

The Second Half – With a Quarter of a Century Delay

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Abstract. We show how results by Diekmann *et al.* (2007) on the qualitative behaviour of solutions of delay equations apply directly to a resource–consumer model with age-structured consumer population.

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1. Age-structure and semigroups

The modern mathematical theory of (linear) age-structured population dynamics started in the beginning of the 20th century with the work of Lotka and Sharpe (Lotka 1907, Sharpe and Lotka 1911), although the fundamental ideas go back as far as Euler (1760). With the exception of McKendrick's (1926) paper, not much happened until 1974, when Gurtin's and MacCamy's (1974) nonlinear extension of McKendrick's model triggered a renewed interest in both linear and nonlinear age-structured models.

Among the different techniques to treat age-structured population models, the theory of semigroups of operators became very much *en vogue* in the late 1970s and early 1980s. This was mainly due to the work by Glenn Webb. He was the first to show rigorously that a nonlinear age-structured population model defined in terms of individual vital rates (birth and death rates) determines a dynamical system (a nonlinear semigroup) on the population state space L^1 with the age-distribution $n(t, \cdot)$ as the population state (Webb 1981). Using the theory of semigroups of linear operators

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he gave (Webb 1984) an elegant proof of *asynchronous exponential growth* of age-structured populations that had been only heuristically derived by Sharpe and Lotka (1911). This result says that (under mild conditions) the population eventually grows exponentially with the *Malthusian parameter* r obtained as the unique real root of the Euler-Lotka equation

$$\int_0^{\infty} e^{-ra} \beta(a) \mathcal{F}(a) da = 1, \quad (1.1)$$

while the age-distribution converges to the stable age distribution

$$n(a) = e^{-ra} \mathcal{F}(a). \quad (1.2)$$

Here β is the age specific fecundity and $\mathcal{F}(a)$ is the probability of surviving to age a . Feller (1941) gave a rigorous proof of the renewal theorem, which also implies eventual exponential growth of the population, but he did not translate this result into the convergence of the age-distribution towards a stable one.

Glenn Webb's work in this area culminated in the first comprehensive book on age-structured population dynamics (Webb 1986), where he proved, among other things, the principle of linearized stability: A steady state is exponentially stable if the spectrum of the infinitesimal generator of the linearized semigroup lies entirely in the open left half-plane, whereas it is unstable if there is at least one spectral value with positive real part. It is worth noting that before that, with the exception of Prüß (1983), only the stability part of the principle of linearized stability had been proved for nonlinear age-structured models, while authors had passed the more difficult instability part with silence (Gurtin and MacCamy 1974; Gyllenberg 1982, 1983).

In the 1980s linear age-structured population dynamics served as motivation for the general theory of positive semigroups (Greiner 1984) and for feedback boundary control problems (Desch *et al.* 1985). Semigroups were also used to study linear models of more general physiologically structured population models, in particular models of the cell cycle (Diekmann *et al.* 1984; Gyllenberg and Heijmans 1987). In the 1990s Horst Thieme used integrated semigroups to prove both parts of the principle of linearized stability for a variety of nonlinear age-structured models (Thieme 1990, 1991; Feng and Thieme 2000). Magal and Ruan (to appear) treated center manifold theory in an integrated semigroup context and applied their results to age-structured models. Many more papers could be mentioned. However, the aim of the present paper is to expose a new approach that allows one to appeal to text book theory in order to derive results and not to give a detailed historical account of the various approaches that have been developed.

2. Suns and stars unify age and delay

About a decade before Glenn Webb introduced semigroups to treat age-structured population problems, semigroups had become a major ingredient in the theory of retarded functional differential equations, largely due to the influence of the books by Jack Hale (1971, 1977). We refer to the recent book edited by Arino *et al.* (2006) for articles on the history of delay equations and many applications related to the topic of the present paper.

