

Exact Finite Dimensional Representations of Models for Physiologically Structured Populations.I: The Abstract Foundations of Linear Chain Trickery

J.A.J. METZ
O. DIEKMANN

Institute of Theoretical Biology, University of Leiden
Center for Mathematics and Computer Science, Amsterdam

1. Prelude: A low dimensional representation of the population dynamics of generalized ectotherms

Suppose we want to model a population of ectothermic animals, *e.g.* the water flea *Daphnia magna*. Experimentally it appears that reproduction depends on the size of the individual animals and this observation motivated KOOIJMAN & METZ (1984) to introduce a size structured model. As the biological assumptions underlying the model are described already in some detail, in METZ & DIEKMANN (1986; I.3), METZ *et al.* (1988), DE ROOS *et al.* (preprint) and DE ROOS & METZ (preprint), we restrict ourselves here to its mathematical formulation:

$$\begin{aligned} \frac{\partial}{\partial t} n(t, \ell) + \frac{\partial}{\partial \ell} (\nu(s, \ell) n(t, \ell)) &= -\mu(s, \ell) n(t, \ell), \\ \nu(s, \ell_b) n(t, \ell_b) &= \int_{\ell_b}^{\ell_{\max}} \beta(s, \ell) n(t, \ell) d\ell. \end{aligned} \tag{1.1}$$

Here ℓ denotes length and s substrate (more precisely: concentration of algae). The individual growth, death and reproduction rates are denoted by, respectively, ν , μ and β . The density n describes the concentration of *Daphnia* as well as their distribution with respect to length. All individuals are born with length ℓ_b and ℓ_{\max} is the maximal attainable length under abundant food conditions.

To describe some experiments one should consider s as a given function of time but to describe others one has to specify the dynamics of s as well. In the latter case we take

$$\frac{ds}{dt} = h(s) - \int_{\ell_b}^{\ell_{\max}} \gamma(s, \ell(n(t, \ell))d\ell, \quad (1.2)$$

where h corresponds to the rate of change of the algae concentration in the absence of daphnids and γ is the per capita consumption rate. Under appropriate assumptions on the ingredients ν, μ, β, γ and h , (1.1) and (1.2) together generate an infinite dimensional nonlinear dynamical system.

Since daphnids are filters feeders it is reasonable to assume that the consumption rate γ is proportional to the surface area which in turn is proportional to ℓ^2 . So we put

$$\gamma(s, \ell) = f(s)\ell^2. \quad (1.3)$$

If a constant fraction of the ingested energy is allotted to reproduction we may put

$$\beta(s, \ell) = \alpha f(s)\ell^2 \quad (1.4)$$

(at this point we deliberately ignore the experimental fact that daphnids don't reproduce if they are still too small; see METZ & DIEKMANN, METZ *et al.* DE ROOS *et al.* and DE ROOS & METZ (op. cit.) for a formulation which does take into account a juvenile period characterized by $\ell < \ell_j$). If the remainder of the ingested energy is allotted to individual growth and maintenance and if maintenance is proportional to weight, which in turn is proportional to ℓ^3 , we may take

$$\frac{d}{dt}\ell^3 = 3\delta f(s)\ell^2 - 3\epsilon\ell^3,$$

and therefore

$$\nu(s, \ell) = \frac{d}{dt}\ell = \delta f(s) - \epsilon\ell. \quad (1.5)$$

Finally we take

$$\mu(s, \ell) = \mu, \quad \text{a constant.} \quad (1.6)$$

To analyze (1.1) together with (1.2) for the special constitutive relations (1.3) to (1.6) we introduce

$$N_i(t) = \int_{\ell_b}^{\ell_{\max}} \ell^i n(t, \ell) dt, \quad i = 0, 1, 2, \quad (1.7)$$

and find, using (1.1) - (1.7) and some straightforward integrations (by parts),

that (N, s) satisfies the *closed* system of ODE's

$$\begin{aligned}\frac{dN_0}{dt} &= \alpha f(s)N_2 - \mu N_0, \\ \frac{dN_1}{dt} &= \ell_b \alpha f(s)N_2 - \delta f(s)N_0 - (\mu + \varepsilon)N_1, \\ \frac{dN_2}{dt} &= \ell_b^2 \alpha f(s)N_2 + 2\delta f(s)N_1 - (\mu + 2\varepsilon)N_2, \\ \frac{ds}{dt} &= h(s) - f(s)N_2.\end{aligned}\tag{1.8}$$

The powerful qualitative theory of finite dimensional dynamical systems now can be brought to bear on (1.8). Moreover one can choose from a multitude of well established schemes to study (1.8) numerically. As one example of the exploitation of these facts we point to DE ROOS (1988), who uses the relationship between (1.8) and (1.1) to investigate the accuracy of the 'escalator boxcar train', a new, efficient method developed by him for the numerical solution of the usual combinations of first order PDE's and non-local side conditions appearing in the theory of physiologically structured populations.

Of course neglecting the juvenile period has consequences, the main difference between the present model and the full one being that the latter not only allows the occurrence of predator prey oscillations due to the lag in recovery of the food population, but in addition oscillations related to the development lag (see METZ *et al.* 1988; DE ROOS *et al.* 1988; DE ROOS *et al.* preprint, and DE ROOS & METZ, preprint).

2. Introduction

The *Daphnia* example shows that it is sometimes possible to faithfully represent a full physiologically structured population model in a low dimensional manner, provided an appropriate choice of the constitutive relations, *viz.* the velocity and mortality functions and birth kernel, is made. The idea to search specifically for modelling approximations allowing such low dimensional representations is affectionately called 'linear chain tickery' by its practitioners. The name arose in the context of delay differential equations, where particular distributed delays can be represented as linear, *i.e.* unbranched, chains of coupled single ODE's (see *e.g.* MAC DONALD, 1978).

The earliest references to a systematic use of linear chain tricks that we are aware of are by VOGEL and by REPIN (1965) who applied them in the context of respectively Volterra integral and delay differential equations. The first analysis of necessary and sufficient conditions for linear chain trickability in the context of systems with hereditary action seems to have been given by FARGUE (1973, 1974). Good general references in this context with a slant towards biological applications are MAC DONALD (1978, 1979). GURTIN & MAC CAMY (1974, 1979) were the first to use linear chain trickery for well specified age structured

population model. GURNEY *et al.* (1986) provided the extension to physiological age, and MURPHY (1983) and EDELSTEIN & HADAR (1983), to size.

