zeta).$$

Now

$$\chi_{A_{-\tau}}(\rho,\zeta) = \chi_A(\rho+\tau,\zeta).$$

The assertion now follows from Levi's theorem of monotone convergence ([33], 12.22) and the fact that non-negative measurable functions f can be pointwise approximated from below by a non-decreasing sequence of measurable functions of the form

$$\sum_{j=1}^{n} \alpha_j \chi_{A_j}.$$ □

Lemma A4. (*Associativity of* $\otimes$)

$$\Phi_1 \otimes (\Phi_2 \otimes \Phi_3) = (\Phi_1 \otimes \Phi_2) \otimes \Phi_3$$

for all kernels Φ_i, $i = 1,2,3$.

Proof: Let $t \in \mathbf{R}, x \in \Omega$ and $A \subseteq \mathbf{R}_+$ be measurable. Then, by definition of $\otimes$,

$$(\Phi_1 \otimes (\Phi_2 \otimes \Phi_3))(t,x)(A) = \int\limits_{\mathbf{R}_+\times\Omega} \Phi_1(t+\rho,\zeta)(A_{-\rho})(\Phi_2 \otimes \Phi_3)(t,x)(d\rho\times d\zeta).$$

By Lemma A4,

$$(\Phi_1 \otimes (\Phi_2 \otimes \Phi_3))(t,x)(A)$$

$$= \int\limits_{\mathbf{R}_+\times\Omega} \left(\int\limits_{\mathbf{R}_+\times\Omega} \Phi_1(t+\rho+\tau,\zeta)\left(A_{-(\rho+\tau)}\right)\Phi_2(t+\tau,\xi)(d\rho\times d\xi) \right) \Phi_3(t,x)(d\tau\times d\xi).$$

By definition of $\otimes$,

$$(\Phi_1 \otimes (\Phi_2 \otimes \Phi_3))(t,x)(A) = \int\limits_{\mathbf{R}_+\times\Omega} (\Phi_1 \otimes \Phi_2)(t+\tau,\xi)(A_{-\tau})\Phi_3(t,x)(d\tau\times d\xi)$$

$$= ((\Phi_1 \otimes \Phi_2) \otimes \Phi_3)(t,x)(A).$$ □

The next two lemmata follow via standard arguments using Levi's theorem of monotone convergence and the fact that measurable non-negative functions can be pointwise approximated from below by a non-decreasing sequence of measurable functions of the form

$$\sum_{j=1}^{n} \alpha_j \chi_{A_j}.$$

Lemma A5. (*Distributivity of* $\otimes$)

$$\Phi_1 \otimes (\Phi_2 + \Phi_3) = \Phi_1 \otimes \Phi_2 + \Phi_1 \otimes \Phi_3$$

$$(\Phi_1 + \Phi_2) \otimes \Phi_3 = \Phi_1 \otimes \Phi_3 + \Phi_2 \otimes \Phi_3$$

for all kernels $\Phi_i, i = 1,2,3$.

Lemma A6. *Assume that* $\Psi_n \uparrow \Psi_\infty$ *then, for any kernel* Φ,

$$\Phi \otimes \Psi_n \uparrow \Phi \otimes \Psi_\infty$$

and

$$\Psi_n \otimes \Phi \uparrow \Psi_\infty \otimes \Phi$$

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