There is an obvious relation between delay equations and age-structured problems. Indeed, those individuals who are presently (at time t) of age a were born at time $t - a$, so in order to compute the present age distribution we need information about the birth rate in the past.

In the mid 1980s the present authors, in collaboration with Ph. Clément, H.J.A.M Heijmans and H.R. Thieme, used the theory of adjoint semigroups (sun-star-calculus) to treat delay differential equations and age-structured population problems (Diekmann 1987; Clément *et al.* 1987,1988). In addition to providing a unified framework for delay differential equations and age-structured population models, the main advantage of this approach is that it turns notoriously difficult quasi-linear problems into more tractable semi-linear problems. This is achieved by a reformulation of the original problem as an abstract integral equation of the variation-of-constants formula type:

$$u(t) = T_0(t)\varphi + \int_0^t T_0^{\odot*}(t-s)G(u(s))ds, \quad (2.1)$$

where T_0 is the semigroup on the population state space X generated by the linear part, $T_0^{\odot*}$ is the extension of T_0 to a larger space $X^{\odot*}$ and $G : X \rightarrow X^{\odot*}$ is the nonlinear perturbation and $\varphi \in X$ is the initial state. The perturbation theory of adjoint semigroups (Clément *et al.* 1987) gave the variation-of-constants formula a precise meaning, whereas it had been somewhat symbolic in the work of Hale (1971, 1977). As in the case of ordinary differential equations, the variation-of-constants formula is the starting point for proving the principle of linearized stability, the Hopf bifurcation theorem and for characterizing the stable, unstable and center manifolds. Indeed, using ideas of Desch and Schappacher (1986), Clément *et al.* (1989) proved the principle of linearized stability and Diekmann *et al.* (1995) proved the Hopf bifurcation theorem and characterized the stable, unstable and center manifolds for semi-linear problems of the form (2.1). The price one has to pay for all this is that one has to extend the state space — an idea already present in the treatment of Hopf bifurcation in delay-differential equations in the paper by Chow and Mallet-Paret (1977).

3. Physiologically structured populations and interaction via the environment

We had hoped that the perturbation theory for adjoint semigroups would apply to models of populations structured by more general physiological features than age. In this respect we were, however, disappointed. A key difficulty is that for higher dimensional individual state space we have translation along characteristics, but no action of the unperturbed semigroup in transversal directions. As a consequence, the characterization of the so-called sun-dual space X^{\odot} (the space of strong continuity of the adjoint semigroup T_0^*) and the domain of the infinitesimal generator of $T_0^{\odot} = T_0^*|_{X^{\odot}}$ turned out to be an insurmountable obstacle. And on top of that the characteristics change dynamically!

In structured population models the nonlinearities enter through so-called environmental interaction (or control) variables often representing quantities such as food concentration, vacant territory or predator density (Metz and Diekmann 1986). If the values of these variables are known

as functions of time, then the population problem becomes a linear time-dependent problem. But by its own activity the population affects the values of these variables, for instance by consuming food, occupying territory or serving as food for a predator. When this feedback is taken into account, one obtains a nonlinear autonomous system.

In most of the earlier work on nonlinear age-structured populations (Gurtin and MacCamy 1974; Webb 1986) the interaction variable was simply the total population $N(t) = \int_0^\infty n(t, a) da$ or some other linear functional $I(t) = \int_0^\infty w(a)n(t, a) da$ of the age-distribution $n(t, \cdot)$. Such a *direct* interaction variable could determine the amount of occupied territory or a quasi steady state approximation of food concentration under the assumption that food consumption is much faster than the demographic processes of birth and death. Haimovici (1979) and Gyllenberg (1982) treated age-structured models with *indirect* interaction variables, which satisfy differential equations with the right hand sides involving the age-distribution, hence taking the form of integro-differential equations. Gyllenberg (1983) proved the stability part of the principle of linearized stability for a model containing both direct and indirect interaction variables. Tucker and Zimmermann (1988) proved the stability part for a class of physiologically structured models that, however, did not allow for a finite number of states-at-birth. Calsina and Saldaña (1995) considered a size-structured model in which all individuals are born with the same size and gave conditions for the existence of a global attractor. As far as we know, the instability part has not been proved for structures other than age. We know of only one paper in which the instability part has been proved for an age-structured model with indirect interaction variables: Martcheva and Thieme (2003) proved it for an epidemic model structured by stage-age, as opposed to chronological age.