Another, practically very useful, extension of the idea of linear chain trickery, which, however, is less amenable to an abstract characterization, is provided by the stage structured models pioneered by the University of Strathclyde group of ecological modellers. Basically these are physiologically structured population models which can be represented in a fairly straightforward manner as systems of delay differential equations with a few, though possibly variable, discrete delays, and hence allow a rapid exploration of their dynamics using only slight extensions of the standard numerical techniques for ODE's. The advantage of aiming at using delay instead of ordinary differential equations in one's modelling approximations is the greater flexibility allowed, in particular if one wishes to keep the number of differential equations involved fairly small. A good introduction to the biological assumptions underlying the stage structure concept can be found in NISBET & GURNEY (1986). The first papers on the subject are GURNEY *et al.* (1983), which treats the case of fixed delay only, and NISBET & GURNEY (1983) which deals with the variable delay case (the symposium paper GURNEY & NISBET (1983) provides a nice summary). Various useful further extensions can be found in BLYTHE *et al.* (1984), GURNEY *et al.* (1986), and NISBET *et al.* (1985).

In the present contribution we report our attempts at elucidating for general population models the structural properties underlying the machinery of deriving faithful finite dimensional representations. This work forms part of an ongoing program, started in METZ & DIEKMANN (1986), aimed at clarifying the abstract mathematical structure inherent in our ways of thinking about the mechanistic basis of population dynamics. Some of the results reported in the present paper, in particular the characterization results from subsection 5.1.2, already appeared in DIEKMANN & METZ (1988,89).

3. An abstract formulation of physiologically structured population models

Let the individuals of a population be characterized by finitely many variables, which together we call the i -state. So the set of feasible i -states Ω is a nice subset of \mathbb{R}^n , for some n . At the individual level a model amounts to a specification of (i) the rate of i -state change, ν , (ii) the death rate, μ , (iii) the birth rate, β , and in particular how (i), (ii) and (iii) depend on the i -state x and the prevailing environmental conditions. The latter are described by a (possibly even infinite dimensional) variable E . In the case of the birth rate we have to specify the (distribution of the) state at birth as well.

Once we have a model at the individual level we can immediately derive balance laws doing the necessary bookkeeping. These balance laws generate the time evolution at the population level. There are two types of balance laws, related to each other by duality. We can use duality since for E a given function of time the equations are linear as a result of our previous assumption that

for a given course of E individuals are fully state-determined. The Kolmogorov backward equation is concerned with the clan mean of a continuous function on Ω (see below). The Kolmogorov forward equation describes infinitesimal changes in the measure which assigns to every measurable subset of Ω the concentration of individuals which have at that instant an i -state which belongs to that particular subset. This measure is called the p -state (p for population) and the space $M(\Omega)$ of regular Borel measures on Ω is called the p -state space. Frequently (but not always) we can restrict our attention to densities, as we did in the case of the *Daphnia* example, and formulate the Kolmogorov forward equation for $L_1(\Omega)$.

Let for a particular course of E the population state at t deriving from an initial condition at t_0 corresponding to a unit mass at x_0 be denoted as $n(t, t_0, \mathbf{1}_{x_0})$. Then the clan mean of $\psi : \Omega \rightarrow \mathbb{R}$ is defined as

$$\nu(t_0, t, \psi)(x_0) := \int_{\Omega} \psi(x) n(t, t_0, \mathbf{1}_{x_0})(\{dx\}).$$

The Kolmogorov backward equation of a general physiologically structured population model is

$$-\frac{d}{dt_0} \nu(t_0, t, \psi) = A(E(t_0)) \nu(t_0, t, \psi) \quad (3.1)$$

with 'final' condition

$$\nu(t, t, \psi) = \psi, \quad (3.2)$$

where

$$A(E) = A_0(E) + B(E) \quad (3.3)$$

with

$$(A_0(E)\psi)(x) = \frac{d\psi}{dx} \nu(x, E) - \mu(x, E)\psi(x) \quad (3.4)$$

the i -state movement *cum* death operators, and

$$(B(E)\psi)(x) = \int_{\Omega} \psi(y) \beta(a, E; \{dy\}) \quad (3.5)$$

with birth operator. To derive this equation from first principles one only has to consider what will and/or may befall an individual who at time $t_0 - dt$ has i -state x_0 , during the next short time interval to t_0 , and then perform the usual averaging at t of ψ , first within and then over the clans generated by (i) what by t_0 has become of her and (ii) her offspring present at t_0 .

The Kolmogorov forward equation can best be introduced as the formal adjoint of the backward equation:

$$\frac{dn}{dt}(t, t_0, n_0) = A(E(t))^* n(t, t_0, n_0). \quad (3.6)$$

The main use of the general decomposition (3.3) derives from the fact that for $B = 0$ we can write down explicit solutions to either (3.1) or (3.6) by the simple expedient of integration along characteristics. Biologically this is equivalent to the following of cohorts.

The description of our population is completed by specifying any outputs, such as total population size, total biomass, or total resources consumption, to be derived from it:

$$y(t, t_0, n_0) = C(E(t))n(t, t_0, n_0). \quad (3.7)$$

When the range of y is finite dimensional, as is usually, but not always, the case, we can write

$$C(E)m = \langle \Gamma(E), m \rangle = \int_{\Omega} \Gamma(E)(x)m(\{dx\}) \quad (3.8)$$

with $\Gamma(E) : \Omega \rightarrow \mathbb{R}^h$. Given any specific initial condition, t_0, n_0 , the previous description should be such as to enable us in principle to calculate y as a function of $t > t_0$ for any sufficiently well behaved environmental input E .

From an applied point of view the main usefulness as well as interest of the previous considerations derives from the fact that many environmental variables, like food, are in turn influenced by the population, *e.g.* through consumption. Thus nonlinear evolution problems arise in a natural manner through the specification of the feedbacks through the environment.

