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CONTINUUM POPULATION DYNAMICS WITH AN APPLICATION TO *DAPHNIA MAGRA*

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ABSTRACT

The paper starts by discussing the formulation of models for the dynamics of populations with physiological structure in the language of continuum mechanics. Subsequently it is indicated how the spectral theory of positive semigroups of operators yields results about stable distributions in linear models. It is shown how the formalism can be used to deduce the population consequences of the physiological effects of toxic chemicals on individuals of, for instance *Daphnia magna*. Finally, the need for mathematical machinery which is well suited to analyse nonlinear problems is stressed.

1. INTRODUCTION

The partial differential equations of continuum mechanics describe the evolution in the course of time of the density of particles in an elastic material, a fluid or a gas. They are derived by combining a mathematical description of the physical forces that act upon the particles with bookkeeping arguments based on conservation of mass, etc. .

A first and crude description of the state of a population is given by the number of individuals. As a next step one may distinguish individuals from each other according to relevant physiological traits (a large codfish is not the same as a small codfish when one considers reproduction and predation). The present paper is concerned with this "next step". Exploiting the similarity with the bookkeeping part of continuum mechanics we shall describe, in section 2, the mathematical structure of a large class of models.

The aim of these models is to describe the behaviour of populations in terms of the behaviour of individuals (such that, for instance, the impact of toxic substances on populations can be inferred from the impact on the individuals). In later sections it will be argued that the explicit incorporation of physiological structure enables one to describe density dependence on the basis of biological facts (or, at least, biologically plausible arguments) as opposed to ad hoc mathematical assumptions in unstructured models.

In section 3 we shall sketch how spectral theory, compactness arguments, positivity arguments and the theory of semigroups of operators can be combined to yield resuls about stable distributions in *linear* models. Without much disadvantage most of this section may be skipped by those readers which are not interested in functional analysis. In section 4 we show how the mathematical machinery (both the existing and some which still has to be developed) is of value for deriving the ecological consequences from physiological effects of toxic chemicals on the individual members of a population. In section 5 we observe that there exists, as yet, no systematic theory for *nonlinear* problems, even if we have some idea how to proceed in some special cases.

This paper describes an odd concoction of mathematical modelling, (functional) analysis and biological experiments, but deliberately so. Among other things we intend to demonstrate that the interplay of mathematics and biology can be profitable for both fields simultaneously.

2. BOOKKEEPING AND MODEL SPECIFICATION

Let the physiological state of each individual be given by the value of an N-vector x. Thus the state space of the individuals is Ω, some subset of $\mathbb{R}^N$. The individuals trace orbits in Ω. The beginning and the end of such orbits are the physiological state at birth and death, respectively ("birth" and "death" have to be interpreted broadly as we shall see in the examples later on). We assume that in between the orbits are determined by an ordinary differential equation

$$\frac{dx}{dt} = v(x) \,, \tag{2.1}$$

where $v: \Omega \to \mathbb{R}^N$ describes the *velocity* with which the individuals move through Ω. Of course v may depend on other variables but we do not, at this point, include this explicitly in our notation.

Let $n(t,.): \Omega \to \mathbb{R}_+$ be the density function at time t, i.e., for each $\Omega_0 \subset \Omega$ the number of individuals at time t with physiological state belonging to Ω_0 is given by

$$\int_{\Omega_0} n(t,x)dx.$$

Then vn is the *flux* of individuals and a standard application of the divergence theorem leads to the *balance law*

$$(2.2) \qquad \frac{\partial n}{\partial t} + \mathrm{div}(vn) = \text{sources} - \text{sinks} \quad ,$$

where sources and sinks describe birth and death (see, for instance, Lin & Segel (1974), Segel (1977) and the papers by Segel and Oster in DiPrima (1977)). We shall assume that the number of individuals in the relevant states is so large that we can use a deterministic approximation to describe inherently stochastic processes. Or, in other words, we shall describe the birth and death processes which involve some element of chance in terms of rates. Formulating a mathematical model now amounts to specifying Ω, v, the sources and sinks, and $-\nu.vn$ (where ν is the outward unit normal) at that part of the boundary $\partial\Omega$ where $\nu.v < 0$ (i.e., where newborn individuals can enter Ω). In order to illustrate the formalism we present two sets of examples which concern unicellular organisms reproducing by fission and ectothermic animals having weight dependant fertility.

Example 1: *Multiplication by division.* For simplicity we shall assume that the organisms do not die. The necessary modifications to incorporate deaths are immediate.

a: Let the cells be characterized by their age (i.e., the time elapsed since the cell was created by a division of her mother). Let b(a) denote the rate at which cells of age a divide into two daughters. Since $\frac{da}{dt} = 1$ and all cells are born with age zero we obtain

$$(2.1) \qquad \begin{aligned} &\frac{\partial}{\partial t} n(t,a) + \frac{\partial}{\partial a} n(t,a) = - b(a)\, n(t,a), \\ &n(t,0) = 2 \int_0^\infty b(\sigma)\, n(t,\sigma)d\sigma. \end{aligned}$$

b: Instead of age we now use "size" s to characterize the cells. If cells divide into two identical daughters exactly when reaching size one we have

$$(2.2) \qquad \begin{aligned} &\frac{\partial}{\partial t} n(t,s) + \frac{\partial}{\partial s} (v(s)n(t,s)) = 0, \\ &v(\tfrac{1}{2})n(t,\tfrac{1}{2}) = 2\, v(1)n(t,1)\ . \end{aligned}$$

Here v(s), the growth rate of cells of size s, is assumed to be positive.
c: Again suppose that cells divide exactly when reaching size one, but now assume that the two daughters are not necessarily identical.

