Naturalis Biodiversity Center

Naturalis Repository

Finite dimensional state representation of linear and nonlinear delay systems

Odo Diekmann, Mats Gyllenberg & J. A. J. Metz

Article 25fa Dutch Copyright Act (DCA) - End User Rights

This publication is distributed under the terms of Article 25fa of the Dutch Copyright Act (Auteurswet) with consent from the author. Dutch law entitles the maker of a short scientific work funded either wholly or partially by Dutch public funds to make that work publicly available following a reasonable period after the work was first published, provided that reference is made to the source of the first publication of the work.

This publication is distributed under the Naturalis Biodiversity Center 'Taverne implementation' programme. In this programme, research output of Naturalis researchers and collection managers that complies with the legal requirements of Article 25fa of the Dutch Copyright Act is distributed online and free of barriers in the Naturalis institutional repository. Research output is distributed six months after its first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and copyrights owner(s) of this work. Any use of the publication other than authorized under this license or copyright law is prohibited.

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the department of Collection Information know, stating your reasons. In case of a legitimate complaint, Collection Information will make the material inaccessible. Please contact us through email: collectie.informatie@naturalis.nl. We will contact you as soon as possible.

Finite Dimensional State Representation of Linear and Nonlinear Delay Systems

Odo Diekmann
Department of Mathematics, University of Utrecht,
P.O. Box 80010, 3508 TA Utrecht, The Netherlands

Mats Gyllenberg
Department of Mathematics and Statistics,
P.O. Box 68
FI-00014 University of Helsinki, Finland

J.A.J. Metz
Mathematical Institute and Institute of Biology,
Leiden University, 2333 CA Leiden, The Netherlands
Evolution and Ecology Program,
International Institute for Applied Systems Analysis,
2361 Laxenburg, Austria
Naturalis Biodiversity Center,
2333 CR Leiden, The Netherlands

May 30, 2017

Abstract

We consider the question of when delay systems, which are intrinsically infinite dimensional, can be represented by finite dimensional systems. Specifically, we give conditions for when all the information about the solutions of the delay system can be obtained from the solutions of a finite system of ordinary differential equations. For linear autonomous systems and linear systems with time-dependent input we give necessary and sufficient conditions

and in the nonlinear case we give sufficient conditions. Most of our results for linear renewal and delay differential equations are known in different guises. The novelty lies in the approach which is tailored for applications to models of physiologically structured populations. Our results on linear systems with input and nonlinear systems are new.

Key words: Linear chain trick, delay-differential equation, renewal equation, Markov chain, physiologically structured populations, epidemic models

MSC2000: 34K17, 93C23, 92D25

1 Introduction

A large class of both epidemic and physiologically structured population models with a finite number of states at birth can be cast in the form of a coupled system of nonlinear renewal equations and differential delay equations (see Gyllenberg 1982,1983; Calsina and Saldaña 1995; Diekmann *et al.* 2017, 2010):

$$b(t) = F_1(X_t, Y_t)b_t, \tag{1.1}$$

$$X(t) = F_2(X_t, Y_t)b_t, \tag{1.2}$$

$$\frac{d}{dt}Y(t) = G\left(Y(t), F_3(X_t, Y_t)b_t\right). \tag{1.3}$$

The subscript t of a function refers to the *history* of the function up to time t, formally,

$$f_t(\theta) = f(t+\theta), \quad \theta \leq 0.$$

In the system (1.1) – (1.3), $b(t)$ is a vector, the jth component of which is the rate at which individuals are born into the state at birth labeled by the number j at time t. The components of the vectors $X(t)$ and $Y(t)$ are the *environmental interaction variables*. Together they form a vector $E(t) = (X(t)\ Y(t))^T$ which we call the *environmental condition* at time t. The difference between X and Y is not conceptual, but in the description of the dynamics as embodied in (1.2) and (1.3), respectively: X is determined directly by feedback while Y is determined by feedback via a differential equation. Often the components of Y represent resources consumed at the same time scale as the population dynamical events, while Equation (1.2) is obtained as a quasi-steady-state approximation after a time scale separation.

Equation (1.1) describes how individuals born in the past have survived to and give birth at the current time t. Similarly, Equation (1.2) describes the contribution to the current $X(t)$ by individuals born in the past (before time t) and Equation

(1.3) describes how the rate of change of $Y(t)$ depends on the current value of $Y(t)$ and the current population composition for instance by consuming resources. Note that, as the notation indicates, the action on b_t is linear on the right hand sides of all the equations. The interpretation of this is that, if the history of the environmental interaction variables is known, the individuals are independent of one another with regard to survival and reproduction as well as contribution to the environment. An individual's survival probability, reproductive success, satiation, etc. depend on the environment it has experienced throughout its life. Therefore the linear operators F_i, $i = 1, 2, 3$, have to depend on the history of the environmental interaction variables.

The equations (1.1) – (1.3) should hold for $t > 0$ and they should be supplemented by appropriate initial conditions prescribing the history, that is, the values of the unknowns for $t \leq 0$.

If $E(t)$ is independent of time t, the environmental condition is constant and Equation (1.1) becomes a linear renewal equation

$$b(t) = \int_0^\infty K(a)b(t-a)da. \tag{1.4}$$

If k is the number of possible states at birth, then b is a function taking on values in $\mathbb{R}^k$ and the kernel K is a $k \times k$-matrix valued function. The element $K_{ij}(a)$ is the rate at which an individual of age a who was born with state j gives birth to individuals with state i. Readers interested primarily in population dynamics may wish to read the rather short Section 5 before they embark on the rest of the paper.

Although basic questions like analysing steady states (Diekmann *et al.* 2003) and determining their local stability properties (Diekmann and Gyllenberg 2012) have been settled for the infinite dimensional dynamical system generated by (1.1) – (1.3), many important questions remain. For instance, in what manner does the population state evolve with time and possibly reach a steady state? What is the structure of the ω-limit sets? Does there exist a global attractor? Because of the infinite dimensionality of the problem these questions are hard to answer in general. In contrast, there is a highly developed qualitative theory for systems of ordinary differential equations, where such questions can be treated. There are also highly efficient packages for solving systems of ODEs numerically, whereas corresponding methods for general structured population models are rare (but see de Roos 1988; de Roos and Persson 2013; Breda *et al.* 2016).

Because of the arguments mentioned above, it is important to find necessary and sufficient conditions for solutions of the system (1.1) – (1.3) to be representable in terms of solutions of a system of ordinary differential equations. This is the main purpose of the present paper.

The representation in terms of ordinary differential equations of solutions of delay equations in general, and structured population models in particular, has a long pedigree. In their pioneering paper, Gurtin and MacCamy (1974) observed that if in the age-structured model

$$\begin{aligned}
\frac{\partial}{\partial t}n(t,a)+\frac{\partial}{\partial a}n(t,a) &= -\mu(a,X(t))n(t,a), \quad ,a>0,\ t>0, && (1.5)\\
n(t,0) &= \int_0^\infty \beta(a,X(t))n(t,a)da, \quad t>0, && (1.6)\\
X(t) &= \int_0^\infty n(t,a)da, && (1.7)\\
n(0,a) &= \phi(a), \quad a>0, && (1.8)
\end{aligned}$$

the death rate μ and the fecundity β are of the form

$$\begin{aligned}
\mu(a,X) &= \mu_0(X), && (1.9)\\
\beta(a,X) &= \alpha\beta_0(X)e^{-\alpha a}, && (1.10)
\end{aligned}$$

then solving the system (1.5) – (1.8) reduces to solving the ODE system

$$\begin{aligned}
\frac{dz_1}{dt} &= \left(\alpha\beta_0(z_2)-\alpha-\mu_0(z_2)\right)z_1, && (1.11)\\
\frac{dz_2}{dt} &= \beta_0(z_2)z_1-\mu_0(z_2)z_2, && (1.12)
\end{aligned}$$

where

$$\begin{aligned}
z_1(t) &= \alpha\int_0^\infty e^{-\alpha a}n(t,a)da, && (1.13)\\
z_2(t) &= X(t). && (1.14)
\end{aligned}$$

Once the system (1.11) – (1.12) has been solved with initial conditions

$$\begin{aligned}
z_1(0) &= \alpha\int_0^\infty e^{-\alpha a}\phi(a)da, && (1.15)\\
z_2(0) &= \int_0^\infty \phi(a)da, && (1.16)
\end{aligned}$$

the solution to the original problem is obtained from the formula

$$n(t,a)=\begin{cases} b(t-a)e^{-\int_{t-a}^t \mu_0(X(s))ds}, & \text{if } t>a,\\ \phi(a-t)e^{-\int_0^t \mu_0(X(s))ds}, & \text{if } t<a, \end{cases} \qquad (1.17)$$

where

$$b(t) := n(t,0) = \beta_0(z_2(t))z_1(t). \tag{1.18}$$

The result above can easily be generalized. The system (1.5) – (1.8) reduces to a system of ordinary differential equations if μ is independent of age and β is of the form

$$\beta(a,X) = \alpha \sum_{k=0}^{p} \beta_k(X) \frac{1}{k!}(\alpha a)^k e^{-\alpha a}. \tag{1.19}$$

For details, we refer to (Gyllenberg 2007).

The above result is related to a well-known fact in the theory of functional differential equations. The scalar equation

$$\frac{dx(t)}{dt} = f\left(x(t), \int_{-\infty}^{t} K(t-s)x(s)ds\right) \tag{1.20}$$

with distributed delay is equivalent to a system

$$\begin{aligned} \frac{dx(t)}{dt} &= f\left(x(t), z_p(t)\right), \\ \frac{dz_1(t)}{dt} &= \alpha\left(x(t) - z_1(t)\right), \\ \frac{dz_k(t)}{dt} &= \alpha\left(z_{k-1}(t) - z_k(t)\right), \quad k = 2,3,\ldots,p \end{aligned} \tag{1.21}$$

of ordinary differential equations whenever the scalar kernel K equals the gamma density

$$g_{\alpha,k}(a) := \frac{\alpha}{k!}(\alpha a)^k e^{-\alpha a}. \tag{1.22}$$

This fact has been employed in the context of biological delay systems by MacDonald (1978, 1989), who also seems to have coined the term 'linear chain trick'. Notice the linear chain structure $x \to z_1 \to z_2 \to \cdots \to z_p$ in (1.21). The system can be interpreted as a compartmental population model in which individuals in the last compartment (z_p) give birth to individuals in the x compartment and maturation consists of recruitment to a compartment from the immediately preceding one.