The mathematical theory of provide a rigorous justification and interpretation of the general framework embodied in equation (3.1) to (3.8) is still in its infancy. Some first steps towards a functional analytic underpinning have been made in CLEMENT *et al.* (1987, 1988, 1989a, 1989b; see DIEKMANN, 1989, for a survey), but much work remains to be done. In the present contribution we restrict ourselves to formal manipulations, ignoring all problems related to the existence and uniqueness of solutions and to the precise interpretation of the differential equations (3.1) and (3.6).

4. An abstract formulation of linear chain trickery

From now on we shall always assume that the required output from the population model is finite (possibly zero) dimensional, and that E itself is the output from a dynamical system allowing a finite dimensional state representation.

4.1. The most general case.

Since our population equations (3.6) and (3.7) are linear in the state we do not loose any generality by assuming that any potential finite dimensional representation of them is linear in the state as well, and that the full model and its finite dimensional representation are related by a linear map $P : M(\Omega) \rightarrow \mathbb{R}^k$. In order that

$$N(t) = Pn(t) \quad (4.1)$$

provides us with a fully selfcontained description of the dynamical relationship between population input E and output y

$$\frac{dN}{dt} = K(E)N, \quad (4.2)$$

$$y = Q(E)N, \quad (4.3)$$

we should have

$$C(E) = Q(E)P \quad (4.4)$$

and

$$PA(E)^* = K(E)P \quad (4.5)$$

for some family of $h \times k$ matrices Q and some family of $k \times k$ matrices K .

Remark. It is not possible to attain greater generality by letting P depend on E as this will lead to a additional term $[\frac{d}{dE}P(E)\frac{dE}{dt}]n$ in (4.2). \square

If and only if (4.4) and (4.5) are fulfilled the dynamics of E and N can be described by a coupled finite dimensional system of ODE's. Once E is determined by solving this reduced system we can treat

$$\frac{dn}{dt} = A(E)^*n \quad (4.6)$$

as a non-autonomous (i.e. time dependent) but linear equation. If for example one can conclude from the (N, E) -system that E approaches a limit (or a periodic solution) for $t \rightarrow \infty$, the linear equation for n is asymptotically autonomous (periodic) and one can base further conclusions on the known asymptotic behaviour for these special cases.

If we are willing to assume that

$$Pm = \langle \Phi, m \rangle \quad (4.7)$$

for some vector Φ with components which are continuous functions of Ω we can reformulate (4.5) as

$$A(E)\Phi = K(E)\Phi, \quad (4.8)$$

provided $\Phi \in \mathcal{D}(A(E))$ for all E .

Remark. Actually $\cap_E \mathcal{D}(A(E))$ may be empty. However, within the context of dual semigroups one can extend $A(E)$ to an operator $A(E)^{\odot*}$ which has its range in a larger space $X^{\odot*}$ and therefore has larger domain as well (see CLEMENT *et al.* 1987, 1988, 1989a, 1989b, or DIEKMANN, 1989). One can then replace (4.8) by

$$A(E)^{\odot*}\Phi = K(E)\Phi.$$

In the following we shall not go into the distinction between this formulation and (4.8) (in fact we shall omit the precise definition of domains of unbounded operators). \square

Furthermore we can use (3.8), to replace (4.4) by

$$\Gamma(E) = Q(E)\Phi. \quad (4.9)$$

(4.8) and (4.9) together provide us with an easy practical recipe for checking whether a particular combination of ν , μ , β and Γ allows a finite dimensional representation. First of all it should be possible to write $\Gamma(E)(x)$ as $Q_1(E)\Phi_1(x)$ for some vector $\Phi_1 = (\varphi_1, \dots, \varphi_{k_1})^T$ of linearly independent functions ϕ_i and some $h \times k$ matrix family Q_1 . If this is the case our problem is linear chain trickable if and only if the space spanned by all possible combinations $A(E_p) \dots A(E_1)\phi_i$ for $i = 1, \dots, k_1$, $p = 0, 1, \dots$, is finite dimensional.

4.2. Two examples.

Example 1. Consider a cell population with size structure and assume that a mother cell divides into two parts without any mass loss, (see HEIJMANS, 1984 and METZ & DIEKMANN, 1986 (sub)section I.4, III.3.3.1, and VI.5, and the references given there). Then

$$(B(E)\psi)(x) = d(x, E)[- \psi(x) + 2 \int_0^1 \psi(\theta x) p(x, \{d\theta\})],$$

where d is the division rate and $p(x, \cdot)$ is the probability distribution of the sizes of the daughters relative to the size of their mother. The assumption of no mass loss implies that $p(x, \cdot)$ is symmetrical about $\theta = 1/2$. Now assume that the uptake of nutrient E by a cell is proportional to its biomass. In that case

$$C(E) = g(E)\langle \phi, \cdot \rangle,$$

with $\phi(x) = x$, i.e. $\langle \phi, \cdot \rangle$ is the total biomass functional. Next we observe that necessarily

$$B(E)\phi = 0$$

in accordance with the initial assumption that biomass is conserved in the division process. Finally we observe that we get

$$A(E)\phi = A_0(E)\phi = ((f - (E) - \mu(E))\phi)$$

if we make in additional assumptions that

$$\nu(x, E) = f(E)x \quad \text{and} \quad \mu(x, E) = \mu(E).$$

The first condition is *i.a.* fulfilled when basal metabolism is proportional to biomass, and cell growth is proportional to nutrient uptake minus loss through basal metabolism:

$$f(E) = \alpha(g(E) - m).$$

The second condition is *i.a.* fulfilled when the only cause of cell loss is washout. If finally we assume chemostat dynamics, so that $\mu(E) = D$, the dilution rate, we arrive at

$$\begin{aligned} \frac{dN}{dt} &= \alpha(g(E) - m)N - DN, \\ \frac{dE}{dt} &= D(E^i - E) - g(E)N, \end{aligned}$$

where E^i is the concentration of the limiting substrate in the inflowing nutrient both. Under appropriate conditions on g the resulting ODE system has a globally stable steady state. \square

Example 2. This example is more contrived. Assume again that individuals acquire food at a rate $g(E)x$ where E is the surrounding food concentration and x is their size. Assume moreover that the acquired food is partitioned into a fraction $\kappa(x)$ which is spent on reproduction and a fraction $1 - \kappa(x)$ spent on basal metabolism and growth, and that the cost of producing offspring biomass equals that of producing parent biomass. Finally assume again that basal metabolism is proportional to size and that the death rate is size independent. In that case

$$(A_0(E)\psi)(x) = (g(E)(1 - \kappa(x)) - m)x\psi'(x) - \mu(E)\psi(x)$$

and

$$(B(E)\psi)(x) = x_b^{-1}g(E)\kappa(x)x\psi(x_b),$$

where x_b is the size of the young. If we choose again $\phi(x)$ to be equal to x we find

$$A(E)\phi = (g(E) - m - \mu(E))\phi. \quad \square$$

4.3. 'Ordinary' LCT.