Let the probability that fission results into one daughter of size s and one of size 1-s be described by the nonnegative function D which is symmetric about $\frac{1}{2}$ and has integral 1. Then

$$(2.3)\qquad \begin{aligned} &\frac{\partial}{\partial t} n(t,s) + \frac{\partial}{\partial s}(v(s)n(t,s)) = 2v(1)\, D(s)\, n(t,1) \\ &v(0)\, n(t,0) = 0 \end{aligned}$$

d: Let b(s) denote the rate at which cells of size s divide into two identical daughters of size $\frac{1}{2}s$. Then

$$(2.4)\qquad \begin{aligned} &\frac{\partial}{\partial t} n(t,s) + \frac{\partial}{\partial s}(v(s)\, n(t,s)) = -\, b(s)\, n(t,s) + 4b(2s)\, n(t,2s), \\ &v(0)\, n(t,0) = 0. \end{aligned}$$

Exercise: explain the factor 4.
e: Asymmetric division into a part of fixed size s_0 (the daughter) and a part of size $s-s_0$ (the mother) is described by

$$(2.5)\qquad \begin{aligned} &\frac{\partial}{\partial t} n(t,s) + \frac{\partial}{\partial s}(v(s)\, n(t,s)) = -\, b(s)\, n(t,s) + b(s+s_0)\, n(t,s+s_0), \\ &v(s_0)\, n(t,s_0) = \int_0^\infty b(\sigma)\, n(t,\sigma)d\sigma. \end{aligned}$$

f: Combining the examples a and d we arrive at the equations

$$(2.6)\qquad \begin{aligned} &\frac{\partial}{\partial t} n(t,a,s) + \frac{\partial}{\partial a} n(t,a,s) + \frac{\partial}{\partial s}(v(a,s)\, n(t,a,s)) = -\, b(a,s)\, n(t,a,s) \\ &n(t,0,s) = 4\int_0^\infty b(\sigma,2s)\, n(t,\sigma,2s)d\sigma. \end{aligned}$$

for the age-size density.

REMARKS. 1. These examples clearly illustrate jump phenomena and non-local coupling: individuals may jump instantaneously from one position in the physiological state space to another or they may produce offspring at some other position. This feature is characteristic for models from population dynamics and it is perhaps the main reason why continuum population problems are, despite many similarities so different from problems in continuum mechanics.

2. In these models both the individual growth rate as well as the division rate may depend on environmental conditions. This will be made more explicit in the next example. When the individuals themselves contribute to the (change in) environmental conditions we end up with a (set of) nonlinear equation(s).

Example 2: *Size dependent reproduction in ectothermic animals.*
In contrast with the previous example we shall immediately specify all the functions involved from first principles. The model was derived with the waterflea *Daphnia magna* in mind as the experimental animal. (However, its applicability appears to be much more general.) More details on the individual level as well as empirical evidence for the correctness of our assumptions can be found in Kooyman & Metz (in press).
a will again denote age, w will denote weight, $\ell \sim w^{1/3}$ length and x food density.

We start with individual growth. It is assumed that ingestion equals $\nu f(x)\ell^2 = \nu f(x)w^{2/3}$ with $f(x) = \frac{\xi x}{1+\xi x}$. The basis for this assumption is that the maximum rate of food intake of an animal should equal the maximum digestion rate which scales with the surface area of the digestive apparatus. Moreover, for filter feeders (and also for many other feeding types) the food intake at low food densities is proportional to food density times the surface area of the food catching apparatus. A hyperbolic relation between food density and intake rate results from many micro models of the food catching process (Holling, 1959; Rashevsky, 1959; Metz & van Batenburg, in press). In the ecological literature it is known as the Holling functional response, in the biochemical and microbiological literature as the Monod curve. Figure 1a shows the fit of the assumed relation between food density, body size and amount eaten per unit of time for some literature data on *Daphnia magna.*

We assume, moreover, that a fraction κ of the ingested energy is channelled to maintenance and growth, and a fraction $1-\kappa$ to reproduction. Finally, maintenance is assumed to be proportional to weight. The result is a growth equation of so-called von Bertalanffy type (Von Bertalanffy, 1934)

$$\frac{dw}{da} = \eta^{-1}(\kappa\nu f(x)w^{2/3} - \zeta w)_+ ,$$

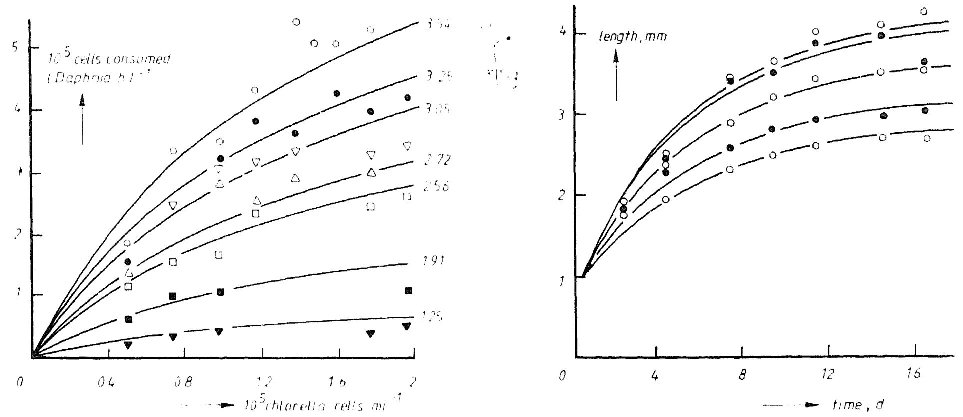

Fig. 1: Left: Feeding rate at 20°C of the waterflea *Daphnia magna* on the alga *Chlorella* as a function of food density x and body length ℓ. The fitted curves are given by $y = \nu \ell^2 f(x)$ with $f(x) = \xi x/(1+\xi x)$, with $\nu = 0.75 \times 10^5$ cells /h.mm^2), $\xi = 0.7 \times 10^{-5}$ml/cell. Data from McMacon & Rigler (1963), reproduced by Wulff (1980).
Right: length ℓ of *Daphnia magna* as a function of age a for various food densities x. The fitted curves are given by
$\ell = f(x)\ell_m - [f(x)\ell_m - \ell_b] \exp(-\gamma a)$, with $f(x)\ell_m = 2.89, 3.24, 3.72, 4.17, 4.31$ mm, $\ell_b = 0.8$mm, $\gamma = 0.17\text{d}^{-1}$.

where η denotes the energy cost of growth. The + accounts for the fact that large animals stop growing, but do not shrink, when food density drops ($z_+ := \max(z,0)$). Transforming to length we find

$$
(2.7) \qquad \begin{aligned} \frac{d\ell}{da} &= \frac{d\ell}{dw}\frac{dw}{da} = \frac{1}{3\eta}(\kappa\nu f(x) - \zeta\ell)_+ =: g(x,\ell) \\ \ell(0) &= \ell_b \end{aligned}
$$

where ℓ_b, the length at birth, is assumed to be fixed. Figure 1b shows the fit of the solution to (2.7) at various constant values of x for some laboratory observations on the growth of *Daphnia magna*.