The example above gives sufficient conditions for when the Gurtin-MacCamy model has a finite dimensional state representation, or, as we shall say, is ODE-reducible. In this paper we give sufficient and necessary conditions for ODE-reducibility for a much larger class of physiologically structured population models. Earlier work in this direction includes (Diekmann and Metz 1988 and Metz and Diekmann 1991). In a companion paper (Diekmann *et al.* (in preparation)) we give

necessary and sufficient conditions for ODE-reducibility in terms of how the basic modelling ingredients, viz. the individual reproduction, death, and growth rates, depend on the individual state and the environmental condition.

Often, as in the example above, the finite dimensional state representation of a structured population model has a biological interpretation and the accompanying ODE-system is a population model in its own right. This is not always the case. It might for instance happen that the equivalent finite dimensional system is not positivity preserving. In this paper we will not consider the problem of when exactly the reduced system is actually interpretable as a population model. However, population dynamical interpretation will serve as motivation for formulating results concerning the finite dimensional systems, in particular in Section 5.

In queueing theory the same idea of choosing (1.22) was introduced by Erlang and is commonly called the method of stages. A customer has to pass through several stages each having an exponentially distributed service time. The stages are served one at a time and the service is completed when all stages have been served. For details we refer to (Asmussen 1987; Section III.6).

Vogel (1965) (see also Fargue (1973)) studied the question of when the solution x of a scalar nonlinear and non-autonomous Volterra integro-differential equation satisfies a system of ordinary differential equations. His result applied to the linear equation

$$x(t) = \int_{-\infty}^{t} K(t,\tau)x(\tau)d\tau \tag{1.23}$$

is that x satisfies a system of ordinary differential equations if and only if the kernel K satisfies a linear ordinary differential equation

$$\frac{\partial^n K}{\partial t^n} + a_{n-1}(t)\frac{\partial^{n-1} K}{\partial t^{n-1}} + \cdots + a_1(t)\frac{\partial K}{\partial t} + a_0(t)K = 0 \tag{1.24}$$

for some time dependent functions $a_0, a_1, \ldots, a_{n-1}$.

We shall start by considering the linear renewal equation (1.4) in Sections 2 and 3 and continue by studying linear integro-differential equations in Section 4. In Section 5 we show how the ODE system can be given an interpretation as a population model in its own right. We also characterize the basic reproduction number and the Malthusian parameter of the finite dimensional system and show that they coincide, as they should, with the corresponding quantities of the original model. In Section 6 we consider the question of minimality of the dimension of the finite dimensional state representation. In Section 7 we extend our previous results to linear renewal equations with input, which are one of the main building blocks of structured population models. In Section 8 we use the results of Section 7 to study

nonlinear problems by closing the feedback loop, that is, by feeding the output back as input to the renewal equation. In Section 9 we consider examples of nonlinear age-structured population models and epidemic models.

2 Linear Renewal Equations

In this paper we denote the space of all $p \times q$-matrices, that is, matrices with p rows and q columns, by $\mathbb{R}^{p\times q}$.

Consider the linear delay equation (renewal equation)

$$x(t) = \int_0^\infty K(\tau)x(t-\tau)d\tau \quad t > 0, \tag{2.1}$$

with initial condition

$$x(t) = \varphi(t), \quad t \leq 0. \tag{2.2}$$

or, equivalently,

$$x(t) = \int_{-\infty}^0 K(t-\tau)\varphi(\tau)d\tau + \int_0^t K(t-\tau)x(\tau)d\tau, \tag{2.3}$$

where K is a given locally integrable $\mathbb{R}^{k\times k}$-valued kernel and the unknown x and the initial history φ take on values in $\mathbb{R}^k$. Of course, one has to assume that $\int_0^\infty K(\tau)\varphi(-\tau)d\tau$ converges.

The *resolvent kernel* $R : \mathbb{R}_+ \to \mathbb{R}^{k\times k}$ of K is, by definition, the solution of the two equations

$$R(t) = K(t) + \int_0^t K(t-\tau)R(\tau)d\tau, \tag{2.4}$$

$$R(t) = K(t) + \int_0^t R(t-\tau)K(\tau)d\tau, \tag{2.5}$$

or,

$$R = K + K * R = K + R * K, \tag{2.6}$$

where we have used the notation

$$(F * G)(t) = \int_0^t F(t-\tau)G(\tau)d\tau. \tag{2.7}$$

It is an easy exercise in algebra to show that whenever $(\mathcal{A}, +, *)$ is a ring and $K \in \mathcal{A}$ is given, then the resolvent kernel is unique whenever it exists. For details, see (Gripenberg *et al.* 1990, Section 9.3).

The importance of the resolvent kernel stems from the fact that the unique solution of (2.3) is given by

$$x(t) = \int_{-\infty}^{0} K(t-\tau)\varphi(\tau)d\tau + \int_{0}^{t} R(t-s)\int_{-\infty}^{0} K(s-\tau)\varphi(\tau)d\tau ds. \tag{2.8}$$

Roughly speaking, the renewal equation (2.3) is ODE-reducible if its solution x can be fully recovered from the solution of a system of linear ordinary differential equations. The purpose of this section is to make this statement mathematically precise and to derive sufficient and necessary conditions for the equation (2.3) to be ODE-reducible.

Because the resolvent kernel R contains all the information to construct the solution x, it is natural to formulate the conditions of finite dimensional state representation in terms of the resolvent kernel.

Definition 2.1. *The renewal equation* (2.3) *has a* state representation of finite dimension $n \in \mathbb{N}$ *(or, for short, is* ODE-reducible*) if there exist matrices* $U, V \in \mathbb{R}^{n\times k}$ *and* $A \in \mathbb{R}^{n\times n}$ *such that* K *has a resolvent kernel* R *given by*

$$R(t) = U^T Z(t), \tag{2.9}$$

where $Z : \mathbb{R}_+ \to \mathbb{R}^{n\times k}$ *is the solution of the initial value problem*

$$\begin{aligned} \frac{d}{dt}Z(t) &= AZ(t), & (2.10)\\ Z(0) &= V. & (2.11) \end{aligned}$$

As a normalisation we always take the columns of V to be unit vectors with respect to the l^1-norm. In the special case $k = n$ this means that, possibly after a change of bases, V is the identity matrix.

To motivate the formulation of our first result, we observe that, by defining $H = A - VU^T$ one can write (2.10) & (2.11) equivalently as

$$\begin{aligned} \frac{d}{dt}Z(t) &= VU^T Z(t) + HZ(t), & (2.12)\\ Z(0) &= V. & (2.13) \end{aligned}$$

Theorem 2.2. *The renewal equation* (2.3) *is ODE-reducible if and only if for some positive integer* n *there are matrices* $U, V \in \mathbb{R}^{n\times k}$ *and* $H \in \mathbb{R}^{n\times n}$ *such that*

$$K(t) = U^T e^{tH} V. \tag{2.14}$$

Proof. To prove sufficiency, assume that $K(t) = U^T e^{tH} V$. Then, by (2.4),

$$\begin{aligned} R(t) &= U^T e^{tH} V + \int_0^t U^T e^{(t-s)H} V R(s) ds \\ &= U^T \left(e^{tH} V + \int_0^t e^{(t-s)H} V R(s) ds \right) \qquad (2.15) \\ &= U^T Z(t), \qquad (2.16) \end{aligned}$$

where

$$Z(t) = e^{tH} V + \int_0^t e^{(t-s)H} V R(s) ds. \qquad (2.17)$$

Direct verification shows that Z defined by (2.17) satisfies (2.12) & (2.13) and thus sufficiency is proved.

Assume now that the resolvent kernel R of K is given by $R(t) = U^T Z(t)$, where Z is the solution of (2.12) & (2.13). From the definition (2.6) of the resolvent kernel we have

$$U^T Z(t) = K(t) + \int_0^t K(t-\tau) U^T Z(\tau) d\tau \qquad (2.18)$$

and by applying the variation of constants formula to (2.12) & (2.13) we have

$$U^T Z(t) = U^T e^{tH} V + \int_0^t U^T e^{(t-\tau)H} V U^T Z(\tau) d\tau. \qquad (2.19)$$

Subtracting (2.19) from (2.18) we get that $Q(t) = K(t) - U^T e^{tH} V$ satisfies

$$Q(t) + \int_0^t Q(t-s) R(s) ds = 0,$$

which has a unique solution $Q(t) = 0$, $t > 0$. This shows that $K(t) = U^T e^{tH} V$ and completes the necessity part of the proof. □

When the renewal equation (2.3) is ODE-reducible one recovers the solution x from the formula (2.8) with K and R given by (2.14) and (2.9), respectively. But there is a quicker and perhaps more instructive way, which we now present.

Let the kernel K be given by (2.14). From (2.1) we then get

$$x(t) = \int_0^\infty U^T e^{sH} V x(t-s) ds = U^T z(t), \qquad (2.20)$$

where

$$z(t) = \int_0^\infty e^{sH} V x(t-s) ds = \int_{-\infty}^t e^{(t-s)H} V x(s) ds. \tag{2.21}$$

Differentiating (2.21) and taking (2.20) into account, one obtains

$$\frac{d}{dt} z(t) = \left(V U^T + H \right) z(t) \tag{2.22}$$

and from (2.21) and (2.2) we infer that

$$z(0) = \int_0^\infty e^{sH} V \varphi(-s) ds. \tag{2.23}$$

We conclude that whenever the renewal equation (2.3) is ODE-reducible its solution is obtained by first solving the ordinary differential equation (2.22) with initial condition (2.23) and then defining

$$x(t) = U^T z(t) \tag{2.24}$$

for $t > 0$.

3 Construction of the matrices H, U and V from a given kernel

It is well-known in the theory of ordinary differential equations that the entries of the matrix exponential e^{tH} contain scalar exponentials $e^{t\lambda_\ell}$ multiplied by powers of t. Thus the kernel $K = U^T e^{tH} V$ giving rise to an ODE-reducible renewal equation is necessarily of the form

$$K(t) = \sum_{\ell=1}^{r} \sum_{j=0}^{p_\ell - 1} \beta_{\ell j} \frac{t^j}{j!} e^{\lambda_\ell t}, \tag{3.1}$$

where the coefficients $\beta_{\ell j}$ are $k \times k$ matrices.

In this section we consider the converse problem: Given a kernel of the form (3.1), construct the matrices H, U and V such that

$$U^T e^{tH} V = K(t). \tag{3.2}$$

3.1 The case of a scalar kernel

We first consider the case of a scalar kernel, in which the coefficients $\beta_{\ell j}$ are scalars and U and V are column vectors of the same length. The general case then follows easily.

