Abstract Delay Equations Inspired by Population Dynamics

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To the memory of Günter Lumer, a source of inspiration to both of us.

Abstract. In this short note we show that delay equations can be reformulated as abstract weak*-integral equations (AIE) involving dual semigroups, even in the case of infinite delay and/or when the solution takes values in a non-reflexive Banach space. The advantage is that for such (AIE) the standard local stability and bifurcation results are already available, see [8]. Our motivation derives from models of physiologically structured populations, as explained in more detail in [12].

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1. Introduction

The perturbation theory for dual semigroups, as developed in the series [3, 4, 5, 6, 7] of papers, turned out to be a very powerful tool in the local stability and bifurcation theory of delay differential equations (DDE) [8]. The key step is the reformulation of the initial value problem for the DDE as an abstract integral equation

$$u(t) = T_0(t)\varphi + j^{-1}\left(\int_0^t T_0^{\odot *}(t-s)G(u(s))ds\right). \tag{AIE}$$

Here T_0 is a strongly continuous semigroup of bounded linear operators on a Banach space X with sun-dual space $X^{\odot}$ (the subspace of the dual space X^* on

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which the adjoint (or dual) semigroup T_0^* is strongly continuous), $T_0^{\odot *}$ is the adjoint semigroup of $T_0^\odot := (T_0^*)_{|X^\odot}$, G is a nonlinear mapping from X into $X^{\odot *}$ and j is the natural injection of X into $X^{\odot *}$ defined by

$$\langle \varphi^\odot, j\varphi \rangle = \langle \varphi, \varphi^\odot \rangle, \quad \varphi \in X, \ \varphi^\odot \in X^\odot. \tag{1.1}$$

We refer to [2, 3, 8, 18] for more background information about dual semigroups.

Recently, it has been shown [12] that the sun-star-calculus based on (AIE) is equally efficient for treating delay equations (DE) which are functional equations of Volterra type prescribing the value of the function itself in the right end point, rather than the value of its derivative. The only real difference between the treatment of (DDE) and of (DE) is the choice of the underlying function space.

In order for (AIE) to make sense, the convolution integral (which by definition is a weak*-Riemann integral on $X^{\odot *}$) should take values in $j(X)$. It is known [3] that it takes values in $X^{\odot\odot}$. So whenever X is sun-reflexive, that is, whenever $j(X) = X^{\odot\odot}$, this is automatically guaranteed.

The theory developed in [3, 4, 5, 8] concentrates on the sun-reflexive case. As a consequence, the application to delay equations requires a finite delay and that the functions take values in a reflexive space. The aim of the present note is to show that delay equations with infinite delay and involving functions that take values in arbitrary Banach spaces can still be written in the form of an abstract integral equation of the form (AIE). Because in the non-sun-reflexive case the convolution integral in (AIE) need not belong to $j(X)$, we have instead to impose a range condition that for functions f taking values in an appropriate subspace of $X^{\odot *}$, which contains the range of the function G, it is true that

$$\int_0^t T_0^{\odot *}(t-s) f(s) ds \in j(X). \tag{1.2}$$

It turns out that for delay equations it is easy to verify by direct computation that (1.2) holds. Once (AIE) is justified, the methods and results of [8, 12] become available and one obtains the principle of linearized stability, the centre manifold theorem and the Hopf bifurcation theorem essentially for free ('essentially', because the spectral analysis of $T(t)$ is a bit more complicated in the case of infinite delay).

It was already noted in [3, 5, 8] that (AIE) also covers age-dependent population models. More recently, Hans Metz and the present authors found a way to formulate population models that incorporate more general physiological structure (e.g., size structure) as abstract integral equations of type (AIE). This formulation employs delay equations (DE) which do not involve any derivative. In a recent joint work with Philipp Getto [12] we elaborated the details of the reformulation as an (AIE) and its analysis in an L^1-setting, assuming sun-reflexivity. In the present paper we consider the same setting, but we neither impose an upper bound on the delay (i.e., on the maximal attainable age), nor assume that the number of possible states-at-birth is finite. Our results also allow the so-called *interaction variables* [9, 10, 11] to take values in an infinite-dimensional space.