Usually the term linear chain trickery is reserved for a special subclass of the general class of tricks discussed in the previous subsections, the restriction being that it should also be possible to calculate the birth rate into the population from the resulting finite-dimensional representation. The reason for the special importance of this smaller class of problems is that once we know the birth rate as a function of time we can easily construct the full population trajectory by using a variation of constants formula involving the explicit solution \tilde{n} of

$$\frac{d\tilde{n}(t, t_0, n_0)}{dt} = A_0(E(t))\tilde{n}(t, t_0, n_0) \quad \text{with} \quad \tilde{n}(t_0, t_0, n_0) = n_0.$$

The ‘ordinary’ LCT problem is characterized by the conditions that there exist a map $P : M(\Omega) \rightarrow \mathbb{R}^k$, a family of maps $R(E) : \mathbb{R}^k \rightarrow M(\Omega)$, and families of $k \times k$ matrices H and $h \times k$ matrices Q such that

$$B(E)^* = R(E)P, \quad (4.10)$$

$$PA_0(E)^* = H(E)P, \quad (4.11)$$

$$C(E) = Q(E)P. \quad (4.12)$$

The resulting system of ODE’s is

$$\frac{dN}{dt} = H(E)N + PR(E)N. \quad (4.13)$$

If we may in addition make the special assumption (4.7), i.e. $P = \langle \Phi, \cdot \rangle$, (4.10) to (4.12) may be replaced by

$$\beta(x, E, \cdot) = \sum b_i(E; \cdot) \phi_i(x), \quad (4.14)$$

$$A_0(E)\Phi(x) = H(E)\Phi(x), \quad (4.15)$$

$$\Gamma(E)(x) = Q(E)\Phi(x) \quad (4.16)$$

for all x .

Remark. In the case of generalized LCT nothing can be said about the component of the p -state in the kernel of the map P . This is unfortunate as a slight perturbation of the model usually brings it out of the LCT class. If unpleasant things happen in the kernel of P this would result in an extreme non-robustness of the conclusions derived from the LCT variants. It is clear from the discussion at the start of this subsection that the situation is much better for ordinary LCT as usually it is quite easy to prove that $\tilde{n}(t, t_0, n_0) \rightarrow 0$ for all n_0 in a very fast manner. As a consequence for example the local linearisation about an equilibrium of a model in the ordinary LCT class always leads to a polynomial characteristic equation, corresponding to a decomposition of the p -state space into a finite number of (generalized) eigenvectors and a remaining component consisting entirely of ‘fast descenders’. \square

5. Necessary and sufficient conditions for linear chain trickery

We shall in this section proceed from (4.14) – (4.16) on the assumption that ν , μ , β and γ are sufficiently smooth in x . Moreover, we shall only consider minimal representations, in the sense that k is as small as possible.

5.1. One dimensional i -state spaces.

Assume that the i -state space is one dimensional. Then (3.4) reduces to

$$((A_0(E))\psi(x) = \nu(x, E)\psi'(x) - \mu(x, E)\psi(x). \quad (5.1)$$

5.1.1. The case of but one single resulting ODE. We first restrict ourselves to the special case where P has one-dimensional range, i.e. our population model can be represented by just a single ODE. The question then is ‘Under which conditions on ν and μ can we find a (continuous) function $\phi(x)$ and a function $\lambda(E)$ such that

$$\nu(x, E)\phi'(x) - \mu(x, E)\phi(x) = \lambda(E)\phi(x)?' \tag{5.2}$$

If we rewrite (5.2) in the form $\frac{\mu(x, E) + \lambda(E)}{\nu(x, E)} = \frac{\phi'(x)}{\phi(x)}$ we see that a necessary as well as sufficient condition for the family $A_0(E)$ to allow linear chain trickery population models is that there exists a function $\lambda(E)$ such that

$$\frac{\mu(x, E) + \lambda(E)}{\nu(x, E)} = f(x) \tag{5.3}$$

independent of E . For the full population model to be linear chain trickable moreover (4.14) and (4.16) should apply with

$$\phi(x) = \exp\left[\int_0^x f(\xi)d\xi\right]. \tag{5.4}$$

Example 1. Let $\nu(x, E) = \nu(E)$, i.e. x is physiological age. In the case A_0 allows linear chain trickable population models iff

$$\mu(x, E) = \nu(E)\mu_1(x) + \mu_2(E). \tag{5.5}$$

Moreover ϕ should be of the form

$$\phi(x) = \exp\left[\int_0^x \mu_1(\xi)dx\right] \cdot \exp[-\alpha x] \tag{5.6}$$

where α still is a free parameter which can be chosen to comply with the conditions on the birth and output operators. \square

Example 2. Let $\mu(x, E) = \mu(E)$, i.e. the i -state of an individual does not influence its chances of dying. In that case $A_0(E)$ allows linear chain trickable population models iff

$$\nu(x, E) = \nu_1(x)\nu_2(E), \tag{5.7}$$

which after a rescaling of x brings us back to the previous example, or

$$\phi(x) = 1 \quad \text{and} \quad \lambda(E) = -\mu(E). \tag{5.8}$$

Note that in the latter case the conditions (4.14) and (4.16) imply that both the *per capita* birth rate and the ‘*per capita* resource consumption rate’ are independent of the i -state, i.e. the classification of individuals by x is population dynamically irrelevant. \square