To calculate the birth rate we recall that a fraction $1-\kappa$ of the ingested energy is channelled to reproduction. Nevertheless we assume that the animals only start making young when their length has reached a certain value, to be called ℓ_J, since they first have to build up their reproductive apparatus. Moreover, there is an exception to the κ-rule: when food density suddenly drops very far, maintenance takes priority for otherwise the animal would die. More precisely we assume that the individual reproductive rate $\beta(x,\ell)$ is given by

$$(2.8)\qquad \beta(x,\ell) = \begin{cases} 0 & \ell < \ell_J \\ (\omega w_b)^{-1}\,(1-\kappa)\nu f(x)\,\ell^2 & \ell_J \le \ell < \underline{\ell} \\ (\omega w_b)^{-1}\,(\nu f(x)\ell^2 - \zeta\ell^3) & \underline{\ell} \le \ell < \bar{\ell} \end{cases}$$

where (i) ωw_b is the energy needed to produce one young; (ii) $\underline{\ell} := \zeta^{-1}\kappa\nu f(x)$ is the size (at the current food density) at which exactly the fraction κ of the ingested energy is needed for maintenance; $\bar{\ell} = \zeta^{-1}\,\nu f(x)$ is the size at which all ingested energy is needed for maintenance. Animals for which $\ell \ge \bar{\ell}$ are assumed to die.

Finally we need the death rate. It appears that, except for death from starvation, this quantity is largely determined by age (and not by size). Some possible choises are

$$(2.9)\quad \begin{cases} (a)\ :\ \mu(a,\ell) = d \\ (b_1)\ :\ \mu(a,\ell) = \begin{cases} d\,, & a \le a_m \\ \infty\,, & a = a_m \end{cases}\ ,\ \text{where } a_m \text{ is the maximum possible age.} \\ (b_2)\ :\ \mu(a,\ell) = d + \psi(a)\ ,\ \text{with for instance, } \psi(a) = \dfrac{1}{a_m - a}\,. \end{cases}$$

The last formula was found empirically in preliminary laboratory observations on individual *Daphnia*.

Our next step is writing down the *population* equations. In the case of (2.9a) the death rate is not age dependent and we may describe the population completely by its size distribution:

$$\begin{aligned} &\frac{\partial}{\partial t}n(t,\ell) + \frac{\partial}{\partial \ell}(g(x,\ell)n(t,\ell)) = -\,dn(t,\ell) && \text{for } \ell < \bar{\ell}(x) \\ &n(t,\ell) = 0 && \text{for } \ell \ge \bar{\ell}(x) \\ &g(x,\ell_b)\,n\,(t,\ell_b) = \int_\Omega \beta(x,\ell)\ n(t,\ell)d\ell \end{aligned}$$

with $\Omega = [\ell_b, \ell_m]$, with $\ell_m = \zeta^{-1}\kappa\nu$ the upper bound to the individual lengths.

When death does depend on age we might naively write

$$\frac{\partial}{\partial t} n(t,a,\ell) + \frac{\partial}{\partial a} n(t,a,\ell) + \frac{\partial}{\partial \ell} (g(x,\ell)\, n(t,a,\ell)) =$$

$$= -\mu(a,\ell)\, n(t,a,\ell)$$

with $\Omega = [0,a_m] \times [\ell_b, \ell_m]$.

However, when we try to formulate the boundary condition we run into some trouble: since both age and size are fixed at birth, we need a delta "function"

$$n(t,0,\ell) = \delta(\ell-\ell_b) \int_\Omega \beta(x,\ell)\, n(t,a,\ell)\, da\, d\ell.$$

Moreover, the deterministic individual growth pushes this delta "function" from the boundary into the interior of Ω: all mass will always be concentrated on some (varying) curve in Ω.

Thus we prefer to work with a function of one variable, for which we choose age, and to do some extra bookkeeping in order to know the relation between age and length. Murphy (1983) has recently introduced a convenient trick to do the latter: to write down a separate partial differential equation for $\ell(t,a)$, the age-length relation at time t

$$(2.10)\quad \left\{\begin{array}{lll} \frac{\partial}{\partial t} \ell(t,a) + \frac{\partial}{\partial a} \ell(t,a) = g(x,\ell(t,a)) & & \\ \ell(t,0) = \ell_b & & \\ \frac{\partial}{\partial t} n(t,a) + \frac{\partial}{\partial a} n(t,a) = -\mu(a,\ell(t,a))n(t,a) & , & \ell(t,a) < \bar{\ell}(x) \\ n(t,a) = 0 & , & \ell(t,a) \geq \bar{\ell}(x) \\ n(t,0) = \int_\Omega \beta(x,\ell(t,a))\, n(t,a) da & & \end{array}\right.$$

where $\Omega = [0,a_m]$. This equation also encompasses the former case of (2.9a) if we allow $a_m = \infty$.

REMARKS. 1. Equations (2.10) can easily be generalized, e.g. to take care of deaths as a result of the accumulation of toxic compound by introduction of additional equations for the internal concentrations of toxic compounds as a function of a and to let μ depend on these concentrations as well.

2. In our derivation we have implicitly assumed that the animal has no energy reserves, so that it dies as soon as energy intake cannot keep pace with maintenance. A more detailed model on the individual level, which takes account of energy reserves, is developed in Kooijman (in press).

3. The derivation contains one hidden assumption which is slightly embarrassing from a biological point of view: the production of young is assumed to depend instantaneously on energy intake. In other words, an individual needs not accumulate the necessary energy ωw_b. Thus we implicitly assume that all individuals at each time add some infinitesimal amount of young tissue to a communal pool from which, by some miracle, the individual young are created. This assumption is commonly made in the literature of mathematical biology, but always implicitly. A rigorous justification of the resulting equations is possible, however, by assuming that the size of the young is very small, that very many young are produced, but that most of them die at a very early age (Heijmans & Metz, in prep.).

3. POSITIVE SEMIGROUPS AND STABLE DISTRIBUTIONS

In this section we assume that the environment is constant and that the equation is linear. If the model specification is complete, adding an *initial condition* $n(0,x) = \phi(x)$ should single out a unique solution $n = n(t,x;\phi)$. So a first mathematical task is proving existence and uniqueness of a solution to the initial value problem. A frequent approach is to use *integration along characteristics* (i.e. along curves in the (t,x) - space determined by the ordinary differential equations $\frac{dt}{ds} = 1$, $\frac{dx}{ds} = v(x)$) to transform the problem to one to which the contraction mapping principle can be applied (the corresponding construction of a solution by successive approximations has the biological interpretation of a "generation" expansion). So usually the first task can be fulfilled without much difficulty, although the precise meaning of "solution" needs further explanation (see below).