4. The role of the history of the environment

As mentioned above, it is obvious that the history of the birth rate is necessary to predict the time-evolution of the age-distribution of a linear age-structured model. A key insight, obtained in collaboration with Hans Metz and presented for the first time by Diekmann *et al.* (2007), is that the history of the birth rate *and* of the interaction variables is *sufficient* to determine the time-evolution of the state of a general physiologically structured population. To be more precise, general structured population models can be written as systems of Volterra functional equations (delay equations) and delay differential equations of the following type:

$$x(t) = F_1(x_t, y_t), \quad (4.1)$$

$$\dot{y}(t) = F_2(x_t, y_t). \quad (4.2)$$

Here the components of the vector $x(t)$ represent the birth rates (there are several if there are several possible states at birth) and the direct interaction variables, whereas $y(t)$ has the indirect interaction variables as its components. As usual, f_t denotes the history of f , that is, $f_t(\theta) = f(t + \theta)$, $\theta \leq 0$. Often the history of y is only needed to compute the growth and survival of individuals born in the past and *not* for determining the dynamics of y itself ! So the “delay” character of y may be a consequence of our particular way of representing the population state. The drawback that, as a consequence, the y -state component becomes infinite dimensional, is compensated by the fact that

we only have to deal with functions of time in the past, a setting that is ideally suited for sun-star calculus. A second insight is that (undifferentiated) delay equations of the type (4.1) can be treated exactly as the delay differential equations were treated using sun-star-calculus by Diekmann *et al.* (1995). The only difference is the choice of the underlying state space (history space). The combination of the two types of equations (4.1) and (4.2) is straightforward (Diekmann *et al.* 2007).

It is the purpose of this short note to illustrate the results of Diekmann *et al.* (2007) by applying them to a model already treated by Gyllenberg (1983).

5. A nonlinear age-dependent population model containing a control variable, revisited

We consider the system

$$\begin{aligned} b(t) &= \int_0^\infty b(t-\tau)\beta(\tau, S(t))\mathcal{F}(\tau; S_t) d\tau, \\ \frac{dS}{dt}(t) &= D(S_0 - S(t)) - \int_0^\infty b(t-\tau)\gamma(\tau, S(t))\mathcal{F}(\tau; S_t) d\tau \end{aligned} \tag{5.1}$$

of delay equations, where

$b(t)$	is the consumer population birth rate at time t
$S(t)$	is the resource (food) concentration at time t
$\beta(\tau, S)$	is the per capita reproduction rate at age τ and food concentration S
$\mathcal{F}(\tau; S_t)$	is the probability that an individual born at time $t - \tau$ will survive to age τ , given that the food concentration in the time interval $[t - \tau, t]$ is given by $S_t(\sigma) = S(t - \sigma)$
$\gamma(\tau, S)$	is the per capita food consumption per unit of time at age τ and food concentration S
D	is the dilution rate of the food
S_0	is the food concentration in the inflowing medium

For the ease of exposition we introduce a maximum age by assuming that, for a certain $h > 0$ and all continuous functions ψ defined on $[-h, 0]$ one has

$$\mathcal{F}(h; \psi) = 0$$

and refer to Diekmann & Gyllenberg (2007) for how to deal with infinite age/delay.