5.1.2. Physiological age models. Let us now make the special assumption that $\nu(x, E) = \nu_1(x)\nu_2(x)E$. Without loss of generality we may set $\nu_2(E_0) = 1$ for some (arbitrarily chosen) E_0 , and $\nu_1(x) = 1$: Just rescale to physiological age

$$\tilde{x} := \int_0^x \frac{d\xi}{\nu_1(\xi)}. \quad (5.9)$$

In this new variable condition (4.15) becomes (from now on we drop the index 2 and the tilda)

$$\nu(E)\Phi'(x) - \mu(x, E)\Phi(x) = H(E)\Phi(x), \quad (5.10)$$

from which we deduce that Φ should take the form

$$\Phi(x) = \exp\left[\int_0^x \mu(\xi, E_0)d\xi\right] \cdot \exp[H(E_0)x] \cdot \Phi(0). \quad (5.11)$$

Substitution of (5.11) and (5.10) gives

$$[\nu(E)\mu(x, E_0) - \mu(x, E)]\Phi(x) = [H(E) - \nu(E)H(E_0)]\Phi(x), \quad (5.12)$$

i.e. $\Phi(x)$ is an eigenvector of $H(E) - \nu(E)H(E_0)$. For fixed E the eigenvalues of $H(E) - \nu(E)H(E_0)$ form a discrete set. On the other hand it is reasonable to assume that the map $x \mapsto \nu(E)\mu(x, E_0) - \mu(x, E)$ is continuous. A continuous function taking values in a discrete set is constant. Therefore we can conclude that we should have

$$\mu(x, E) = \nu(E)\mu(x, E_0) - \lambda(E), \quad (5.13)$$

where $\lambda(E)$ is only subject to the consistency condition $\lambda(E_0) = 0$, and

$$H(E) = \nu(E)H(E_0) + \lambda(E)I, \quad (5.14)$$

where $H(E_0)$ may still be chosen freely to comply with (4.14) and (4.16).

As a final consideration we note that a function $\phi(x)$ can be written as $q^T \exp[H(E_0)x]\Phi(0)$ if and only if it can be written as a weighted sum of polynomials times (complex) exponentials. This tells us what freedom we have in choosing birth and output operators.

5.1.3. Death rate independent of the i -state. If we try to generalize the approach from the previous subsection to i -states moving in a less restricted manner we end up with

$$\left[\frac{\nu(x, E)}{\nu(x, E_0)}\mu(x, E_0) - \mu(x, E)\right]\Phi(x) = \left[H(E) - \frac{\nu(x, E)}{\nu(x, E_0)}H(E_0)\right]\Phi(x) \quad (5.15)$$

the *Daphnia* example from section 1. Note also that (5.20) definitely does not belong to the family (5.18), in accordance with the remark made at the start of this subsection.

To prove our result we first choose a environment value E_0 and rescale x so that $\nu(x, E_0) = 1$ (we assume that a value of E_0 exists such that $\nu(x, E_0) > 0$ on the whole interior of Ω). Next we rearrange (5.15) into

$$\tilde{H}(E)\Phi(x) = \nu(x, E)\tilde{H}(E_0)\Phi(x) \quad (5.21)$$

with

$$\tilde{H}(E) = H(E) + \mu(E)I. \quad (5.22)$$

Moreover

$$\Phi(x) = \exp[\tilde{H}(E_0)x]\Phi(0). \quad (5.23)$$

As a next step we observe that our choice of ϕ_i is to a large extent arbitrary as long as the set of ϕ_i 's spans one and the same subspace of the continuous functions on Ω . Therefore we may without loss of generality write

$$\Phi(x) = (e^{\lambda_1 x}, x e^{\lambda_1 x}, \dots, x^{k_1-1} e^{\lambda_1 x}, e^{\lambda_2 x}, \dots, x^{k_r-1} e^{\lambda_r x})^T, \quad (5.24)$$

where the λ_i are the eigenvalues of $\tilde{H}(E_0)$. Note that (5.24) corresponds to the particular choice $\tilde{H}(E_0) = \Lambda$. Note also that all possible $\tilde{H}(E_0)$ can be obtained from this particular choice by a change of basis for $N = Pn$. Restriction of our attention to minimal representations moreover guarantees that all the λ_i are different.

Substitution of (5.24) into (5.21) yields

$$\nu(x, E)(qx^{q-1} + x^q \lambda_p) e^{\lambda_p x} = \sum_{i=1}^r \sum_{j=0}^{k_i-1} \tilde{h}_{(p,q)(i,j)}(E) x^j e^{\lambda_i x}, \quad (5.25)$$

where the symbols (p, q) and (i, j) relate in an obvious manner to the indices characterizing the components of Φ . To proceed further we need several lemmas.

Lemma 1a. *Let $\lambda_i \in \mathbb{C}$ for $i = 1, \dots, r$ be all different and let $U_p := \{\lambda_p - \lambda_i | i = 1, \dots, r\}$ then $\cap_{p=1}^r U_p = \{0\}$.*

Proof. $\cap_{p=1}^r U_p \neq \{0\}$ iff there exists a complex number $\alpha \neq 0$ common to all U_p . Assume that such an α exists. This allows us to define a relation \rightarrow on $E_r := \{1, \dots, r\}$ by $i \rightarrow p \Leftrightarrow \lambda_i - \lambda_p = \alpha$. Under \rightarrow every element of E_r connects in the forward and backward direction to at most one other element of E_r since (i) $\lambda_i - \lambda_p = \alpha \lambda_i - \lambda_{p'} \Rightarrow \lambda_{p'} = \lambda_p$ and (ii) $\lambda_{i'} - \lambda_p = \alpha = \lambda_{i''} - \lambda_p \Rightarrow \lambda_{i'} = \lambda_{i''}$. Since we have r sets U_p we should have at least r connections under \rightarrow . As E_r has but r elements this would mean that there has to exist at least one cycle. But this is inconsistent with the geometrical interpretation (in \mathbb{C}) of the relation \rightarrow . (Note that the existence of a nonzero common element to only $r - 1$ of the U_p implies that the λ_i lie at fixed distance on a straight line in \mathbb{C} .) \square

Exactly the same argument yields

Lemma 1b. Let $\lambda_i \in \mathbb{C}$ for $i = 1, \dots, r$ be all different and let $U_p := \{\lambda_p - \lambda_i | i = 1, \dots, r\}$. Assume $\lambda_1 = 0$. Then either

$$\bigcap_{p=2}^r U_p = \{0\}$$

or, possibly after renumbering the λ_i 's,

$$\lambda_i = (i-1)\alpha \quad \text{and} \quad \bigcap_{p=2}^r U_p = \{0, +\alpha\}$$

for some $\alpha \in \mathbb{C}$.