It is convenient to conceive of ϕ and $n(t,.;\phi)$ as elements of a Banach function space X (the population state space, e.g. $L_2(\Omega)$ or $C(\Omega)$) and to write

$$n(t,.;\phi) = T(t)\phi \quad , \tag{3.1}$$

where $\{T(t)\}$ is a strongly continuous semigroup of bounded linear operators on X, i.e.,

$$\begin{cases} \text{(i)} & T(0) = I \ , \\ \text{(ii)} & T(t)\ T(\tau) = T(t+\tau), \quad t,\ \tau \geq 0 \\ \text{(iii)} & \lim\limits_{t \downarrow 0} \| T(t)\ \phi - \phi \| = 0, \ \forall\ \phi \in X. \end{cases} \tag{3.2}$$

The *infinitesimal generator* A is defined by

$$A\ \phi = \lim_{t \downarrow 0} \frac{1}{t}\ (T(t)\ \phi - \phi) \tag{3.3}$$

for those $\phi \in X$ for which this limit exists. The original partial differential equation can now be interpreted as the abstract ordinary differential equation

$$\frac{dn}{dt} = An, \tag{3.4}$$

and thus one can define "solution" in terms of a semigroup and its generator (Pazy, 1983).

REMARK: For parabolic partial differential equations it is customary to start by defining A and to prove, by verifying the Hille-Yoshida conditions, that it generates a semigroup. However, for the present class of first order equations it is usually much easier to first construct a semigroup directly and only later re-interpret the original equation as one involving the generator.

Example. We illustrate the general remarks above by elaborating in some detail the very simple example 1a. We begin by specifying the assumptions on b and by making a preliminary transformation.

Suppose that each cell has to divide before reaching a maximal age, say a = 1. Since the probability that a newborn cell does not divide before reaching age a is given by

$$(3.5)\qquad F(a) = \exp(-\int_0^a b(\sigma)d\sigma),$$

we assume

b is nonnegative and integrable on $[0,1-\varepsilon]$ for each $\varepsilon \in (0,1)$ but b has a non-integrable singularity in $a = 1$.

The transformation

$$(3.6)\qquad n(t,a) = m(t,a)\, F(a)$$

leads to

$$(3.7)\qquad \begin{cases} \frac{\partial}{\partial t} m(t,a) + \frac{\partial}{\partial a} m(t,a) = 0 \\ m(t,0) = \int_0^1 K(\sigma)\, m(t,\sigma)d\sigma \\ m(0,a) = \psi(a) \end{cases}$$

where

$$(3.8)\qquad K(a) = 2b(a)\, F(a)$$

is nonnegative and integrable on $[0,1]$ (and zero for $a > 1$) and where

$$(3.9)\qquad \psi(a) = \frac{n(0,a)}{F(a)} = \frac{\phi(a)}{F(a)}\ .$$

We assume that $\psi \in L_1[0,1]$. Since $F(1) = 0$ this is, among other things, an assumption on the behaviour of ϕ near $a = 1$. Define

$$(3.10)\qquad y(t) := \int_0^1 K(\sigma)\, m(t,\sigma)d\sigma\ ,$$

and pretend that y is known. Then m is readily expressed in terms of ψ and y:

$$(3.11)\qquad m(t,a;\psi) = \begin{cases} \psi(a-t)\ , & a \geq t\ , \\ y(t-a)\ , & a < t. \end{cases}$$

Substituting this result into (3.10) we find the *renewal equation*

$$(3.12) \qquad y(t) = \int_0^t K(\sigma)\, y(t-\sigma)\, d\sigma + f(t)$$

where

$$(3.13) \qquad f(t) = \int_t^1 K(\sigma)\psi(\sigma-t)\, d\sigma .$$

Existence and uniqueness of an integrable solution y is easy to prove and this solution is represented by the infinite series

$$(3.14) \qquad y = f + K * f + K * K * f + \dots ,$$

where * denotes the convolution product (see, for instance, Miller 1971). Define

$$(3.15) \qquad S(t)\,\psi = m(t,.;\psi)$$

with m given by (3.11), y being the solution of (3.12). It is rather straightforward to verify that $\{S(t)\}$ is a strongly continuous semigroup on $L_1[0,1]$ with infinitesimal generator

$$(3.16) \qquad \begin{aligned} B\psi &= -\frac{d\psi}{da} \\ \mathcal{D}(B) &= \{\psi \in L_1[0,1] \mid \psi \text{ is absolutely continuous and } \\ &\qquad\qquad \psi(0) = \int_0^1 K(\sigma)\, \psi(\sigma)\, d\sigma\} \end{aligned}$$

(the generator of translation is always differentiation). Let X denote the weighted L_1 - space

$$(3.17) \qquad X = \{\phi \in L_1[0,1] \mid a \mapsto \frac{\phi(a)}{\mathcal{F}(a)} \text{ is in } L_1\,[0,1]\}$$

with norm

$$\| \phi \|_X = \int_0^1 \left| \frac{\phi(a)}{\mathcal{F}(a)} \right| da ,$$

and define $L : X \to L_1[0,1]$ by $(L\phi)(a) = \frac{\phi(a)}{\mathcal{F}(a)}$.

The semigroup $T(t)$ is defined on X by

$$T(t) = L^{-1} S(t) L \tag{3.18}$$

and its generator A is given by $A = L^{-1}BL$ with $\mathcal{D}(A) = \{\phi \mid L\phi \in D(B)\}$. Hence

$$\begin{aligned} A\phi &= -\frac{d\phi}{da} - b\phi \\ \mathcal{D}(A) &= \{\phi \in X \mid a \mapsto \frac{\phi(a)}{F(a)} \text{ is absolutely continuous and} \\ &\qquad \phi(0) = 2\int_0^1 b(\sigma)\,\phi(\sigma)d\sigma\}. \end{aligned} \tag{3.19}$$

<u>End of example.</u>

The next mathematical problem is to analyse the *asymptotic behaviour* for $t \to \infty$. Fortunately a powerful mathematical tool, *spectral theory*, is at our disposal. The standard approach involves two steps:

(i) the derivation of certain relations between the spectra of $T(t)$ and A,

(ii) an analysis of the spectrum of A.

(Note that the constructive definition of the semigroup is, in general, not suited at all to determine the spectrum of $T(t)$ directly.) We shall first describe some general results for step (i) and we shall formulate a theorem which implies, under some *compactness* condition, the convergence towards a *stable distribution*. Subsequently we discuss the influence of *positivity* on the position of the spectra.