Let

$$\begin{aligned} X &:= L^1([-h, 0]; \mathbf{R}), \\ Y &:= C([-h, 0]; \mathbf{R}). \end{aligned}$$

We require that (5.1) holds for $t \geq 0$ and supplement the system by the initial condition

$$\begin{aligned} b(t) &= \varphi(t), & -h \leq t \leq 0, \\ S(t) &= \psi(t), & -h \leq t \leq 0, \end{aligned} \tag{5.2}$$

where $(\varphi, \psi) \in X \times Y$. The maps $F_i : X \times Y \rightarrow \mathbf{R}$, $i = 1, 2$ are defined by

$$\begin{aligned} F_1(\varphi, \psi) &= \int_0^h \varphi(-\tau) \beta(\tau, \psi(0)) \mathcal{F}(\tau; \psi) d\tau, \\ F_2(\varphi, \psi) &= D(S_0 - \psi(0)) - \int_0^h \varphi(-\tau) \gamma(\tau, \psi(0)) \mathcal{F}(\tau; \psi) d\tau. \end{aligned} \tag{5.3}$$

This allows us to rewrite (5.1) in the form

$$\begin{aligned} b(t) &= F_1(b_t, S_t), \\ \frac{dS}{dt}(t) &= F_2(b_t, S_t). \end{aligned} \tag{5.4}$$

This brings us into exactly the setting studied in Section 4 of (Diekmann *et al.* 2007). It remains to formulate assumptions on β, γ and \mathcal{F} that guarantee that the maps F_i are continuously differentiable.

Note first of all that for any $\psi \in Y$ the maps

$$\varphi \mapsto F_i(\varphi, \psi), \quad i = 1, 2$$

are linear! This is not a coincidence, see (Diekmann *et al.* 2003). We represent the dual space X^* by $L^\infty([0, h]; \mathbf{R})$ with the pairing given by

$$\langle \varphi, \varphi^* \rangle := \int_0^h \varphi(-\tau) \varphi^*(\tau) d\tau$$

and consider $\psi \mapsto F_i(\cdot, \psi)$ as a map from Y into X^* , that we require to be C^1 .

We need the following hypotheses:

(H1) For any $S \geq 0$ the functions

$$\begin{aligned} \tau &\mapsto \beta(\tau, S), \\ \tau &\mapsto \gamma(\tau, S) \end{aligned}$$

define positive elements of $L^\infty([0, h]; \mathbf{R})$.

(H2) For any $\psi \in Y$ the function

$$\tau \mapsto \mathcal{F}(\tau; \psi)$$

is decreasing with $\mathcal{F}(0; \psi) = 1$ and $\mathcal{F}(h; \psi) = 0$.

(H3) The maps

$$S \mapsto \beta(\cdot, S),$$

$$S \mapsto \gamma(\cdot, S)$$

from \mathbf{R}_+ into $L^\infty([0, h]; \mathbf{R})$ are C^1 and so is the map

$$\psi \mapsto \mathcal{F}(\cdot; \psi)$$

from Y into $L^\infty([0, h]; \mathbf{R})$.

Lemma 5.1. *The maps $F_i : X \times Y$, $i = 1, 2$ are C^1 under the hypotheses (H1) – (H3).*

In steady state both b and S are constant. We shall make no notational distinction between a constant function and the value that such a function takes. With that convention we can state that in steady state the food level \bar{S} should be such that the basic reproduction number under the corresponding conditions is one:

$$1 = \int_0^h \beta(\tau, \bar{S}) \mathcal{F}(\tau; \bar{S}) d\tau. \quad (5.5)$$

Once \bar{S} has been determined from (5.5), the steady birth rate is given explicitly by

$$\bar{b} = \frac{D(S_0 - \bar{S})}{\int_0^h \gamma(\tau, \bar{S}) \mathcal{F}(\tau; \bar{S}) d\tau}. \quad (5.6)$$

Note that under the natural monotonicity assumptions that for any $\tau \in [0, h]$ the maps

$$S \mapsto \beta(\tau, S),$$

$$\psi \mapsto \mathcal{F}(\tau; \psi)$$

are increasing, the equation (5.5) has exactly one solution provided that

(i) $\int_0^h \beta(\tau, 0) \mathcal{F}(\tau; 0) d\tau < 1$,

(ii) $\int_0^h \beta(\tau, S) \mathcal{F}(\tau; S) d\tau > 1$ for large S .