Taking the Laplace transform of (3.2) with K given by (3.1) one obtains

$$U^T (\lambda I - H)^{-1} V = \sum_{\ell=1}^{r} \sum_{j=0}^{p_\ell - 1} \beta_{\ell j} (\lambda - \lambda_\ell)^{-(j+1)}. \tag{3.3}$$

Let P_ℓ be the identity matrix of dimension $p_\ell \times p_\ell$ and let N_ℓ be the shift operator (ones on the first subdiagonal, zeros everywhere else) of dimension $p_\ell \times p_\ell$. Let P and N be the $(p_1 + \cdots + p_r) \times (p_1 + \cdots + p_r)$ dimensional block matrices

$$P = \begin{pmatrix} P_1 & 0 & \cdots & 0 \\ 0 & P_2 & & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & 0 & P_r \end{pmatrix}, \quad N = \begin{pmatrix} N_1 & 0 & \cdots & 0 \\ 0 & N_2 & & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & 0 & N_r \end{pmatrix}. \tag{3.4}$$

Abusing symbols, we also use P_ℓ and N_ℓ to denote the $(p_1 + \cdots + p_r) \times (p_1 + \cdots + p_r)$ dimensional matrices obtained by putting $P_j = 0$ and $N_j = 0$ for $j \neq \ell$ in (3.4). We then have

$$I = P_1 + P_2 + \cdots + P_r, \tag{3.5}$$

$$N = N_1 + N_2 + \cdots + N_r. \tag{3.6}$$

Define

$$H = \sum_{\ell=1}^{n} (\lambda_\ell P_\ell + N_\ell). \tag{3.7}$$

Note that H is almost the Jordan normal form of a $(p_1 + \cdots + p_r) \times (p_1 + \cdots + p_r)$ dimensional matrix with n distinct eigenvalues λ_ℓ of multiplicity p_ℓ. The standard Jordan form has ones on the diagonal immediately above the main diagonal, whereas H has ones on the first subdiagonal. The reason for this unorthodox choice is that in applications to population dynamics H can be interpreted as the state-transition matrix for the process of survival and i-state development (see Section 5). Often an individual progresses through the different states in a particular order during its life and it is natural to number the states in the same order. This leads to a matrix with non-zero elements only on the main diagonal and first subdiagonal and it is natural to keep this structure for the Jordan normal form, too.

The resolvent of H is given by

$$(\lambda I - H)^{-1} = \sum_{\ell=1}^{r} \left((\lambda - \lambda_\ell)^{-1} P_\ell + \sum_{j=0}^{p_\ell - 1} (\lambda - \lambda_\ell)^{-(j+1)} N_\ell^j \right). \tag{3.8}$$

Inserting (3.8) into (3.3) we find that we have to determine U and V such that the following equations are satisfied.

$$U^T P_\ell V = \beta_{\ell 0}, \quad \ell = 1, 2, \ldots, r, \tag{3.9}$$

$$U^T N_\ell^j V = \beta_{\ell j}, \quad \ell = 1, 2, \ldots, r, \ j = 0, 1, \ldots, p_\ell - 1. \tag{3.10}$$

We now fix the $(p_1 + \cdots + p_r)$ dimensional vector V with components v_k by defining

$$v_1 = v_{p_1+1} = v_{p_1+p_2+1} = \cdots = v_{p_1+p_2+\cdots+p_{r-1}+1} = 1 \tag{3.11}$$

and

$$v_k = 0 \tag{3.12}$$

for all other indices k. With this choice of V we can solve the system (3.9)–(3.10) for the components of U obtaining

$$\begin{array}{ccccccccc} u_1 & = & \beta_{10} & u_{p_1+1} & = & \beta_{20} & u_{p_1+\cdots+p_{r-1}+1} & = & \beta_{r0} \\ u_2 & = & \beta_{11} & u_{p_1+2} & = & \beta_{21} & u_{p_1+\cdots+p_{r-1}+2} & = & \beta_{r1} \\ & \vdots & & & \vdots & & & \vdots & \\ u_{p_1} & = & \beta_{1,p_1-1} & u_{p_1+p_2} & = & \beta_{2,p_2-1} & u_{p_1+\cdots+p_{r-1}+p_n} & = & \beta_{r,p_r-1} \end{array} \tag{3.13}$$

We have thus solved the problem.

The biological interpretation is as follows: There are $p_1 + \cdots + p_r$ discrete states (compartments). The matrix H is the transition matrix describing movement between these states. Newborns enter r of the states (states numbered $1, p_1 + 1, p_1 + p_2 + 1, \ldots, p_1 + p_2 + \cdots + p_{r-1} + 1$). For $\ell = 1, 2, \ldots, r, \ j = 0, 1, \ldots, p_\ell - 1$ the number $\beta_{\ell, p_\ell - j - 1}$ is the rate at which individuals in state $p_1 + \cdots + p_\ell - j$ give birth to offspring (distributed uniformly over the states $1, p_1 + 1, p_1 + p_2 + 1, \ldots, p_1 + p_2 + \cdots + p_{r-1} + 1$).

The solution presented above is of course not unique. The choice of V made in (3.11)–(3.12) was made for mathematical convenience. A different choice of V is often more appropriate from the point of view of biological interpretation. Let $\tilde{V}$ be *any* non-zero $(p_1 + \cdots + p_r)$ dimensional vector and choose an invertible matrix Q such that

$$Q\tilde{V} = V,$$

where V is the vector chosen in (3.11)–(3.12). Then

$$U^T e^{tH} V = U^T Q Q^{-1} e^{tH} Q Q^{-1} V = U^T Q e^{tQ^{-1}HQ} Q^{-1} V = U^T Q e^{tQ^{-1}HQ} \tilde{V}. \qquad (3.14)$$

So a different choice of V is compensated by a similarity transformation of H.

Because the given kernel K is a scalar valued function, there is essentially only one state-at-birth represented by a fixed linear combination of states as determined by $\tilde{V}$. The choice $\tilde{V} = (1\,0\,0\,\ldots\,0)^T$ is therefore rather natural.

Example: Let

$$K(t) = \beta_{10} e^{\lambda_1 t} + (\beta_{20} + \beta_{21} t)\, e^{\lambda_2 t}.$$

According to the solution above, we have

$$H = \begin{pmatrix} \lambda_1 & 0 & 0 \\ 0 & \lambda_2 & 0 \\ 0 & 1 & \lambda_2 \end{pmatrix}, \quad V = \begin{pmatrix} 1 \\ 1 \\ 0 \end{pmatrix}, \quad U = \begin{pmatrix} \beta_{10} \\ \beta_{20} \\ \beta_{21} \end{pmatrix}$$

The ODE

$$\frac{dx}{dt} = Hx$$

is easy to solve and yields

$$e^{tH} = \begin{pmatrix} e^{\lambda_1 t} & 0 & 0 \\ 0 & e^{\lambda_2 t} & 0 \\ 0 & t e^{\lambda_2 t} & e^{\lambda_2 t} \end{pmatrix}$$

Direct verification shows that

$$U^T e^{tH} V = K(t)$$

as it should.

Finally we consider the case $\tilde{V} = (1\,0\,0)^T$. The invertible matrix

$$Q = \begin{pmatrix} 1 & 0 & 0 \\ 1 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

maps $\tilde{V}$ to V. One has

$$Q^{-1} H Q = \begin{pmatrix} \lambda_1 & 0 & 0 \\ -\lambda_1 + \lambda_2 & \lambda_2 & 0 \\ 1 & 1 & \lambda_2 \end{pmatrix}, \qquad U^T Q = (\beta_{10} + \beta_{20}\ \beta_{20}\ \beta_{21}).$$

The biological interpretation going with this finite state representation is that everyone is born in state 1, individuals are recruited to state 2 from state 1 and to state 3 from state 2 and also directly from state 1. The vector $U^T Q$ gives the fecundity rates in the different states.

3.2 The general case

In the general case the kernel $K(t)$ is a $k \times k$ matrix of the form (3.1), where the coefficients $\beta_{\ell j}$ are $k \times k$ matrices. The construction of Section 3.1 works *mutatis mutandis*. The main change is that the non-zero components v_k in (3.11) are no longer the scalar 1, but the $k \times k$ identity matrix, while the zero components in (3.12) are the $k \times k$ zero matrix. The matrix V is built up by these blocks of identity and zero matrices and has dimension $k \times k(p_1 + \cdots + p_r)$.

4 Linear delay differential equations

In this section we consider the linear delay differential equation

$$\dot{y}(t) = \int_0^\infty dL(s)y(t-s), \quad t > 0 \tag{4.1}$$

with initial condition

$$y(t) = \psi(t), \quad t \leq 0. \tag{4.2}$$

As in (Diekmann and Gyllenberg 2012; see the references therein for earlier work) we work with continuous functions ψ with values in $\mathbb{R}^k$ and require $\theta \mapsto e^{\varrho\theta}\psi(\theta)$ to be continuous and to vanish at $-\infty$ for some $\varrho > 0$. The kernel L is a $k \times k$ matrix-valued function defined on $\mathbb{R}_+$, the entries of which are normalized functions of bounded variation such that

$$e^{\varrho t}V(t)$$

is bounded (here V is the total variation function, see (Diekmann *et al.* 1995)). Normalization is done such that $L(0) = 0$ and L is continuous from the right on the open interval $(0, \infty)$.

Exactly as in the finite delay case treated by Diekmann *et al.* (1995; Section I.2) one shows that the solution of (4.1) & (4.2) coincides for $t \geq 0$ with the solution of the linear renewal equation

$$y(t) = \int_0^t L(s)y(t-s)ds + f(t), \tag{4.3}$$

where

$$f(t) = \psi(0) + \int_0^\infty \left(L(t+\sigma) - L(\sigma)\right)\psi(-\sigma)d\sigma. \tag{4.4}$$

Therefore, as in the case of (2.1) & (2.2), all the information of the solution of (4.1) & (4.2) is contained in the resolvent kernel R of L and we define ODE-reducibility of

(4.1) & (4.2) by Definition 2.1 (with L instead of K). As an immediate consequence we get the following theorem:

Theorem 4.1. *The problem* (4.1) & (4.2) *is ODE-reducible if and only if there are matrices* $U, V \in \mathbb{R}^{n\times k}$ *and* $H \in \mathbb{R}^{n\times n}$ *such that*

$$L(t) = \begin{cases} 0, & t = 0, \\ U^T e^{tH} V, & t > 0. \end{cases} \tag{4.5}$$

As in the preceding section, we close by showing how one recovers the solution y of an ODE-reducible delay differential equation (4.1). To this end, assume that L is given by (4.5). Equation (4.1) is then equivalent to

$$\frac{d}{dt}y(t) = U^T V y(t) + U^T H z(t), \tag{4.6}$$

where

$$z(t) = \int_0^\infty e^{sH} V y(t-s) ds = \int_{-\infty}^t e^{(t-s)H} V y(s) ds. \tag{4.7}$$

Differentiating (4.7) one obtains

$$\frac{d}{dt}z(t) = V y(t) + H z(t). \tag{4.8}$$

The solution y of an ODE-reducible delay differential equation (4.1) is thus obtained by solving the system (4.6) & (4.8) with initial condition

$$y(0) = \psi(0), \tag{4.9}$$

$$z(0) = \int_0^\infty e^{sH} \psi(-s) ds. \tag{4.10}$$

However, we can go one step further to arrive at an ODE system in z only, which is almost identical to the corresponding system (2.22) for the case of a renewal equation.