Lemma 2a. Let $k \geq 1$ be a given integer. Suppose there exist complex numbers $\lambda \neq 0$ and α_{jq} , $j, q \in \{0, \dots, k-1\}$ such that

$$R(q, x) = \sum_{j=0}^{k-1} \frac{\alpha_{jq} x^j}{qx^{q-1} + \lambda x^q}, \quad q = 0, \dots, k-1,$$

is independent of q . Then R is independent of x as well.

Proof. By taking $q = 0$ we find that R is a polynomial in x of degree $\leq k-1$. By taking $q = k-1$ we obtain that $((k-1)x^{k-2} + \lambda x^{k-1})R(q, x)$ is a polynomial degree $\leq k-1$. Therefore the degree of R is necessarily zero. \square

Lemma 2b. Let $k \geq 2$ be a given integer. Suppose there exist complex numbers α_{jq} , $j, q \in \{1, \dots, k-1\}$ such that

$$R(q, x) = \sum_{j=0}^{k-1} \frac{\alpha_{jq} x^j}{qx^{q-1}}, \quad q = 1, \dots, k-1,$$

is independent of q . Then R is necessarily of the form $a + bx$.

Proof. By taking $q = 1$ we find that R is a polynomial in x of degree $\leq k-1$. By taking $q = k-1$ we obtain that $(k-1)x^{k-2}R(q, x)$ is a polynomial of degree $\leq k-1$. Therefore the degree of R is necessarily ≤ 1 . \square

Lemma 3. Let for $j, q \in \mathbb{N}, \theta \in \mathbb{C}$

$$U(j, q, \beta, \theta) := \frac{x^j}{qx^{q-1} + \beta x^q} e^{\theta x}$$

then a necessary condition for $U(j_0, q_0, \beta_0, \theta_0)$ to be in the linear span of $\{U(j_i, q_i, \beta_i, \theta_i) | i = 1, \dots, k-1\}$ is that $\theta_0 \in \{\theta_i | i = 1, \dots, k-1\}$.

Proof. Suppose that $U(j_0, q_0, \beta_0, \theta_0) = \sum_{i=1}^{k-1} \xi_i U(j_i, q_i, \beta_i, \theta_i)$. Multiply both sides with $\prod_{i=0}^{k-1} (q_i x^{q_i-1} + \beta_i x^{q_i})$. At the left and right hand side we now only have polynomials times exponentials in x . Any collection of functions $x^{m_i} e^{\theta_i}$ for which the pairs (m_i, θ_i) are all different are linearly independent. Therefore the factor $e^{\theta_0 x}$ has to appear on both sides of the equal sign. \square

If either $\lambda_p \neq 0$ or $q \neq 0$ we can rewrite (5.25) in the form

$$\nu(x, E) = \sum_{i=1}^r \sum_{j=0}^{k_i-1} \tilde{h}_{(p,q)(i,j)}(E) \frac{x^j}{qx^{q-1} + x^q \lambda_p} e^{(\lambda_i - \lambda_p)x}. \tag{5.26}$$

If for all p either $\lambda_p \neq 0$ or $k_p > 1$ we thus find at least r (in fact $k = \sum_{i=1}^r k_i$) expressions for ν .

First assume that for all p either $\lambda_p \neq 0$ or $k_p > 1$. In that case (5.26), Lemma 3 and Lemma 1a together imply that

$$\tilde{h}_{(p,q)(i,j)}(E) = 0 \quad \text{for } i \neq p$$

and therefore that

$$\nu(x, E) = \sum_{j=0}^{k_p-1} \tilde{h}_{(p,q)(p,j)}(E) \frac{x^j}{qx^{q-1} + x^q \lambda_p}. \tag{5.27}$$

We can now apply Lemma 2a to conclude that ν is independent of x provided 0 is not the only λ . We are then in the situation described by (5.16) and (5.19). When $\lambda = 0$ is the only eigenvalue we apply Lemma 2b to conclude that ν is linear in x . This brings us to the situation described by (5.17) and (5.20).

Next we assume that $r \geq 2$ and, say, $\lambda_1 = 0, k_1 = 1$. We still obtain (5.26) for $p = 2, \dots, r$. When not $\lambda_i = (i-1)\alpha$ for some $\alpha \neq 0$ Lemma 1b tells us that we are in the first of the two situations encountered before. When, on the other hand, $\lambda_i = (i-1)\alpha$ we deduce from Lemma 3 together with Lemma 1b that

$$\begin{aligned} \nu(x, E) &= \sum_{j=0}^{k_p-1} \tilde{h}_{(p,q)(p,j)}(E) \frac{x^j}{qx^{q-1} + x^q \lambda_p} \\ &+ \sum_{j=0}^{k_p-1-1} \tilde{h}_{(p,q)(p-1,j)}(E) \frac{x^j e^{-\alpha x}}{qx^{q-1} + \lambda_p x^q} \end{aligned} \tag{5.28}$$

for $p \geq 2$. Applying Lemma 2a to each of the sums we infer that

$$\nu(x, E) = \frac{1}{\alpha}(g(E) + f(E)e^{-\alpha x}) \tag{5.29}$$

(the reason for this particular ‘parameterization’ with g, f and $1/\alpha$ will become clear below). We claim that in this situation necessarily $k_p = 1$ for all p . We proceed by induction. Suppose $k_2 > 1$ then we can take $p = 2, q = 1$ in (5.28) to obtain

$$\nu(x, E) = \sum_{j=0}^{k_2-1} \tilde{h}_{(2,1)(2,j)}(E) \frac{x^j}{1 + \lambda_2 x} + \tilde{h}_{(2,1)(1,0)}(E) \frac{e^{-\alpha x}}{1 + \lambda_2 x}.$$

Since $\lambda_2 \neq 0$ this is incompatible with (5.29). We conclude that $k_2 = 1$. We then use the same argument for $p = 3$ etc.