Our next aim is to determine criteria for the stability or instability of a steady state. As usual, these criteria are based on linearization or, in other words, they involve the derivatives of F evaluated at the steady state. Because of the linearity with respect to φ , it suffices to compute

$$\begin{aligned} D_2 F_1(\bar{b}, \bar{S})\psi &= \bar{b} \int_0^h D_2 \beta(\tau, \bar{S}) \mathcal{F}(\tau; \bar{S}) d\tau \psi(0) \\ &\quad + \bar{b} \int_0^h \beta(\tau, \bar{S}) D_2 \mathcal{F}(\tau; \bar{S}) \psi d\tau, \end{aligned} \tag{5.7}$$

$$\begin{aligned} D_2 F_2(\bar{b}, \bar{S})\psi &= -D\psi(0) - \bar{b} \int_0^h D_2 \gamma(\tau, \bar{S}) \mathcal{F}(\tau; \bar{S}) d\tau \psi(0) \\ &\quad - \bar{b} \int_0^h \gamma(\tau, \bar{S}) D_2 \mathcal{F}(\tau; \bar{S}) \psi d\tau. \end{aligned}$$

To make things a little more explicit, we now make the natural assumption that the survival probability \mathcal{F} is given in terms of a mortality rate μ by the formula

$$\mathcal{F}(\tau; \psi) = \exp\left(-\int_0^\tau \mu(\sigma, \psi(-\tau + \sigma)) d\sigma\right) \tag{5.8}$$

and that

$$D_2 \mathcal{F}(\tau; \bar{S}) = -\int_0^\tau D_2 \mu(\sigma, \bar{S}) \psi(-\tau + \sigma) d\sigma \mathcal{F}(\tau; \bar{S}). \tag{5.9}$$

Of course we require $\mu \geq 0$ but there are various possibilities for stating assumptions in terms of μ that guarantee both that $\mathcal{F}(h; \psi) = 0$ and that $\psi \mapsto \mathcal{F}(\cdot, \psi)$ is smooth. The simplest of these is to assume that (5.8) holds for $\tau < h$, to define $\mathcal{F}(h; \psi) = 0$ and to assume that $S \mapsto \mu(\cdot, S)$ is C^1 as a map from \mathbf{R}_+ into $L^\infty([0, h]; \mathbf{R})$. This means that individuals may survive to age h , but then die instantaneously upon reaching this age; note that we may choose h , once μ has been specified such that it is bounded away from zero for large ages, such that $\lim_{\tau \uparrow h} \mathcal{F}(\tau, \psi)$ is as small as we wish, uniformly in ψ . A second option is to assume separability, that is,

$$\mu(\tau, S) = \mu_0(\tau) \mu_1(S)$$

and to require that μ_1 is C^1 and that μ_0 is locally bounded but has a non-integrable singularity at h , that is,

$$\lim_{\tau \uparrow h} \int_0^\tau \mu_0(\sigma) d\sigma = +\infty.$$

In that case one should interpret the right hand side of both (5.8) and (5.9) as zero for $\tau = h$ (concerning (5.9), recall that $x e^{-x} \rightarrow 0$ as $x \rightarrow \infty$).