The point spectra of A and $T(t)$ are related by

$$e^{tP\sigma(A)} \subset P\sigma(T(t)) \subset (e^{tP\sigma(A)} \cup \{0\}).$$

A similar relation exists for the residual spectrum, but the continuous spectrum may not be "faithful" (Pazy, 1983). In the present context, however, another subdivision of the spectrum is more useful. The *essential spectrum* $\sigma_e(L)$ (in the sense of Browder) of a closed operator L is defined as the set of those $\lambda \in \sigma(L)$ for which at least one of the following conditions is satisfied

(a) $R(\lambda I - L)$ is not closed,

(b) λ is an accumulation point of $\sigma(L)$,

(c) the generalized eigenspace corresponding to λ is infinite-dimensional.

If $\lambda \in \sigma(l) \setminus \sigma_e(L)$ then λ is an isolated pole of finite order of the resolvent. Let p be the order of the pole, then

$$X = N((\lambda I-L)^p) \oplus R((\lambda I-L)^p).$$

The elements of $\sigma(L) \setminus \sigma_e(L)$ are called *normal eigenvalues.*

The measure-of-noncompactness $\alpha(V)$ of a bounded set $V \subseteq X$ is the infimum of the positive numbers d for which V can be covered by finitely many sets of diameter less than or equal to d. The measure-of-noncompactness $\gamma(L)$ of a bounded linear operator $L : X \to X$ is the infimum of the positive numbers k for which

$$\alpha(L(V)) \leq k\, \alpha(V)$$

for all bounded sets $V \subseteq X$.

For a bounded operator L we have the well-known identity

$$r(L) = \lim_{n\to\infty} \|L^n\|^{\frac{1}{n}}$$

for the spectral radius of L. Nussbaum (1970) has proved the analogue for the essential spectral radius:

$$r_e(L) = \lim_{n\to\infty} (\gamma(L^n))^{\frac{1}{n}}.$$

Here the essential spectral radius is of course defined by

$$r_e(L) = \sup\{|\lambda| \mid \lambda \in \sigma_e(L)\}.$$

Let A be the generator of the strongly continuous semigroup T(t). We define

$$\omega_0 = \omega_0(A) = \lim_{t\to\infty} \frac{1}{t} \log \|T(t)\|,$$

$$\omega_1 = \omega_1(A) = \lim_{t\to\infty} \frac{1}{t} \log \gamma\, (T(t)).$$

(with the convention $\log 0 = -\infty$)

It can be proved that

$$r(T(t)) = e^{\omega_0 t},$$

$$r_e(T(t)) = e^{\omega_1 t}.$$

(with the convention $e^{-\infty} = 0$)

The relation between ω_0, ω_1 and the spectrum of A is rather complicated. There are examples, even of positive semigroups, where

$$\omega_0 \neq \sup \{\mathrm{Re}\,\lambda \mid \lambda \in \sigma(A)\}.$$

(See Greiner, Voigt & Wolf (1981).)
However, it can be shown that

$$\omega_0 = \max \{\omega_1, \omega_2\},$$

where

$$\omega_2 = \omega_2(A) = \sup \{\mathrm{Re}\,\lambda \mid \lambda \text{ is a normal eigenvalue of } A\}.$$

(See Webb (in press), and Prüss (1983)). Thus one can characterize ω_0 precisely in terms of A provided a suitable estimate for ω_1 can be given. And knowledge of ω_0 yields exponential estimates for the semigroup.

THEOREM A. *Assume that*

1) A *has a simple real eigenvalue* λ_d *which is a pole of the resolvent.*
2) *There exists an* $\varepsilon > 0$ *such that*

$$\sigma(A) \cap \{\lambda \mid \mathrm{Re}\,\lambda \geq \lambda_d - \varepsilon\} = \{\lambda_d\}$$

3) $T(t) = U(t) + V(t)$ *where* $U(t)$ *is compact, and for some* $\eta > 0$, $M > 0$
$\|V(t)\| \leq M\exp(\lambda_d - \eta)t, \quad t \geq 0$

then $T(t)\,\phi = e^{\lambda_d t} P\,\phi + O(e^{(\lambda_d - \nu)t})$, $t \to \infty$, *where* $\nu = \min\{\varepsilon, \eta\}$ *and* P *is the spectral projection on the eigenvector corresponding to* λ_d.

PROOF. Since P commutes with T(t), the restriction $\hat{T}(t)$ to the subspace $\mathcal{R}(I-P)$ defines a strongly continuous semigroup having generator $\hat{A}$ which is the restriction of A to $\mathcal{R}(I-P)$. It follows directly that $\omega_1(\hat{A}) = \omega_1(A) \le \lambda_d - \eta$ and $\omega_2(\hat{A}) \le \lambda_d - \varepsilon$. Therefore $\omega_0(\hat{A}) \le \lambda_d - \nu$, from which we conclude that for all $t \ge 0$ $\| (I-P)T(t)\phi \| = \| \hat{T}(t)(I-P)\phi \|$

$$\le K e^{(\lambda_d-\nu)t} \|(I-P)\phi\| \le K e^{(\lambda_d-\nu)t} \|\phi\|,$$

for some positive constant K.
Since $T(t)\phi = T(t)\,((I-P)\phi + P\phi) = (I-P)T(t)\phi + e^{\lambda_d t} P\phi$, the result follows. □

An implication of the theorem is that, as $t \to \infty$, the dynamics becomes one-dimensional: the population will grow or decay (depending on the sign of λ_d) exponentially while the x-distribution becomes stationary. The eigenvector corresponding to the so-called strictly dominant eigenvalue λ_d is called the *stable x-distribution*.

This theorem covers many population problems, although there exist cases, such as example 1^b, which exhibit a different type of asymptotic behaviour.

The assumptions 1) and 2) of theorem A may seem, at first sight, rather special and restrictive. So let us now briefly explain how in many problems from population dynamics, positive operator theory can be exploited to prove that these assumptions are satisfied.

Let us first give some definitions. Let X_+ be a convex closed cone in the Banach space X. A bounded operator $L : X \to X$ is called positive if it leaves X_+ invariant, i.e.

$$L(X_+) \subseteq X_+.$$

We denote by X_+^* the dual cone, i.e.

$$X_+^* = \{ f \in X^* \mid \langle f, \phi \rangle \ge 0, \ \forall \phi \in X_+ \}.$$

For an introduction to positive operator theory we refer to Schaeffer (1974) and Krasnosel'skiĭ (1964).