Finally we transform to $\tilde{x} = e^{\alpha x}$. This yields $\tilde{\nu}(\tilde{x}, E) = f(E) + g(E)\tilde{x}$ and $\tilde{\Phi}(\tilde{x}) = (1, \tilde{x}, \dots, \tilde{x}^{r-1})$ which, modulo tilda’s and $r \rightarrow k$, is precisely (5.17). \square

Remark 1. When judging the generality of the linear growth law (5.17) one should keep in mind that one can still employ an E -independent change of i -state variable to bring a particular biological growth law in that form. For example, the growth laws most commonly encountered in the literature

- (i) von Bertalanffy: $\frac{dy}{dt} = \alpha y^{2/3} - \beta y$
- (ii) logistic: $\frac{dy}{dt} = \alpha y - \beta y^2$
- (iii) Gompertz: $\frac{dy}{dt} = \alpha y - \beta y \log y$

can all be linearized:

- (i) $x = y^{1/3} \Rightarrow \frac{dx}{dt} = \frac{1}{3}(\alpha - \beta x)$
- (ii) $x = \frac{1}{y} \Rightarrow \frac{dx}{dt} = \beta - \alpha x$
- (iii) $x = \log y \Rightarrow \frac{dx}{dt} = \alpha - \beta x$

(we thank Y. Iwasa for reminding us to (ii) and (iii)). \square

Remark 2. If we set $\mu(x, E) = \nu(x, E)\mu_1(x) + \mu_2(E)$ the combinations (5.16) and (5.17) with the old $\Phi(x)$ replaced by $\Psi(x) = \exp(\int^x \mu_1(\xi)d\xi)\Phi(x)$ still satisfy (4.15) with the same $H(E)$ as when $\mu_1 = 0$. \square

5.2. Higher dimensional i -state spaces.

We do not have any general results for the case where Ω is higher dimensional. What we do have is a whole zoo of weird and wonderful examples. We just give three of them.

Example 1. Let Ω be two-dimensional and let ν be given by

$$\nu(x, E) = \begin{bmatrix} a(E) + b(E)x_1 \\ c(E) \end{bmatrix}.$$

Define

$$\Phi(x) = \begin{bmatrix} 1 \\ x_1 \\ x_1^2 \\ e^{-kx_2} \\ x_1 e^{-kx_2} \\ x_1^2 e^{-kx_2} \end{bmatrix}$$

and

$$L(E) = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ a & b & 0 & 0 & 0 & 0 \\ 0 & 2a & 2b & 0 & 0 & 0 \\ 0 & 0 & 0 & -kc & 0 & 0 \\ 0 & 0 & 0 & a & (b - kc) & 0 \\ 0 & 0 & 0 & 0 & 2a & 2b - kc \end{bmatrix}.$$

A straightforward calculation then shows that

$$\frac{d\Phi}{dx}(x) \cdot \nu(x, E) = L(E)\Phi(x)$$

which is the required relation $A_0(E)\Phi = H(E)\Phi$ for $\mu = 0$. When μ is nonzero but still independent of x , $L(E)$ has to be replaced by $H(E) = L(E) - \mu(E)I$.

The biological interest of this example is that we may interpret x_1 as size and x_2 as physiological age. Moreover Φ is chosen in such a way that we can choose

$$\beta(x, E) = f(E)(1 - e^{-kx_2})x_1^2$$

as an age and size dependent birth rate of individuals. \square

The next two examples do not allow immediate biological applications. They do show, however, that in the case of higher dimensional i -state spaces there exist also cases with nonlinear i -state dynamics which are yet linear chain trickable.

Example 2. Let again Ω be two dimensional, and let

$$\nu(x, E) = \begin{pmatrix} a(E) + b(E)x_1 \\ c(E)x_1^2 \end{pmatrix}, \quad \Phi(x) = \begin{pmatrix} 1 \\ x_1 \\ x_1^2 \\ x_2 \end{pmatrix},$$

$$L(E) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ a & b & 0 & 0 \\ 0 & 2a & 2b & 0 \\ 0 & 0 & c & 0 \end{pmatrix}. \quad \square$$

Example 3. Let Ω be three dimensional and let

$$\nu(x, E) = \begin{pmatrix} a_1(E) \\ a_2(E) \\ c_1(E)e^{\lambda_1 x_1} + c_2(E)e^{\lambda_2 x_2} + c_3(E)e^{\lambda_1 x_1 + \lambda_2 x_2} \end{pmatrix},$$

$$\Phi(x) = \begin{pmatrix} e^{\lambda_1 x} \\ e^{\lambda_2 x} \\ e^{\lambda_1 x_1 + \lambda_2 x_2} \\ x_3 \end{pmatrix},$$

$$L(E) = \begin{pmatrix} \lambda_1 a_1 & 0 & 0 & 0 \\ 0 & \lambda_2 a_2 & 0 & 0 \\ 0 & 0 & \lambda_1 a_1 + \lambda_2 a_2 & 0 \\ c_1 & c_2 & c_3 & 0 \end{pmatrix}. \quad \square$$

6. Discussion

Understanding the precise nature of the necessary and sufficient conditions for linear chain trickery to be possible is of interest of three reasons. First of all there is the intrinsic esthetic appeal of the problem. Secondly its solution amounts to a *complete* catalogue of cases for which a reduction of finite dimension is possible. No doubt this catalogue will contain useful cases which thus far escaped our attention (like the first example from section 5.2). Thirdly solving the general linear chain trickery problem will tell us which (classic) ODE models can be reinterpreted reduced structured models. (In our, admittedly somewhat biased, opinion the justification of any ODE population model should derive from the fact that such an interpretation is possible).

In this paper we to a large extent have solved the ordinary, or special, linear chain trickery problem for the case of a one-dimensional i -state space. A full characterization of linear chain trickable models with higher dimensional i -state spaces is still lacking. And we have only scratched the surface of the generalized linear chain trickery problem. However, we plan to keep working on these problems.

Acknowledgments. Hans Metz wishes to thank the Department of Physics and Applied Physics of the University of Strathclyde, Glasgow, for its hospitality during part of the research reported here.

Note added in print. In the meantime we have also solved the 'ordinary' LCT characterization problem for one dimensional i -state spaces in a general manner, i.e., without assuming any restrictions on either the rate of i -state change ν or the death rate μ . The result is bizarre.