Using (5.9) we find that

$$\bar{b} \int_0^h \beta(\tau, \bar{S}) D_2 \mathcal{F}(\tau; \bar{S}) \psi d\tau = \int_0^h k_{12}(\sigma) \psi(-\sigma) d\sigma$$

with

$$k_{12}(\sigma) = -\bar{b} \int_0^{h-\sigma} \beta(\tau + \sigma, \bar{S}) D_2 \mu(\tau, \bar{S}) \mathcal{F}(\tau + \sigma; \bar{S}) d\tau. \quad (5.10)$$

Defining

$$k_{11}(\sigma) = \beta(\sigma, \bar{S}) \mathcal{F}(\sigma; \bar{S}), \quad (5.11)$$

$$k_{21}(\sigma) = -\gamma(\sigma, \bar{S}) \mathcal{F}(\sigma; \bar{S}), \quad (5.12)$$

$$k_{22}(\sigma) = \bar{b} \int_0^{h-\sigma} \gamma(\tau + \sigma, \bar{S}) D_2 \mu(\tau, \bar{S}) \mathcal{F}(\tau + \sigma; \bar{S}) d\tau, \quad (5.13)$$

$$c_1 = \bar{b} \int_0^h D_2 \beta(\tau, \bar{S}) \mathcal{F}(\tau; \bar{S}) d\tau, \quad (5.14)$$

$$c_2 = -D - \bar{b} \int_0^h D_2 \gamma(\tau, \bar{S}) \mathcal{F}(\tau; \bar{S}) d\tau, \quad (5.15)$$

we can write the linearized version of (5.4) as

$$y(t) = c_1 z(t) + \int_0^h (k_{11}(\sigma) y(t - \sigma) + k_{12}(\sigma) z(t - \sigma)) d\sigma, \quad (5.16)$$

$$\frac{dz}{dt}(t) = c_2 z(t) + \int_0^h (k_{21}(\sigma) y(t - \sigma) + k_{22}(\sigma) z(t - \sigma)) d\sigma.$$

The system (5.16) has a solution of the form

$$\begin{pmatrix} y(t) \\ z(t) \end{pmatrix} = e^{\lambda t} \begin{pmatrix} y_0 \\ z_0 \end{pmatrix}$$

if and only if λ is a solution of the *characteristic equation*

$$\left(1 - \widehat{k}_{11}(\lambda)\right) \left(\lambda - c_2 - \widehat{k}_{22}(\lambda)\right) = \widehat{k}_{21}(\lambda) \left(c_1 + \widehat{k}_{12}(\lambda)\right), \quad (5.17)$$

where the hat denotes Laplace transform, that is,

$$\widehat{k}_{ij}(\lambda) := \int_0^h e^{-\lambda t} k_{ij}(\tau) d\tau.$$

The results presented in (Diekmann *et al.* 2007), in particular those of Section 4, Corollary 2.19 and Theorem 2.17, now allow us to formulate our main conclusion.

Theorem 5..2. (i) *If all roots of (5.17) have negative real part, then the steady state (\bar{b}, \bar{S}) of (5.4) is exponentially stable.*

(ii) *If at least one root of (5.17) has positive real part, then the steady state (\bar{b}, \bar{S}) of (5.4) is unstable*

We reiterate that part (i) is contained in (Gyllenberg 1983) but that, as far as we know, part (ii) is new. We emphasize that Diekmann *et al.* (2007) also showed that the results presented in (Diekmann *et al.* 1995) concerning unstable, stable and center manifolds, as well as those concerning Hopf bifurcation, apply directly to the system (5.4). So, by considering as part of the initial condition the *history* of S (even though there is no need for this at all if one would consider the present age distribution, rather than the history of the birth rate, as the initial condition for the consumer population), the local stability and bifurcation theory derived for abstract integral equations in the sun-star framework is at once at our disposal!

In work in progress (together with Hans Metz, Shinji Nakaoka and André de Roos, under the preliminary title “*Daphnia revisited*”), we show that also in the case of a size structured consumer population, the linearized system is given by (5.16) but, obviously, with a kernel k and a vector c that involve many more terms reflecting the influence of the resource on the growth of the individuals. These results provide, at last, a rigorous mathematical foundation for studies like (de Roos *et al.* 1990; de Roos & Persson 2003). Only with considerable delay did we realize that these population models are, after all, described by delay equations.

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