In our models from population dynamics the interpretation of $T(t)\,\phi$ as a population density requires that $T(t)$ leaves the cone

$$X_+ = \{\phi \in X \mid \phi(x) \geq 0, \quad \forall x \in \Omega\}$$

invariant. Now the identity

$$(\lambda I - A)^{-1}\,\phi = \int_0^\infty e^{-\lambda t}\, T(t)\,\phi\, dt, \text{ Re } \lambda \text{ large,}$$

(See Pazy (1983)) yields that the resolvent $(\lambda I-A)^{-1}$ defines a positive operator for every large real λ.

The famous Krein-Rutman theorem and its variants describe the spectrum of a bounded, positive operator on the circle with radius equal to the spectral radius, thus generalizing the Perron-Frobenius theorem on the eigenvalues of a positive matrix.

THEOREM B. *Let* X_+ *be reproducing,* (i.e. $\{\phi-\psi \mid \phi,\psi \in X_+\} = X$) *and normal*

(i.e. $\exists_{\delta>0}\, \forall_{\phi,\,\psi \in X_+} : \|\phi + \psi\| \geq \delta\, \|\phi\|$).

Let L *be a bounded, positive operator such that for all* $\phi \in X_+$, $\phi \neq 0$ *and* $f \in X_+^*$, $f \neq 0$ *there exists an integer* p *such that* $\langle f, L^n\,\phi\rangle > 0$ *for all* $n \geq p$. *Moreover let* $\lambda = r(L)$ *be a pole of the resolvent of* L *(which is true if* L *is compact) Then*

(i) r(L) *is an algebraically simple eigenvalue and the corresponding eigenvector belongs to* X_+.

(ii) *No other eigenvector belongs to* X_+.

(iii) *If* $\lambda \in \sigma(L)$ *and* $\lambda \neq r(L)$ *then* $|\lambda| < r(L)$.

This theorem is formulated in Marek (1970). We refer to Krasnosel'skiǐ (1964) for similar theorems for so-called u_0-positive operators.

In several cases it is possible to show that the resolvent of A satisfies the hypotheses of theorem B and subsequently the correctness of the assumptions 1) and 2) of theorem A is a straightforward consequence of the relation between the spectra of A and it's resolvent. We refer to Heijmans (in press) for more details in a specific example.

If we do not have some kind of strong positivity (such as $<f,L^n\phi>>0$) conclusion (iii) of theorem B has to be weakened in the sense that the spectrum of L on the circle of radius r(L) is a cyclic set, i.e. if $r(L)e^{i\theta} \in \sigma(L)$, then $r(L)e^{ik\theta} \in \sigma(L)$, for all $k \in \mathbb{Z}$. We refer to Schaefer (1974) for precise formulations. Greiner (1981) has shown that, under certain conditions, the spectrum of the generator A of a positive semigroup on the vertical line $\mathrm{Re}\,\lambda = \lambda_d$ is necessarily additive cyclic (i.e. if $\lambda_d+iy \in \sigma(A)$ then $\lambda_d + iky \in \sigma(A)$ for all $k \in \mathbb{Z}$; also see Davies (1980)), and that $\lambda_d = \omega_0$. This result is consistent with the multiplicative cyclicity of the spectrum of T(t) on the circle with radius $e^{\omega_0 t}$. In such a situation the asymptotic behaviour for $t \to \infty$ is determined by the projection onto an infinite dimensional subspace of X (i.e. infinitely many 'properties' of the initial condition remain manifest for all time). A trivial example of this type of behaviour is provided by example 1b, and a more subtle one by example 1d with $v(x) = cx$, for some constant c. (See Diekmann, Heijmans & Thieme, (in press).)

In many cases (with x one-dimensional) it is actual possible to derive a (transcendental) *characteristic equation* from which the eigenvalues of A can be computed. In that case one finds the necessary information about the spectrum of A directly, and any appeal to general results can be avoided. (See Heijmans (in press)). Nevertheless these general results are important for putting things in their true perspective.

Example. Again we illustrate the general outline by analysing example 1a. We formulate the results in terms of S(t) and B. The abstract equation $(\lambda I-B)\psi = f$ implies

$$\psi'(a) = -\lambda\psi(a) + f(a)$$

and consequently

$$\psi(a) = e^{-\lambda a}\psi(0) + \int_0^a e^{-\lambda(a-\sigma)} f(\sigma)d\sigma$$

However, ψ is an element of $\mathcal{D}(B)$ iff

$$\psi(0) = \int_0^1 K(\sigma)e^{-\lambda\sigma}d\sigma\ \psi(0) + \int_0^1 K(\sigma)\int_0^\sigma e^{-\lambda(a-\tau)}f(\tau)d\tau\ d\sigma.$$

This equation can be solved for $\psi(0)$ iff $\int_0^1 K(\sigma)e^{-\lambda\sigma}\,d\sigma \neq 1$. We conclude that $\lambda \in \rho(B)$, the resolvent set of B, if $\int_0^1 K(\sigma)\,e^{-\lambda\sigma}\,d\sigma \neq 1$ and that the zeros of $1-\int_0^1 K(\sigma)e^{-\lambda\sigma}\,d\sigma$ of order p are poles of the resolvent of order p and eigenvalues of B. The fact that $K(a) \geq 0$ implies that there exists one *simple* real zero λ_d and that all other zeros satisfy $R_e\,\lambda \leq \lambda_d - \varepsilon$ for some $\varepsilon > 0$ (use the analyticity and the lemma of Riemann-Lebesque).

For $t \geq 1$ the influence of the initial condition ψ on the solution m in (3.11) is through y defined by (3.12) only. One can use standard estimates to show that, as a consequence, T(t) is compact for $t \geq 1$.

REMARKS 1. Of course the conclusion can, for this simple example, also be derived directly from (3.12) using Laplace transformation.

2. If we study example 1 with $a \in [0,\infty)$, i.e. without maximal age, the direct influence of the initial condition on the solution remains for all times although, under suitable conditions on b, its "strength" diminishes as $t \to \infty$. In such a case one can exploit a representation $T(t) = U(t) + V(t)$ (see Webb, in press, and Prüß, 1981 and in press).
3. In the case of example 1d the compactness as well as the existence of a nontrivial additive group of eigenvalues on the line $\mathrm{Re}\lambda = \lambda_d$ hinge upon the behaviour of the function $v(2x) - 2v(x)$. We refer to Diekmann, Heijmans & Thieme (in press) for the details and the biological interpretation of the "cyclic" case.
4. In certain situations the choice of topology is of some importance. Heijmans (in prep.) uses the weak * topology and duality to demonstrate the existence of a stable distribution for a model of predatory behaviour introduced in Metz & van Batenburg (in press).