It follows from (4.6) and (4.8) that

$$\frac{d}{dt}y(t) = U^T \frac{d}{dt} z(t)$$

and hence that

$$y(t) - U^T z(t) = y(0) - U^T z(0) = \psi(0) - U^T \int_0^\infty e^{sH} V \psi(-s) ds$$

for all $t \geq 0$. We can therefore rewrite (4.8) as

$$\frac{d}{dt}z(t) = Vy(t) + Hz(t) = \left(VU^T + H\right) z(t) + Vc,$$

where c is the constant vector

$$c = \psi(0) - U^T \int_0^\infty e^{sH} V\psi(-s)ds. \tag{4.11}$$

The solution y of a linear ODE-reducible delay differential equation (4.1) can thus alternatively be obtained by solving the initial value problem

$$\frac{d}{dt}z(t) = \left(VU^T + H\right) z(t) + Vc, \tag{4.12}$$

$$z(0) = \int_0^\infty e^{sH} V\psi(-s)ds \tag{4.13}$$

and then defining

$$y(t) = U^T z(t) + c. \tag{4.14}$$

Note that the only difference between the initial value problem (4.12) & (4.13) with output (4.14) and the corresponding system (2.22) – (2.24) for the renewal equation is manifested in the constant vector c. When $c = 0$ the two systems coincide.

5 Markov chain population models with finitely many individual states

In the previous sections we gave necessary and sufficient conditions for when solving a renewal equation or a delay differential equation can be reduced to solving a system of ordinary differential equations, but we neither fully interpreted the resulting ODE system biologically nor considered whether it was the most economical reduction. Structured populations with a finite number n of individual states (i-states for short) can be modelled directly as a system of ODEs

$$\frac{d}{dt}N(t) = (B + H)N(t), \tag{5.1}$$

where the unknown N takes on values in $\mathbb{R}^n$. The jth component of $N(t)$ represents the density of individuals with i-state j. The $n \times n$ matrix H generates the process of survival and i-state development: for $i \neq j$, H_{ij} is the rate at which an individual

with i-state j jumps to i-state i, while $-H_{jj}$ is the rate at which an individual with i-state j either changes state or dies. The $n \times n$ matrix B represents reproduction. The component B_{ij} is the rate at which an individual with i-state j gives birth to an individual with i-state i.

In this section we will relate the system (5.1) to a linear ODE-reducible renewal equation and characterize the next generation matrix, the basic reproduction number and the Malthusian parameter.

In many (perhaps most) population models the possible states at birth form a proper subset of all i-states. This means that the dimension k of the range $\mathcal{R}(B)$ of B is usually less than n and in any case $k \leq n$. Moreover, it may happen that individuals produce offspring of different i-states, but in a fixed proportion. When this is the case the dimension of $\mathcal{R}(B)$ will be further reduced (see also (Diekmann *et al.* 2010)). To take advantage of this, we let $V \in \mathbb{R}^{n\times k}$ be a matrix, the columns of which are unit vectors (with respect to the l^1-norm) that form a basis for the range of B. Because V is an injection, there is a unique matrix $U \in \mathbb{R}^{n\times k}$ such that $B = VU^T$. The system (5.1) is now of the same form as (2.22):

$$\frac{d}{dt}N(t) = (VU^T + H)N(t). \tag{5.2}$$

Define the birth rate vector $b(t) \in \mathbb{R}^k$ at time t by

$$b(t) = U^T N(t). \tag{5.3}$$

Equation (5.2) can now be written as

$$\frac{d}{dt}N(t) = Vb(t) + HN(t). \tag{5.4}$$

The definition of H implies that all its eigenvalues have negative real part and so

$$\lim_{t\to-\infty} e^{-tH} = 0. \tag{5.5}$$

We make the biologically obvious assumption that the population vector $N(t)$ remains bounded as $t \to -\infty$ after which (5.5) and an application of the variation of constants formula yields

$$N(t) = \int_{-\infty}^{t} e^{(t-s)H} Vb(s)ds. \tag{5.6}$$

Substituting (5.6) into (5.3) one finds that b satisfies the renewal equation

$$b(t) = \int_{-\infty}^{t} U^T e^{(t-s)H} Vb(s)ds, \tag{5.7}$$

which is simply equation (2.1) with the ODE-reducible kernel (2.14).

Recall from the introduction that the entry $K_{ij}(a)$ of the kernel in the renewal equation (1.1) is the rate at which an individual of age a who was born with i-state j produces offspring of i-state i. The life time contribution of a set of individuals with i-state distribution at birth given by the vector $b \in \mathbb{R}^k$ to the next generation is therefore

$$\Lambda b := \int_0^\infty K(a)\, b\, da. \tag{5.8}$$

The matrix

$$\Lambda = \int_0^\infty K(a) da \tag{5.9}$$

is called the *next generation matrix*. The basic reproduction number R_0 is, by definition, the spectral radius of Λ. In population problems Λ is a positive matrix and the spectral radius is an eigenvalue.

The Malthusian parameter r is the exponential growth rate of the population (and hence of the birth rate b). It is the real $\lambda = r$ such that the matrix

$$\int_0^\infty e^{-\lambda a} K(a) da \tag{5.10}$$

has dominant eigenvalue 1.

Let us now return to the equation (5.1). Because of the biological interpretation we assume that the transition matrix H has positive off-diagonal elements (thus e^{tH} is a positive matrix for all t) and that B is positive. Because H involves the death rates (which by assumption are not all equal to zero) it is plain that all the eigenvalues of H have negative real part. Therefore H is invertible. Again from the interpretation, $e^{aH}\phi$ is the (defective) probability distribution over the different i-states of a cohort of age a who had i-state distribution ϕ at birth, that is, at $a = 0$. So the next generation matrix is

$$\Lambda = \int_0^\infty B e^{aH} da = -BH^{-1}.$$

To find R_0 we have to solve the eigenvalue problem

$$-BH^{-1}\xi = \lambda\xi$$

for $\lambda > 0$ and $\xi \in \mathbb{R}^n_+$. Obviously ξ has to belong to the range of B and by construction of V there is a unique $\eta \in \mathbb{R}^k$ such that

$$\xi = V\eta.$$

Remembering that $B = VU^T$, we get the eigenvalue problem

$$-VU^T H^{-1} V\eta = \lambda V\eta,$$

which, because V is injective, reduces to

$$-U^T H^{-1} V\eta = \lambda\eta. \tag{5.11}$$

On the other hand, if the renewal equation is ODE-reducible, then $K(t) = U^T e^{tH} V$ and the next generation matrix is

$$\Lambda = \int_0^\infty U^T e^{tH} V dt = -U^T H^{-1} V. \tag{5.12}$$

We conclude that the problem (5.11) of finding R_0 for the model (5.1) is the same as finding R_0 for the ODE-reducible renewal equation model.

The Malthusian parameter of the model (5.1) is the positive eigenvalue of the matrix $B + H$. So we consider

$$(B + H)\xi = \lambda\xi.$$

This can be written as

$$VU^T\xi = (\lambda I - H)\xi.$$

Put

$$\eta = U^T\xi.$$

Then, if λ is not an eigenvalue of H,

$$\xi = (\lambda I - H)^{-1} V\eta$$

and hence

$$U^T(\lambda I - H)^{-1} V\eta = \eta,$$

which says that $U^T(\lambda I - H)^{-1}V$ has eigenvalue 1. Notice that for an ODE-reducible kernel K we have

$$\int_0^\infty e^{-\lambda t} K(t)dt = \int_0^\infty e^{-\lambda t} U^T e^{tH} V dt = U^T(\lambda I - H)^{-1} V,$$

which shows that finding the Malthusian parameter for (5.1) and for an ODE-reducible renewal equation amount to the same thing.

6 Minimality of the finite dimensional state space representation

When we in the last section built a structured population model directly in terms of ODEs, positivity of the resulting dynamical system was automatic. We now return to our general framework in which we do not pay attention to positivity.

As already noticed in Section 3, the matrices U, V and H in the representation $K(t) = U^T e^{tH} V$ are not unique as a similarity transformation of H together with corresponding transformations of U^T and V does not change the kernel K, see (3.14). Neither is the dimension n of the reduced state space unique. This is obvious because adding an arbitrary number of zero rows and columns to H and the same number of arbitrary rows to U and V will not have any effect on K. It is of course desirable to choose the finite dimensional state space as economically as possible. So we want to eliminate extra dimensions that do not contribute to the kernel K. In this section we consider the problem of minimality in the case of a scalar renewal equation ($k = 1$) which in a population dynamical context corresponds to the assumption of only one individual state at birth. The general case can be treated similarly.

As explained in Section 5 the vector V corresponds to the state at birth and U^T gives the rates at which individuals in different states produce offspring. If a state cannot be reached from the state at birth, then this state is, from the point of view of renewal, superfluous. Our first requirement of minimality is thus:

(M1) The set $\left\{e^{tH} V : t \geq 0\right\}$ spans the whole space $\mathbb{R}^n$ of column vectors.

Assume now that the set $\left\{U^T e^{tH} : t \geq 0\right\}$ does not span the whole space $\mathbb{R}^n$ (of row vectors). This would mean that there are states such that individuals in these states will never reproduce, neither at the current time nor in the future (when they might have moved to another state). Such states do not affect the renewal process and should be removed. We are thus led to our second condition of minimality, which is dual to the first one.

(M2) The set $\left\{U^T e^{tH} : t \geq 0\right\}$ spans the whole space $\mathbb{R}^n$ of row vectors.

Definition 6.1. *A finite dimensional state space representation defined by U, V and H is said to be* minimal *if conditions* (M1) *and* (M2) *hold.*

The terminology of Definition 6.1 is justified by the following theorem.

Theorem 6.2. *Let H and $\tilde{H}$ be n by n and $\tilde{n}$ by $\tilde{n}$ matrices, respectively. If*

$$K(t) = U^T e^{tH} V = \tilde{U}^T e^{t\tilde{H}} \tilde{V}$$

for all $t \geq 0$ and if the finite dimensional state space representation defined by U, V and H is minimal, then $\tilde{n} \geq n$.