References

- [1] S.P. Blythe, R.M. Nisbet, W.S.C. Gurney (1984), *The dynamics of population models with distributed maturation period*, Theor. Pop. Bio. **25**, 289–311.
- [2] Ph. Clement, O. Diekmann, M. Gyllenberg, H.J.A.M. Heijmans, C.H.R. Thieme (1987, 1988, 1989a, 1989b), *Perturbation theory for dual semigroups*,
 I. *The sun-reflexive case*, Math. Ann. **277**, 709–725.
 II. *Time-dependent perturbations in the sun-reflexive case*, Proc. Roy. Soc. Edinburgh A **109**, 145–172.
 III. *Nonlinear Lipschitz continuous perturbations in the sun-reflexive case*, in “Volterra Integro-Differential Equations in Banach Spaces and Applications”, G. Da Prato, M. Iannelli, Eds., Longman, 67–89.
 IV. *The intertwining formula and the canonical pairing*, in “Trends in Semigroup Theory and Applications”, Ph. Clement, S. Invernizzi, E. Mitidieri, I.F. Vrabie, Eds., Marcel Dekker, 95–116.
- [3] O. Diekmann (1989), *On semigroups and populations*, Advanced Topics in the Theory of Dynamical Systems, G. Fusco, M. Iannelli, L. Salvadori, Eds., Academic Press, 125–135.
- [4] O. Diekmann, H. Metz (1988,89), *Exploring linear chain trickery for physiologically structured populations*, TW in Beeld, CWI, Amsterdam, 73–84. Also: CWI Quarterly **2**, 3–14.
- [5] L. Edelstein, Y. Hadar (1983), *A model for pellet size distribution in submerged mycelial cultures*, J. Theor. Biol. **105**, 427–457.
- [6] D. Fargue (1983), *Reducibilité des systèmes héréditaires à des systèmes dynamiques (régis des équations différentielles ou aux dérivés partielles)*, C.R. Acad. Sc. Paris B **277**, 471–473.
- [7] D. Fargue (1984), *Reducibilité des systèmes héréditaires*, Int. J. Non-linear Mechanics **9**, 331–338.
- [8] W.S.C. Gurney, R.M. Nisbet (1983), *The systematic formulation of delay-differential models of age or size structured populations*, Population Biology, M.I. Freeman & C. Strobeck, Eds., Springer Lect. Notes in Biomath. **52**, 163–172.
- [9] W.S.C. Gurney, R.M. Nisbet, S.P. Blythe (1986), *The systematic formulation of models of stage-structured populations*, The Dynamics of Physiologically Structured Populations, J.A.J. Metz & O. Diekmann, Eds., Springer Lect. Notes in Biomath. **68**, 474–494.
- [10] W.S.C. Gurney, R.M. Nisbet, J.H. Lawton (1983), *The systematic formulation of tractable single species models incorporating age-structure*, J. Anim. Ecol. **52**, 479–496.
- [11] M.E. Gurtin, R.C. MacCamy (1974), *Non-linear age-dependent population dynamics*, Archive for Rational Mechanics and Analysis **54**, 281–300.
- [12] M.E. Gurtin, R.C. MacCamy (1979), *Some simple models for non-linear age-dependent population dynamics*, Math. Biosc. **43**, 199–211.
- [13] H.J.A.M. Heijmans (1984), *On the stable size distribution of populations reproducing by fission into two unequal parts*, Math. Biosc. **72**, 19–50.
- [14] S.A.L.M. Kooijman, J.A.J. Metz, *On the dynamics of chemically stressed populations: the deduction of population consequences from effects on individuals*, Ecotox. Env. Saf. **8**, 254–274.
- [15] M. MacDonald (1978), *Time lags in biological models*, Springer Lect. Notes in Biomath **27**.
- [16] M. MacDonald (1989), *Biological delay systems: linear stability theory*, Cambridge U Press, Cambridge.
- [17] J.A.J. Metz, O. Diekmann (Eds.) (1986), *The Dynamics of Physiologically Structured Populations*, Springer Lect. Notes in Biomath. **68**.
- [18] J.A.J. Metz, A.M. De Roos, F. van den Bosch (1988), *Population models incorporating physiological structure: a quick survey of the basic concepts and an application to size-structured population dynamics in waterfleas*, Size-structured Populations: Ecology and Evolution, E. Ebenman & L. Persson, Eds, Springer, Berlin, Heidelberg, 106–124.

- [19] L.F. Murphy (1983), *A non-linear growth mechanism in size structured population dynamics*, J. Theor. Biol. **104**, 493–506.
- [20] R.M. Nisbet, W.S.C. Gurney (1983), *The systematic formulation of population models for insects with dynamically varying instar duration*, Theor. Pop. Biol. **23**, 114–135.
- [21] R.M. Nisbet, W.S.C. Gurney (1986), *The formulation of age-structured models*, Mathematical Ecology, T.G. Hallam & S.A. Levin, Eds., Springer, Berlin, Heidelberg, 95–115.
- [22] R.M. Nisbet, S.P. Blythe, W.S.C. Gurney, J.A.J. Metz (1985), *Stage-structure models of populations with distinct growth and development processes*, IMA J. Math. Appl. in Med. & Biol. **2**, 57–68.
- [23] Y.M. Repin (1965), *On the approximate replacement of systems with lag by ordinary differential equations*, J. Appl. Math. and Mech **29**, 254–264.
- [24] A.M. De Roos, O. Diekmann, J.A.J. Metz (1988), *The escalator boxcar train: basic theory and an application to Daphnia population dynamics*, Report AM-R8814, Center for Mathematics and Computer Science, Amsterdam.
- [25] A.M. De Roos, J.A.J. Metz (preprint), *Stabilizing and destabilizing mechanisms in a planktonic system: modelling Daphnia population dynamics*.
- [26] A.M. De Roos, J.A.J. Metz, E. Evers, A. Leipoldt (preprint), *A size dependent predator-prey interaction; who pursues whom?*.
- [27] T. Vogel (1965), *Théorie des Systèmes Evolutifs*, Gauthier Villars, Paris.

J.A.J. Metz

Institute of Theoretical Biology

University of Leiden

Kaiserstraat 63

NL-2311 GP Leiden, The Netherlands

O. Diekmann

Center for Mathematics and Computer Science

Kruislaan 413

NL-1098 SJ Amsterdam, The Netherlands