4. THE POPULATION DYNAMICS OF ECTOTHERMS

In this section we shall concentrate on the second example from section 2. In order to simplify the discussion we shall assume that $a_m < \infty$. For the sake of convenience we repeat formula (2.10) as formula (4.1):

$$\text{(4.1a)}\qquad \frac{\partial}{\partial t}\ell(t,a) + \frac{\partial}{\partial a}\ell(t,a) = g(x,\ell(t,a)) \quad , \quad \ell(t,0) = \ell_b$$

$$\text{(4.1b)}\qquad \begin{cases} \frac{\partial}{\partial t} n(t,a) + \frac{\partial}{\partial a} n(t,a) = -\mu(a,\ell(t,a))\,n(t,a), & \text{for } \ell(t,a) < \bar{\ell}(x) \\ n(t,a) = 0 & , \ \text{for } \ell(t,a) \geq \bar{\ell}(x) \\ n(t,0) = \int_\Omega \beta(x,\ell(t,a))\,n(t,a)da\ . & \end{cases}$$

When x is constant, equation (4.1a) has a stationary (i.e. time independent) solution and any solution of an initial value problem will be identical to the stationary one after finite time. Therefore we can restrict the attention to the linear (4.1b) and apply the theory of the last section. In Kooijman & Metz (in press) the value of the dominant eigenvalue λ_d was studied as a function of x.

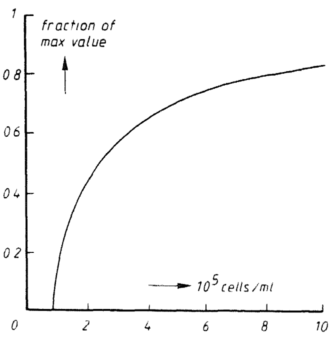

Fig. 2: Dominant eigenvalue λ_d for the waterflea *Daphnia magna* feeding on the alga *Chlorella* at 20°C as a function of food density.

Figure 2 shows the result for the growth parameters of *Daphnia magna* and with formula (2.9 b1) with d = 0 for the death rate. It can be seen from theis figure that near x_{crit} defined by $\lambda_d(x_{crit}) = 0$ the dependence of λ_d on x is very steep indeed. This means that for *Daphnia* and ecologically similar organisms a small fluctuation in the food density x in the neighbourhood of x_{crit} has a very drastic effect on population growth. This is one possible explanation for the frequently erratic appearance of population counts of daphnids recorded in the literature.

Since in the Daphnia model all parameters have a direct physiological interpretation it becomes possible to study the population effects of toxic compounds affecting these parameters in dependence on the food density x. This is very important since routine laboratory toxicity testing is almost always done at high food densities whereas in nature food is generally scarce. Figure 3 shows the result of such an exercise for *Daphnia magna*.

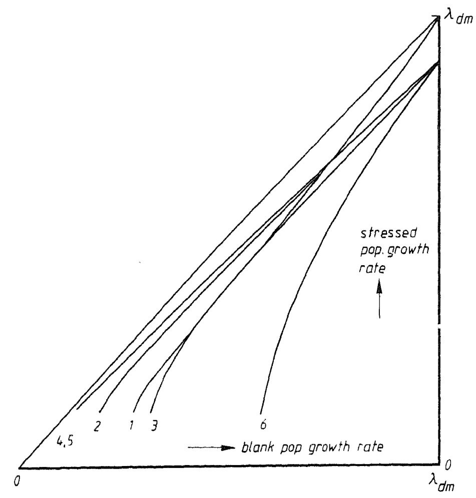

Fig. 3: Dominant eigenvalue λ_d under stressed conditions as a function of $\lambda_d(x)$ under unstressed conditions for compounds affecting (1) feeding rate ξ, (2) digestion ν, (3) basal metabolism ζ, (4) growth η, (5) reproductive rate ω, and (6) survival a_m. Except for the feeding rate the concentration of the toxic compound is chosen such that the maximum stressed value of λ_d is 90% of the maximum blank value λ_{dm}; parameter values of the waterflea *Daphnia magna* feeding on the alga *Chlorella* at 20°C.

In this figure the value of $\lambda_d(x)$ under chemically stressed conditions is plotted as a function of $\lambda_d(x)$ in the unstressed situation (that is, we vary x but put $\lambda_d(x)$ on the horizontal axis) for various types of physiological effects, The level of chemical stress is (arbitrarily) chosen such that λ_d is reduced by 10% at very high food densities (in the case of an effect on the filtering rate which manifests itself in a lowering of ξ another choice is made since this effect never manifests itself in λ_d at high food densities). It can be seen from Figure 3 that for effects on growth and reproduction the relative reduction of λ_d is hardly depending on x (extrapolation is "safe"). On the contrary compounds affecting survival bring about a far more drastic relative reduction of λ_d at lower food densities. These predictions are consolidated for all regions of the parameter space which we have explored so far.

As yet we have not done any laboratory experiments on *Daphnia magna* to test the theory.

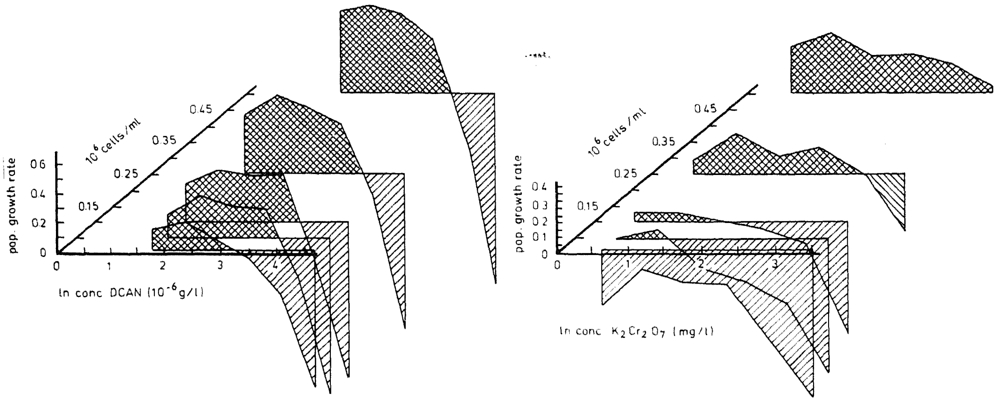

Fig. 4: Observed population growth rates (λ_d, vertical in d^{-1}) at 20°C of the rotator *Brachionus rubens* for various concentrations of 3,4-dichloroaniline (left) and potassium dichromate (right) (horizontal) feeding at various Chlorella densities (backwards). The leftmost concentration is the blank and should be positioned at minus infinity.