The basic idea of the proof is the following: The generalized eigenspaces corresponding to an eigenvalue λ of H are the nullspaces of $(H - \lambda I)^k$ and hence they are naturally ordered by the power k. One can eliminate the span of a generalized eigenvector corresponding to the highest rank without affecting subspaces corresponding to lower powers. But if one eliminates the span of a generalized eigenvector corresponding to some lower rank, automatically additional directions in subspaces corresponding to higher values of k are eliminated too. Therefore minimality is characterized by the requirement that the generalized eigenvectors of highest rank cannot be missed.

Instead of giving a formal proof of Theorem 6.2 we verify it in the case where H is a 3×3 matrix with only one eigenvalue of algebraic multiplicity 3. In the general case each Jordan block can be treated separately in te same way. Recall from Section 3 that we use a slightly unorthodox representation of Jordan blocks.

Let H have the following Jordan normal form:

$$H = \begin{pmatrix} \lambda_1 & 0 & 0 \\ 1 & \lambda_1 & 0 \\ 0 & 1 & \lambda_1 \end{pmatrix}.$$

Then

$$e^{tH} = \begin{pmatrix} e^{\lambda_1 t} & 0 & 0 \\ te^{\lambda_1 t} & e^{\lambda_1 t} & 0 \\ \frac{1}{2}t^2 e^{\lambda_1 t} & te^{\lambda_1 t} & e^{\lambda_1 t} \end{pmatrix}. \tag{6.1}$$

From (6.1) it is obvious that condition (M1) holds if and only if $v_1 \neq 0$. The general condition is that the inner product of V and all (true) eigenvectors must not vanish.

Next we investigate the implications of condition (M2). By (6.1) we have

$$U^T e^{tH} = \begin{pmatrix} u_1 e^{\lambda_1 t} + u_2 te^{\lambda_1 t} + u_3 \frac{1}{2}t^2 e^{\lambda_1 t} \\ u_2 e^{\lambda_1 t} + u_3 te^{\lambda_1 t} \\ u_3 e^{\lambda_1 t} \end{pmatrix}^T, \tag{6.2}$$

from which it is immediate that condition (M2) holds if and only if $u_3 \neq 0$.

We finally examine the way the conditions (M1) and (M2) influence the kernel K. From (6.2) we get

$$K(t) = U^T e^{tH} V = (u_1 v_1 + u_2 v_2 + u_3 v_3)e^{\lambda_1 t} + (u_2 v_1 + u_3 v_2)te^{\lambda_1 t} + u_3 v_1 \frac{1}{2}t^2 e^{\lambda_1 t}.$$

It is now clear that if either (M1) or (M2) (or both) are violated, the dimension of the system can be reduced. If $u_3 = 0$ or $v_1 = 0$, then the direction of the generalized eigenvector of rank 3 corresponding to the eigenvalue λ_1 can be removed without affecting the kernel K. If $u_2v_1 + u_3v_2 = 0$, but $u_3v_1 \neq 0$ then one cannot remove the direction of the generalized eigenvector of rank 2.

It is also clear that if conditions (M1) and (M2) hold, then any other representation producing the same kernel must have at least dimension 3, so the conditions indeed define minimality.

7 Finite dimensional state representation of renewal equations with input

In this section we consider linear renewal equations with an $\mathbb{R}^m$ valued function E of time as *input*.

Assume that to every given function $E : \mathbb{R} \to \mathbb{R}^m$ there corresponds a two parameter matrix valued kernel $K_E(t, s)$. The corresponding *linear renewal equation with input* is

$$x(t) = \int_{-\infty}^{t} K_E(t, s)x(s)ds, \quad t > 0 \tag{7.1}$$

with initial condition

$$x(t) = \varphi(t), \quad t \leq 0, \tag{7.2}$$

or, equivalently

$$x(t) = \int_{-\infty}^{0} K_E(t, \tau)\varphi(\tau)d\tau + \int_{0}^{t} K_E(t, \tau)x(\tau)d\tau. \tag{7.3}$$

The resolvent kernel R_E is now a two parameter kernel satisfying

$$R_E(t, s) = K_E(t, s) + \int_s^t K_E(t, \tau)R_E(\tau, s)d\tau = K_E(t, s) + \int_s^t R_E(t, \tau)K_E(\tau, s)d\tau. \tag{7.4}$$

Equation (7.4) is of the form (2.6) with the product $*$ in the ring of two parameter families of matrices defined by

$$(F * G)(t, s) = \int_s^t F(t, \tau)G(\tau, s)d\tau. \tag{7.5}$$

Definition 7.1. *The renewal equation* (7.3) *with input E has a* state representation of finite dimension $n \in \mathbb{N}$ *(is* ODE-reducible*) if there are functions $U : \mathbb{R}^m \to \mathbb{R}^{n\times k}$, $V : \mathbb{R}^m \to \mathbb{R}^{n\times k}$ and $H : \mathbb{R}^m \to \mathbb{R}^{n\times n}$, such that*

$$R_E(t,s) = U(E(t))^T \Psi_E(t,s) V(E(s)), \tag{7.6}$$

where $\Psi_E(t,s)$ is the fundamental matrix solution for the linear non-autonomous system of ordinary differential equations

$$\frac{d}{dt} Z(t) = \big(V(E(t))U(E(t))^T + H(E(t))\big)\, Z(t), \tag{7.7}$$

Note that in Definition 7.1 we assume that n is independent of E, but allow the normalised columns of V to depend on E. In the setting of Section 5 this corresponds to the range of $B(E)$ having fixed dimension, but the basis for this range being E-dependent. In the examples that we know of, one can actually choose one and the same V for all E. So we are inclined to conclude that, as a rule, V does not depend on E.

Theorem 7.2. *The renewal equation* (7.3) *with input E is ODE-reducible if and only if there are functions $U : \mathbb{R}^m \to \mathbb{R}^{n\times k}$, $V : \mathbb{R}^m \to \mathbb{R}^{n\times k}$ and $H : \mathbb{R}^m \to \mathbb{R}^{n\times n}$, such that*

$$K_E(t,s) = U(E(t))^T \Phi_E(t,s) V(E(s)), \tag{7.8}$$

where $\Phi_E(t,s)$ is the fundamental matrix solution of the linear non-autonomous system

$$\frac{d}{dt} Z(t) = H(E(t)) Z(t). \tag{7.9}$$

Proof. Let $K_E(t,s)$ have the form (7.8) for some matrices $U(E(t)), V(E(t))$ and $H(E(t))$ and let $\Psi_E(t,s)$ be the fundamental matrix solution corresponding to the system (7.7). By the variation of constants formula

$$\Psi_E(t,s)V(E(s)) = \Phi_E(t,s)V(E(s)) + \int_s^t \Phi_E(t,\sigma)V(E(\sigma))U(E(\sigma))^T \Psi_E(\sigma,s)V(E(s))d\sigma. \tag{7.10}$$

Multiplying (7.10) from the left by $U(E(t))^T$ one obtains

$$\begin{aligned} &U(E(t))^T \Psi_E(t,s)V(E(s)) = \\ &U(E(t))^T \Phi_E(t,s)V(E(s)) + \int_s^t U(E(t))^T \Phi_E(t,\sigma)V(E(\sigma))U(E(\sigma))^T \Psi_E(\sigma,s)V(E(s))d\sigma, \end{aligned} \tag{7.11}$$

or, equivalently,

$$U(E(t))^T \Psi_E(t,s) V(E(s)) = \tag{7.12}$$
$$K_E(t,s) + \int_s^t K_E(t,\sigma) U(E(\sigma))^T \Psi_E(\sigma,s) V(E(s)) d\sigma,$$

Thus $U(E(t))^T \Psi_E(t,s) V(E(s))$ satisfies the first equation in (7.4). It follows by the uniqueness of the resolvent that $R_E(t,s)$ is given by (7.6) and hence that (7.3) is ODE-reducible.

Conversely, assume that the resolvent $R_E(t,s)$ of $K_E(t,s)$ has the form (7.6) and define

$$Q_E(t,s) = K_E(t,s) - U(E(t))^T \Phi_E(t,s) V(E(s))$$

Subtracting (7.11) from the first equation in (7.4) one obtains

$$0 = Q_E(t,s) + \int_s^t Q_E(t,\sigma) R_E(\sigma,s) ds,$$

which has the unique solution $Q_E = 0$. This shows that $K_E(t,s) = U(E(t))^T \Phi_E(t,s) V(E(s))$ and completes the proof. □

It is of practical importance to be able to determine, directly from a given kernel, whether the system is ODE reducible or not. The result by Vogel (1965) expressed in (1.24) yields an algorithm for checking this. Given a kernel $K(t,s)$, differentiate it with respect to time t and check whether K and $\partial K/\partial t$ are linearly dependent, that is, whether there exist functions a_0 and a_1 such that

$$a_1(t) \frac{\partial K(t,s)}{\partial t} + a_0(t) K(t,s) = 0. \tag{7.13}$$

If they are, we are done and conclude that the system is ODE-reducible. If not, we differentiate K once more and check, whether K, $\partial K/\partial t$ and $\partial^2 K/\partial t^2$ are linearly dependent, and so on. If this process stops after a finite number of steps the system is ODE-reducible, otherwise not.

Remark 7.3. In Definition 7.1 we allowed the matrix V to depend on the value of the input. As a matter of fact, if the renewal equation (7.1) or, equivalently (7.3), is ODE-reducible in the sense of Definition 7.1., then its solution can always be recovered from the solution of an other renewal equation, possibly of higher dimension, that is ODE-reducible with $V = I$.