Figure 4 shows the results of laboratory experiments with another animal, the rotifer *Brachionus rubens*, for which population experiments are more easily done. It can be concluded that the predictions are borne out by the data, at least qualitatively.

In many population dynamical experiments x is not a given quantity but it is dynamically dependent on the population trajectory (consumption!). Some possible simple assumptions about the dynamics of x are

$$(4.2a)\qquad \frac{dx}{dt} = \alpha - \gamma x - \nu f(x)p$$

or

$$(4.2b)\qquad \frac{dx}{dt} = \alpha x - \gamma x^2 - \nu f(x)p$$

where in both cases

$$p(t) = \int_\Omega \ell^2(t,a)\ n(t,a)da.$$

To arrive at (4.2a) we assume that we feed the population at a constant rate and that uneaten food deteriorates at a constant relative rate, e.g. through sinking to the bottom of the experimental container or through overflow in chemostat-like set ups. Equation (4.2b) corresponds to the so-called logistic growth of the food population.

Together (4.1) and (4.2) form a nonlinear pair of equations which we only just began studying. We shall finish this section with a short overview of our present lines of approach.

To find all possible equilibria the time derivatives in (4.1) and (4.2) are set equal to zero. Not unexpectedly it turns out that there is a unique nontrivial equilibrium $\hat{\ell}$, $\hat{n}$, $\hat{x}$ with $\hat{n} > 0$ if and only if the trivial equilibrium ($\hat{n} = 0$, $\hat{x} = \gamma^{-1}\alpha$) is unstable. This in turn happens if and only if the dominant eigenvalue λ_d of the linear problem which results from setting x equal to $\gamma^{-1}\alpha$ for all time, is positive.

For the nontrivial equilibrium $\hat{\ell}$ increases with a and $\hat{\ell}(a_m) < \underline{\ell}(\hat{x})$, i.e. we remain well away from the kink in g. Therefore we can study, at least formally, local stability by using a linearization procedure. This leads to a characteristic equation (of a type which one also encounters in delay differential equations) which is far more difficult than the one corresponding to the trivial equilibrium. Some idea of the behaviour of the roots of the characteristic equation can be got already from the experimental results reproduced in Figure 5: the oscillations resulting from a temperature change from 18°c to 25°c strongly suggest the occurrence of a Hopf bifurcation.

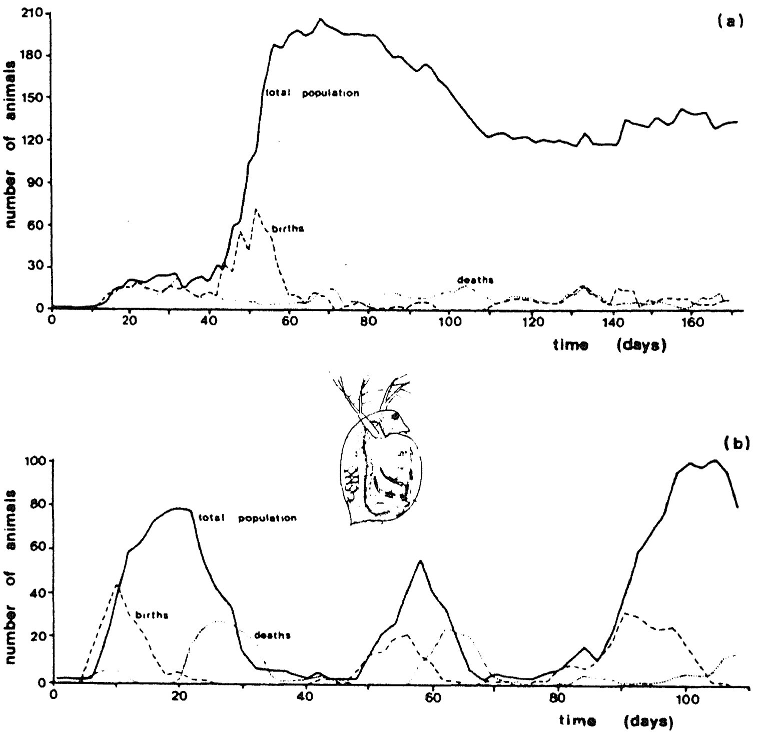

Fig. 5: Population growth in the waterflea *Daphnia Magna* at (a) 18^{o}C, and (b) 25^{o}C in 50 cc of pond water. (Reproduced from Pratt (1943), reproduced by Krebs (1972), reproduced by Nisbet & Gurney (1982).)

5. DENSITY DEPENDENCE: GENERAL REMARKS

Unlimited population growth does not exist. A growing population influences its environment and therefore its own growth. Many such biological feedback loops can only be described properly in terms of the interaction of the physiological processes within the individuals (e.g. growth, reproduction) and environmental factors (e.g. the availability of food). Consequently models of the type described in section 2 are an ideal tool to give a realistic mathematical formulation of density dependence (Streifer, 1974). Once one knows the general structure of the models it is hardly more difficult to formulate a nonlinear model than a linear one(there are, however, some subtilities and pitfalls; see Diekmann, Lauwerier, Aldenberg &

Metz, 1983, for an example), but unfortunately this resemblance ceases when we consider the mathematical analysis of the resulting problems.

If the conditions at the beginning of section 3 are relaxed one usually still can solve the problem of the existence and uniqueness of a solution for the initial value problem and subsequently define a semigroup of non-linear operators (possibly only on a closed subset W of X such that solutions starting in W remain in W and do not blow up in finite time; for instance, the definition of W may involve nonnegativity). However, the catalogue of possible asymptotic behaviour is much richer now and, in fact, so rich that we cannot say anything in general. We expect that progress will be made by analysing specific problems in detail using bifurcation theory (Chow & Hale, 1982, Guckenheimer & Holmes, 1983) and numerical experiments (Gurney & Nisbet, in press). Much work has to be done in order to generalize such basic theoretical results as the principle of linearized stability and the Hopf bifurcation theorem to the present class of dynamical systems (Webb, in press, Cushing, 1983, and Prüss, 1981, 1983, contain results for age-dependent population growth which is a rather special case since the growth rate $\frac{da}{dt}$ is always one and never density dependent). However, a perhaps much more pressing problem is the development of powerful methods to derive results about roots of characteristic equations which are not of the simple kind discussed in section 3 (Cooke & Grossman, 1982). These arise when linearizing about some non-zero steady state.

Anyhow, except for the case of age dependence there exists at this moment no general nonlinear mathematical theory at all and we've had our say on this matter.

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