To see this, assume that (7.1) is ODE-reducible. Then, according to Theorem 7.2.,

$$x(t) = \int_{-\infty}^{t} U(E(t))^T \Phi_E(t,s) V(E(s)) x(s) ds. \tag{7.14}$$

Define

$$\tilde{x}(t) = V(E(t))x(t) \tag{7.15}$$

and multiply Equation (7.14) from the left by $V(E(t))$ to obtain

$$\tilde{x}(t) = \int_{-\infty}^{t} V(E(t))U(E(t))^T \Phi_E(t,s)\tilde{x}(s) ds, \tag{7.16}$$

Applying Theorem 7.2 once again, we see that Equation (7.16) is ODE-reducible with $U(E)V(E)^T$ playing the role of $U(E)$ and the identity matrix that of $V(E)$. Once $\tilde{x}$ has been solved, we recover the solution x of the original problem from

$$x(t) = \int_{-\infty}^{t} U(E(t))^T \Phi_E(t,s)\tilde{x}(s) ds. \tag{7.17}$$

8 Closing the feedback loop

In this section we consider the nonlinear problem (1.1) – (1.3), or

$$b(t) = \int_{-\infty}^{t} K_E^{(1)}(t,s) b(s) ds, \quad t > 0, \tag{8.1}$$

$$X(t) = \int_{-\infty}^{t} K_E^{(2)}(t,s) b(s) ds \quad t > 0, \tag{8.2}$$

$$\frac{d}{dt} Y(t) = G\left(Y(t), \int_{-\infty}^{t} K_E^{(3)}(t,s) b(s) ds \right), \quad t > 0, \tag{8.3}$$

$$E(t) = (X(t), Y(t))^T. \tag{8.4}$$

The unknowns b, X and Y take on values in $\mathbb{R}^k$, $\mathbb{R}^{m_1}$ and $\mathbb{R}^{m_2}$, respectively. Thus E takes on values in $\mathbb{R}^m$ with $m = m_1 + m_2$. Therefore we have to assume that $K_E^{(1)}(t,s) \in \mathbb{R}^{k\times k}$, $K_E^{(2)}(t,s) \in \mathbb{R}^{k\times m_1}$, $K_E^{(3)}(t,s) \in \mathbb{R}^{k\times m_3}$ and that the nonlinear function G maps $\mathbb{R}^{m_2} \times \mathbb{R}^{m_3}$ into $\mathbb{R}^{m_2}$ for some integer m_3. Note that the kernels $K_E^{(i)}(t,s)$ depend on the history of E. Therefore we need to prescribe the initial history of the unknowns for $t \leq 0$:

$$b(t) = \varphi_1(t), \tag{8.5}$$

$$X(t) = \varphi_2(t), \tag{8.6}$$

$$Y(t) = \varphi_3(t). \tag{8.7}$$

As explained by Diekmann and Gyllenberg (2012), it is natural, both from a mathematical and from a biological point of view, to choose a weighted L^1-space of functions on $\mathbb{R}_-$ as state space for b, whereas Y should be taken continuous. The undifferentiated equation (1.2) or (8.2) is often obtained by a quasi-steady-state approximation in an equation of the differentiated type (1.3) or (8.3). Ideally the state space should not be affected by this approximation and so X should be continuous. But experience shows that jump discontinuities may develop, so we should be prepared to enlarge, if necessary, the state space to the space of bounded measurable functions (and giving up on strong continuity of the semigroup of solution operators). Yet the initial condition (8.6) specifies the history of X pointwise exactly as (8.7) specifies the history of Y, whereas the initial condition (8.5) for b cares only about integrals.

The distinctive feature of equation (8.1) is that it is linear in b and that the nonlinearity enters only through feedback via the environmental condition E. In particular, if the environmental condition is a given function of time, then equation (8.1) for b is a linear renewal equation with input of the type considered in Section 7. Theorem 7.2 gives necessary and sufficient conditions on the kernel $K_E^{(1)}(t,s)$ for this renewal equation to be ODE-reducible. In this section we refrain from seeking necessary and sufficient conditions for the full system (8.1) – (8.4) to be ODE-reducible or even giving an exact definition of ODE-reducibility. Instead we notice that because the action on b has the same form in all three equations, it is plausible that if the kernels $K_E^{(i)}(t,s)$, $i=1,2,3$ have the same form as the kernel $K_E(t,s)$ in Theorem 7.2, a reduction to a finite dimensional system should be possible. In this section we show that this is indeed the case.

We assume that for $i=1,2,3$, there are integers n_i and functions $U_i : \mathbb{R}^m \to \mathbb{R}^{n_i\times k}$, $V_i : \mathbb{R}^m \to \mathbb{R}^{n_i\times k}$ and $H_i : \mathbb{R}^m \to \mathbb{R}^{n_i\times n_i}$, such that

$$K_E^{(i)}(t,s) = U_i(E(t))^T \Phi_E^{(i)}(t,s) V_i(E(s)), \tag{8.8}$$

where $\Phi_E^{(i)}(t,s)$ is the fundamental matrix solution of the linear non-autonomous system

$$\frac{d}{dt}Z(t) = H_i(E(t))Z(t). \tag{8.9}$$

Substituting (8.8) into (8.1) – (8.3) and defining

$$z_i(t) = \int_{-\infty}^{t} \Phi_E^{(i)}(t,s) V_i(E(s)) b(s) ds, \quad i=1,2,3, \tag{8.10}$$

one obtains

$$\begin{aligned}
\frac{d}{dt}z_i(t) &= V_i(X(t),Y(t))U_1(X(t),Y(t))^T z_1(t) + H_i(X(t),Y(t))z_i(t), \quad (8.11)\\
&\quad i = 1,2,3,\\
X(t) &= U_2(X(t),Y(t))^T z_2(t), \quad (8.12)\\
\frac{d}{dt}Y(t) &= G\left(Y(t), U_3(X(t),Y(t))^T z_3(t)\right). \quad (8.13)
\end{aligned}$$

The system (8.11) – (8.13) is a semi-explicit system of differential-algebraic equations (Kunkel and Mehrmann 2006). In addition to the $n_1 + n_2 + n_3 + m_2$ scalar differential equations given by (8.11) & (8.13) there are m_1 undifferentiated or "algebraic" equations given by (8.12). If X can be solved explicitly in terms of z_2 and Y from equation (8.12), then this solution can be substituted into (8.11) and (8.13) and the system can be reduced to a system of $n_1 + n_2 + n_3 + m_2$ scalar differential equations.

If the matrix-valued function U_2 is continuously differentiable, then

$$\frac{dX}{dt} = \left(\frac{\partial}{\partial X}U_2(X,Y)^T\frac{dX}{dt}\right)z_2 + \left(\frac{\partial}{\partial Y}U_2(X,Y)^T\frac{dY}{dt}\right)z_2 + U_2(X,Y)\frac{dz_2}{dt}. \quad (8.14)$$

If, in addition, the map $\Lambda(X,Y,z_2) : \xi \mapsto \xi - \left(\frac{\partial}{\partial X}U_2(X,Y)^T\xi\right)z_2$ is invertible, then (8.14) can be solved for dX/dt in terms of $X, Y, z_2, dz_2/dt, dY/dt$ and the system (8.11) – (8.13) can be transformed into a system of $n_1+n_2+n_3+m$ scalar differential equations.

As in the linear cases we can recover the solution (b, X, Y) from the solution of the finite dimensional system as we now proceed to show. It follows from the definition (8.10) and the initial conditions (8.5) – (8.7) that

$$z_i(0) = \int_{-\infty}^{0} \Phi^{(i)}_{(\varphi_2,\varphi_3)}(0,s)V_i(\varphi_2(s),\varphi_3(s))\varphi_1(s)ds \quad (8.15)$$

and

$$Y(0) = \varphi_3(0). \quad (8.16)$$

Once the system (8.11) – (8.13) has been solved with the initial conditions (8.15) and (8.16), one obtains b from the formula

$$b(t) = U_1(X(t),Y(t))^T z_1(t), \quad t > 0. \quad (8.17)$$

We collect our findings into a theorem

Theorem 8.1. *Assume that for $i = 1, 2, 3$, there are integers n_i and functions $U_i : \mathbb{R}^m \to \mathbb{R}^{n_i \times k}$, $V_i : \mathbb{R}^m \to \mathbb{R}^{n_i \times k}$ and $H_i : \mathbb{R}^m \to \mathbb{R}^{n_i \times n_i}$, such that*

$$K_E^{(i)}(t,s) = U_i(E(t))^T \Phi_E^{(i)}(t,s) V_i(E(s)),$$

where $\Phi_E^{(i)}(t,s)$ is the fundamental matrix solution of the linear non-autonomous system

$$\frac{d}{dt} Z(t) = H_i(E(t)) Z(t).$$

Then the nonlinear system (8.1) – (8.7) *is equivalent with the finite dimensional differential-algebraic system* (8.11) – (8.13), (8.15), (8.16) *in the sense that if (b, X, Y) satisfies the former system, then (z_1, z_2, z_3, X, Y) satisfies the latter system and vice versa, where the correspondence between b and z_1, z_2, z_3 is given by* (8.10) *in one direction and by* (8.17) *in the other.*

9 Examples of nonlinear models with finite dimensional state representation

9.1 The Gurtin-MacCamy model

We illustrate the reduction to a finite dimensional system by applying it to the Gurtin-MacCamy model (1.5) – (1.8) mentioned in the introduction. The delay formulation (8.1) & (8.2) of the Gurtin-MacCamy model is

$$b(t) = \int_{-\infty}^{t} \beta(t-s, X(t)) e^{-\int_s^t \mu(\tau - s, X(\tau)) d\tau} b(s) ds, \tag{9.1}$$

$$X(t) = \int_{-\infty}^{t} e^{-\int_s^t \mu(\tau - s, X(\tau)) d\tau} b(s) ds, \tag{9.2}$$

which with the choice (1.9) and (1.10) for μ and β, respectively, becomes

$$b(t) = \beta_0(X(t)) \int_{-\infty}^{t} e^{-\int_s^t (\alpha + \mu_0(X(\tau))) d\tau} \alpha b(s) ds, \tag{9.3}$$

$$X(t) = \int_{-\infty}^{t} e^{-\int_s^t \mu_0(X(\tau)) d\tau} b(s) ds. \tag{9.4}$$

From this we infer that

$$\begin{array}{ccc} U_1(X) = \beta_0(X), & V_1 = \alpha, & H_1(X) = -(\alpha + \mu_0(X)), \\ U_2 = 1, & V_2 = 1, & H_2(X) = -\mu_0(X). \end{array} \tag{9.5}$$

According to (8.10), z_1 and z_2 should be defined by

$$z_1(t) = \int_{-\infty}^{t} e^{-\int_s^t (\alpha+\mu_0(X(\tau)))d\tau} \alpha b(s) ds, \tag{9.6}$$

$$z_2(t) = \int_{-\infty}^{t} e^{-\int_s^t \mu_0(X(\tau))d\tau} b(s) ds \tag{9.7}$$

and the equations (8.11) become

$$\frac{dz_1}{dt} = (\alpha\beta_0(z_2) - \alpha - \mu_0(z_2))\, z_1, \tag{9.8}$$

$$\frac{dz_2}{dt} = \beta_0(z_2) z_1 - \mu_0(z_2) z_2, \tag{9.9}$$

which are precisely the equations (1.11) & (1.12). Equation (8.12) simply reduces to

$$X(t) = z_2(t).$$

9.2 Age-structured growth in a chemostat

Consider a chemostat with dilution rate D in which an age-structured consumer with birth rate b feeds on an unstructured substrate S. We neglect mortality other than that caused by washout from the chemostat. The model for such a system is

$$b(t) = \int_{-\infty}^{t} \beta(t-s, S_t) e^{-D(t-s)} b(s) ds, \tag{9.10}$$

$$\frac{d}{dt} S(t) = D\left(S^0 - S(t)\right) - \int_{-\infty}^{t} \gamma(t-s, S_t) e^{-D(t-s)} b(s) ds. \tag{9.11}$$

Here $\beta(a, S_t)$ and $\gamma(a, S_t)$ are the age-specific per capita fecundity and consumption rate, respectively, given the history S_t of the substrate.

Assume that consumers are either juvenile or adult, that only adults produce offspring at an otherwise age-independent rate $\beta_0(S)$ and that juveniles and adults have different consumption rates $\gamma_J(S)$ and $\gamma_A(S)$, respectively. Assume further that juveniles are recruited to the adult stage at a rate $\alpha(S)$. The probability that an individual born at time s is still alive and in the juvenile stage at time t is

$$e^{-D(t-s)} e^{-\int_s^t \alpha(S(\sigma))d\sigma},$$

while the probability that it is in the adult stage is

$$e^{-D(t-s)} \left(1 - e^{-\int_s^t \alpha(S(\sigma))d\sigma}\right).$$

As a consequence, the equations become

$$b(t) = \int_{-\infty}^{t} \beta_0(S(t)) \left(1 - e^{-\int_s^t \alpha(S(\sigma))d\sigma}\right) e^{-D(t-s)} b(s) ds, \tag{9.12}$$

$$\frac{d}{dt}S(t) = D\left(S^0 - S(t)\right) \tag{9.13}$$

$$- \int_{-\infty}^{t} \left(\gamma_J(S(t)) e^{-\int_s^t \alpha(S(\sigma))d\sigma} + \gamma_A(S(t)) \left(1 - e^{-\int_s^t \alpha(S(\sigma))d\sigma}\right)\right) e^{-D(t-s)} b(s) ds,$$

which is simply (9.10) – (9.11) with

$$\begin{aligned} \beta(a, S_t) &= \beta_0(S(t)) \left(1 - e^{-\int_s^t \alpha(S(\sigma))d\sigma}\right), \\ \gamma(a, S_t) &= \gamma_J(S(t)) e^{-\int_s^t \alpha(S(\sigma))d\sigma} + \gamma_A(S(t)) \left(1 - e^{-\int_s^t \alpha(S(\sigma))d\sigma}\right). \end{aligned}$$

The kernel in (9.12) is of the form

$$K_S^{(1)}(t, s) = U_1(S(t))^T \Phi_S(t, s) V(S(s)),$$

with

$$U_1(S) = (0 \ \beta_0(S)^T, \quad V = (1 \ 0)^T$$

and $\Phi_S(t, s)$ the fundamental matrix solution corresponding to the matrix

$$H(S) = \begin{pmatrix} -(\alpha(S) + D) & 0 \\ \alpha(S) & -D \end{pmatrix}.$$

The kernel $K_S^{(3)}(t, s)$ in (9.13) is almost the same as $K_S^{(1)}(t, s)$, the only difference being that $U_1(S)$ is replaced by

$$U_3(S) = (\gamma_J(S) \ \gamma_A(S))^T.$$

Because V_1 and V_3 are the same (and denoted simply by V) it follows from (8.10) that also z_1 and z_3 coincide. The components of this variable correspond to the densities of juveniles and adults, respectively, so we denote $z_1 = z_3 = (J \ A)^T$. The finite dimensional representation of (9.12) – (9.13) is thus

$$\frac{dJ}{dt} = \beta_0(S)A - (D + \alpha(S))J, \tag{9.14}$$

$$\frac{dA}{dt} = \alpha(S)J - DA, \tag{9.15}$$

$$\frac{dS}{dt} = D\left(S^0 - S\right) - \gamma_J(S)J - \gamma_A(S)A, \tag{9.16}$$

exactly as one would obtain when formulating the model right from the beginning in terms of J and A.

9.3 Epidemic models

In their 1927 classic, Kermack and McKendrick (1927) introduced as their key modelling ingredient

$$K(\tau) \;:=\; \text{expected contribution to the force of infection by an individual that was itself infected } \tau \text{ units of time ago}$$

Let

$$\begin{aligned} F(t) &:= \text{force of infection at time } t, \\ S(t) &:= \text{density (= number per unit area) of susceptibles at time } t. \end{aligned}$$

Then the incidence $b(t)$ (= number of new cases per unit of time and area) is given by

$$b(t) = F(t)S(t)$$

and the interpretation of $K(\tau)$ translates into the equation

$$F(t) = \int_{-\infty}^{t} K(t-\tau)b(\tau)d\tau$$

Now suppose K is of the form (2.14) for $k = 1$. Define

$$Z(t) = \int_{-\infty}^{t} e^{(t-\tau)H} V b(\tau) d\tau.$$

Then

$$\begin{aligned} \frac{dZ}{dt} &= HZ + Vb, \\ F &= U^T Z, \\ b &= FS \end{aligned}$$

so

$$\frac{dZ}{dt} = HZ + SVU^T Z$$

and if we add a differential equation for S like

$$\frac{dS}{dt} = -FS = -SU^T Z$$

(closed population, i.e., no demographic turnover) or

$$\frac{dS}{dt} = g(S) - FS = g(S) - SU^T Z$$

(births and deaths incorporated in g; beware that K, too, has now to incorporate the possibility of death) we have a closed nonlinear ODE system for (S, Z).

Note that for fixed S one has a linear system for Z and the discussion about R_0 and r presented in Section 5 carries over verbatim.

In the standard SIR compartmental model an individual becomes infectious immediately upon becoming infected and stays infectious for an exponentially distributed amount of time with rate parameter α, i.e., the mean of the infectious period is α^{-1}. During the infectious period it produces new cases at rate βS. This corresponds to $n = 1$, $H = -\alpha, U = \beta, V = 1$ and the relabeling $Z = I$. Beware that the symbol I now refers to "infectious" and not to "identity".

Similarly the SEIR model (where individuals are 'exposed' for an exponentially distributed amount of time, with rate parameter γ, before becoming infectious) corresponds to $n = 2$,

$$H = \begin{pmatrix} -\gamma & 0 \\ \gamma & -\alpha \end{pmatrix}, \quad V = (1\ 0)^T, \quad U = (0\ \beta)^T$$

and relabelling $Z_1 = E$ and $Z_2 = I$. Beware that the symbol E now refers to "exposed" and not to "environment".

Currently network models are en vogue in infectious disease epidemiology, so let us have a brief look at one of those. A key feature is that individuals have repeated contacts with the same partner(s). For static configuration networks a nonlinear renewal equation is informally derived by Leung and Diekmann (2017); see (Barbour and Reinert 2013) for a rigorous derivation. It reads

$$x(t) = \mathcal{F}(\infty) - \int_{-\infty}^{t} g(x(\sigma))\mathcal{F}'(t-\sigma)d\sigma \tag{9.17}$$

where $\mathcal{F}(\tau)$ is the probability that transmission of the infectious agent to a partner has not (yet) occurred at disease-age τ and

$$g(x) = \frac{\sum_{k=1}^{\infty} k p_k x^{k-1}}{\sum_{k=1}^{\infty} k p_k}$$

with p_k the probability that an individual has k partners/neighbours, i.e., has degree k. The kernel $\mathcal{F}$ is rather similar to the Kermack-McKendrick kernel K in the sense that it captures the progress of disease, in particular infectiousness, within an individual, but it also takes into account that any partner can be infected at most once.

Consequently we should consider a Markov process that describes both progress of the disease in an infected individual and the status, in terms of susceptible versus infected, of a partner. For example, consider the modified standard SIR model where during the infectious period any susceptible partner is infected with probability per unit of time β. At $\tau = 0$ we start with an (I,S)-couple. The transition (I,S) $\to$ (I,I) occurs at rate β and the transition (I,S) $\to$ (R,S) at rate α. So the probability $P_{\rm IS}$ that the state is still (I,S) at disease-age τ equals $e^{-(\alpha+\beta)\tau}$. Since $\mathcal{F}(0) = 1$ and $\mathcal{F}'(\tau) = -\beta P_{\rm IS}(\tau)$ we find

$$\mathcal{F}(\tau) = 1 - \beta \int_0^\tau e^{-(\alpha+\beta)\sigma} d\sigma = \frac{\alpha}{\alpha+\beta} + \frac{\beta}{\alpha+\beta} e^{-(\alpha+\beta)\tau}$$

For this choice of $\mathcal{F}$ differentiation of (9.17) yields the ODE

$$\frac{dx}{dt} = \beta g(x) - (\alpha+\beta)x + \alpha$$

see (Miller 2011).

The generalization

$$\mathcal{F}(\tau) = 1 - \beta^T \int_0^\tau e^{(H-\mathrm{diag}\beta)\sigma} d\sigma V$$

involves n-vectors β and V and an $n \times n$-matrix H and derives from

$$\frac{dP}{dt} = (H - \mathrm{diag}\beta)P, \quad P(0) = V, \quad \frac{d\mathcal{F}}{dt} = -\beta^T P, \quad \mathcal{F}(0) = 1.$$

If we define

$$Z(t) = \int_{-\infty}^t g(x(\sigma)) e^{(H-\mathrm{diag}\beta)(t-\sigma)} d\sigma V$$

then

$$\frac{dZ}{dt} = g(x)V + (H - \mathrm{diag}\beta)Z$$

and since (9.17) amounts to $x = \mathcal{F}(\infty) - \beta^T Z$ this is, in fact, a closed ODE system for Z. As a particular example, we mention the $\mathrm{SEI_1I_2R}$ system defined by $n = 3$ and

$$V = (1\ 0\ 0)^T, \quad \beta = (0\ \beta_1\ \beta_2)^T, \quad H = \begin{pmatrix} -\gamma & 0 & 0 \\ \gamma & -\alpha_1 & 0 \\ 0 & \alpha_1 & -\alpha_2 \end{pmatrix}$$

We conclude that by an appropriate modification the Markov approach of Section 5 extends to models of the spread of infection over static configuration networks. In particular many of the ODEs derived by Miller and Volz (2013) follow from (9.17) by a choice of two n-vectors β and V and an $n \times n$-matrix H.

10 Conclusions

In this paper we have considered finite dimensional state representations of a class of both linear and nonlinear infinite dimensional systems corresponding to delay-equations. Most of the results for linear renewal and delay differential equations are known, in particular to researchers in systems and/or control theory. They are either part of the folklore or presented in slightly different guises in works such as (Vogel 1965; Zadeh and Desoer 1963; Zadeh and Polak 1969; Fargue 1973). The novelty of our presentation lies in the approach which is tailored for applications to models of physiologically structured populations. Our results on linear systems with input and nonlinear systems are new.

When applied to population dynamics the unknown $b(t)$ in (1.1) represents the birth *rate*. There are relevant population models in which the reproduction process cannot fully be described by rates. One example is when individuals reproduce exactly upon reaching a certain fixed size. For this reason we considered in the paper (Diekmann et al. 2001) the *cumulative* number of births in the following manner: Instead of a kernel K_E in the form of a matrix valued function, our basic ingredient was a kernel Λ_E with the interpretation that $\Lambda_E(t,s)(\xi,\omega)$ is the expected number of offspring, with state-at-birth in the measurable subset ω of the individual state space Ω, produced by an individual with i-state ξ at time s, within the time interval $[s,t)$, given the course of the environmental condition E on the interval $[s,t)$. The resolvent equation then became

$$\Lambda_E^c = \Lambda_E + (\Lambda * \Lambda^c)_E = \Lambda_E + (\Lambda^c * \Lambda)_E\,, \tag{10.1}$$

where the $*$ stands for a convolution-like product involving Stieltjes integrals with respect to time. In the present paper we have defined ODE-reducibility by requiring that the resolvent (Λ_E^c in (10.1)) should be (a linear operator applied to) the solution of a finite dimensional system of ODEs. But such a solution is continuously differentiable and hence we can differentiate (10.1) obtaining an equation which in full detail reads as follows:

$$\begin{aligned}\lambda_E^c(t,s)(\xi,\omega) &= \lambda_E(t,s)(\xi,\omega) + \int_s^t \int_\Omega \lambda_E(t,\tau)(\eta,\omega)\lambda_E^c(\tau,s)(\xi,d\eta)d\tau \\ &= \lambda_E(t,s)(\xi,\omega) + \int_s^t \int_\Omega \lambda_E^c(t,\tau)(\eta,\omega)\lambda_E(\tau,s)(\xi,d\eta)d\tau.\end{aligned} \tag{10.2}$$

In this equation, which is an analogue of (7.4), the kernel $\lambda_E(t,s)(\xi,\omega)$ is the rate at which an individual, which had i-state ξ at time s, produces offspring in the set

ω at time t, given the environment E. The convolution-like product does no longer contain Stieltjes integrals. This shows that for the problem of finding conditions for ODE-reducibility there was no loss of generality in abandoning cumulative outputs and Stieltjes integrals.

The equations from Section 8 exemplify how people generally build community dynamical models, to wit by combining single populations models in a lego-like fashion, taking population outputs as inputs for other populations or for similarly represented inanimate resources. The "community equation" from Section 8 is of the simplest possible type, with X the effect of the population on the condition of instantaneously reacting resources, like the density of occupied nestboxes (supposing that b refers to the birth rate of, say, great tits), and Y the densities of dynamically reacting resources like nitrogen availability (supposing that b refers to the birth rate of, say, planktonic algae). $K_E^{(1)}$ then depends on the density of occupied nest boxes x_i through the intervening variable $n - x_i$, where n is the total density of nest boxes, affecting the stochastic dynamics of a binary i-state component — have or have-not — which in turn affects an individual's metabolism, death rate and reproduction, while $K_E^{(2)}$ tells how nest boxes are monopolised by individuals born some time ago, with a similar story in the case of nitrogen availability affecting algae.

From this "lego point of view" the models of Section 7 are prospective building blocks for the construction of community models. If all building blocks of a community model are ODE-reducible, then so is the full model. This is the gist of Section 7. In general the converse need not be true, as the coupling of the populations imposes constraints on the inputs, while the reasoning in Section 8 implicitly assumed the absence of such constraints. However, the lego point of view offers an alternative formulation for a converse: suppose that our lego set is so rich that by changing the community embedding of our focal population we can produce a sufficiently diverse variety of inputs from its output, and moreover all other building blocks are ODE-reducible, then for all these communities to be ODE-reducible, our focal population should satisfy the conditions put forward in Section 7, with K extended to include the output generating kernels (the analogues of $K^{(2)}$ and $K^{(3)}$ of Section 8). This heuristic phrasing leaves open the following difficult problems: What sets of inputs "vary sufficiently" (all inputs considered in Theorem 7.2 certainly suffice but maybe we can do with less)? How to test whether a set of building blocks when coupled in various combinations and fed with the population output, together produce such a sufficiently variying set?

In the other direction, but within the same model building spirit, we want to know how the ingredients making up our building blocks relate to their ODE-reducibility. In a follow-up paper (Diekmann et al. in preparation) we will take Equation (10.2) as

starting point and obtain necessary and sufficient conditions, in terms of individual birth, death and growth rates, for a population model to be representable by a finite system of ordinary differential equations.

Acknowledgement We thank Michael Mackey for turning our attention to the works (Vogel 1965) and (Fargue 1973). Hans Metz' work benefitted from the support from the "Chair Modélisation Mathématique et Biodiversité of Veolia Environnement-École Polytechnique-Muséum National d'Histoire Naturelle-Fondation X".

References

S. Asmussen (1987). "Applied Probability and Queues," John Wiley & Sons, New York.

A.D. Barbour and G. Reinert (2013). Approximating the epidemic curve, Electron. J. Probab., 18, paper 54.

D. Breda, O. Diekmann, M. Gyllenberg, F. Scarabel, and R. Vermiglio (2016). Pseudospectral discretization of nonlinear delay equations: new prospects for numerical bifurcation analysis, SIAM Journal on Applied Dynamical Systems, 15, 1-23.

À. Calsina and J. Saldaña (1995). A model of physiologically structured population dynamics with a nonlinear individual growth rate, J. Math. Biol., 33, 335-364.

O. Diekmann and M. Gyllenberg (2012). Equations with infinite delay: blending the abstract and the concrete, Journal of Differential Equations, 252, 819-851.

O. Diekmann, M. Gyllenberg, H. Huang, M. Kirkilionis, J.A.J. Metz, and H.R. Thieme (2001). On the formulation and analysis of general deterministic structured population models. II. Nonlinear theory, Journal of Mathematical Biology 43, 157-189.

O. Diekmann, Ph. Getto, and M. Gyllenberg (2007). Stability and bifurcation analysis of Volterra functional equations in the light of suns and stars, SIAM Journal on Mathematical Analysis, 39, 1023-1069.

O. Diekmann, M. Gyllenberg, J.A.J. Metz, S. Nakaoka, and A.M. de Roos (2010). Daphnia revisited: local stability and bifurcation theory for physiologically structured population models explained by way of an example, Journal of Mathematical Biology, 61,277-318.

O. Diekmann, M. Gyllenberg, and J.A.J. Metz (in preparation). Finite dimensional state representation of physiologically structured population models.

O. Diekmann, S.A. van Gils, S.M. Verduyn Lunel and H.-O. Walther (1995). "Delay Equations. Functional-, Complex-, and Nonlinear Analysis," Springer-Verlag, New York.

O. Diekmann, J.A.P. Heesterbeek, and M.G. Roberts (2010). The construction of next-generation matrices for compartmental epidemic models, J.R. Soc. Interface, 7, 873-885.

O. Diekmann and H. Metz (1988). Exploring linear chain trickery for physiologically structured populations. In: Bij het afscheid van Prof. Dr. H.A. Lauwerier, TW in Beeld (Amsterdam: CWI), pp. 73-84.

D. Fargue (1973) Réductibilité des systèmes héréditaires à des systèmes dynamiques (régis par des équations différentielles ou aux dérivées partielles), C.R. Acad. Sc. Paris, Série B, 277, 471-473.

G. Gripenberg, S.-O. Londen and O. Staffans (1990). "Volterra Integral and Functional Equations," Cambridge University Press, Cambridge.

M.E. Gurtin and R.C. MacCamy (1974). Non-linear age-dependent population dynamics, Archive for Rational Mechanics and Analysis, 54, 281-300.

M. Gyllenberg (1982). Nonlinear age-dependent population dynamics in continuously propagated bacterial cultures, Math. Biosci., 62, 45-74.

M. Gyllenberg (1983). Stability of a nonlinear age-dependent population model containing a control variable, SIAM J. Appl. Math., 43, 1418-1438.

M. Gyllenberg (2007). Mathematical aspects of physiologically structured populations: the contributions of J. A. J. Metz, Journal of Biological Dynamics, 1, 3-44.

K.Y. Leung and O. Diekmann (2017). Dangerous connections : on binding site models of infectious disease dynamics, Journal of Mathematical Biology **74**, 619-671.

W.O.Kermack and A.G. McKendrick (1927). A contribution to the mathematical theory of epidemics, Proc. Royal Soc. London, Ser. A., 115, 700-721.

P. Kunkel and V. Mehrmann (2006). "Differential-algebraic equations: analysis and numerical solution," European Mathematical Society, Zürich.

M. MacDonald (1978). *Time lags in biological models*, Lecture Notes in Biomathematics **27**, Springer-Verlag, Berlin.

M. MacDonald (1989). *Biological delay systems*, Cambridge University Press, Cambridge.

J.A.J. Metz and O. Diekmann (1991). Exact finite dimensional representations of models for physiologically structured populations. I: The abstract foundations of linear chain trickery. In: J.A. Goldstein, F. Kappel and W. Schappacher (Eds) Differential Equations with Applications in biology, Physics and Engineering, Lecture Notes in Pure & Applied Mathematics, vol. 133 (New York: Marcel Dekker), pp. 269289.

J.C. Miller (2011). A note on a paper by Erik Volz : SIR dynamics in random networks, J. Math. Biol., 62, 349-358.

J.C. Miller and E.M. Volz (2013). Incorporating disease and population structure into models of SIR disease in contact networks, PLoS ONE [E], vol 8, issue 8, Public Library of Science, San Francisco USA, pp. 1-14.

A.M. de Roos (1988). Numerical methods for structured population models: The Escalator Boxcar Train, Numerical Methods for Partial Differential Equations, 4, 173-195.

A.M. de Roos and L. Persson (2013). Population and Community Ecology of Ontogenetic Development, Princeton University Press, Princeton, New Jersey, USA.

T. Vogel (1965). *Théorie des systèmes évolutifs,* Gauthier-Villars, Paris.

L.A. Zadeh and C.A. Desoer (1963)."Linear system theory : the state space approach", McGraw-Hill, New York.

L. A. Zadeh and E. Polak (1969). "System theory", McGraw-Hill, New York.