As a general reference concerning (DDE) with infinite delay we mention [16], while for (DDE) in infinite-dimensional spaces we refer to [1], [14, Ch. VI.6] and [21].

2. The abstract setting

Let Y be a Banach space and let $\varrho \geq 0$. As the state space we choose the space $X = L^1(\mathbf{R}_-;Y)$ of all measurable functions $\varphi : \mathbf{R}_- = (-\infty, 0] \to Y$ such that the weighted Bochner integral

$$\|\varphi\|_1 = \int_{\mathbf{R}_-} e^{\varrho\theta} \|\varphi(\theta)\| \, d\theta \tag{2.1}$$

is finite. On X we consider the strongly continuous semigroup T_0 defined by translation and extension by zero:

$$(T_0(t)\varphi)(\theta) = \begin{cases} \varphi(t+\theta), & -\infty < \theta \leq -t, \\ 0, & -t < \theta \leq 0, \end{cases} \qquad \varphi \in X, \quad t \geq 0. \tag{2.2}$$

The reason that we chose $X = L^1(\mathbf{R}_-;Y)$ and not a space of continuous functions as state space is that in applications to delay equations the semigroup T_0 occurs and it does not leave the continuous functions invariant. It is also the right choice for our biological applications, which is not the case of L^p, $1 < p < \infty$, which from a purely mathematical point of view could have been used.

It does not seem possible to give the dual space X^* a representation in terms of familiar functions or measures unless Y^* has the Radon-Nikodym property, in which case X^* is isometrically isomorphic to $L^\infty(\mathbf{R}_+;Y^*)$ [13, Theorem 1, p. 98]. And for the function spaces Y that most frequently occur in our applications, viz. C and L^1, the dual space Y^* does *not* possess the Radon-Nikodym property. However, this is no problem because Greiner and van Neerven [15] (see also [18, Theorem 7.3.11, p. 135]) have characterized the sun-dual $X^\odot = L^1(\mathbf{R}_-;Y)^\odot$ with respect to the translation semigroup (2.2).

Proposition 2.1. *Let Y be a Banach space and let the semigroup T_0 be defined on $X = L^1(\mathbf{R}_-;Y)$ by (2.2). Then $X^\odot$ is isometrically isomorphic to the space of all functions $\varphi^\odot : \mathbf{R}_+ \to Y^*$ such that $\theta \mapsto e^{\rho\theta}\varphi^\odot(\theta)$ is bounded and uniformly continuous with the norm*

$$\left\|\varphi^\odot\right\|_\infty = \sup_{\theta\in\mathbf{R}_+} e^{\varrho\theta} \left\|\varphi^\odot(\theta)\right\| < \infty \tag{2.3}$$

and the pairing

$$\left\langle \varphi, \varphi^\odot \right\rangle = \int_{\mathbf{R}_+} \left\langle \varphi(-\theta), \varphi^\odot(\theta) \right\rangle d\theta. \tag{2.4}$$

The sun-dual semigroup $T^\odot$ is given by

$$\left(T_0^\odot(t)\varphi^\odot\right)(\theta) = \varphi^\odot(t+\theta), \quad 0 \leq \theta < \infty, \quad \varphi^\odot \in X^\odot, \quad t \geq 0. \tag{2.5}$$

Note that on the right-hand side of (2.4) we have the duality pairing between the spaces Y and Y^*.

Proof. In [15] and [18] it was proven (without weights, $\varrho = 0$) that $L^1(\mathbf{R}; Y)^{\odot} = BUC(\mathbf{R}; Y^*)$ with respect to the translation semigroup on the whole real line. The proof for the half-line case is identical. Because we work on weighted spaces, the exponential weight enters in the characterization of $X^{\odot}$. □

Because by Proposition 2.1 the elements of $X^{\odot}$ are represented by continuous functions, we can unambiguously talk about the value $\varphi^{\odot}(\theta)$, $\theta \in \mathbf{R}_+$, of any element $\varphi^{\odot} \in X^{\odot}$. In particular, the *evaluation-in-zero map* $\delta : X^{\odot} \to Y^*$ is well defined through

$$\delta\varphi^{\odot} = \varphi^{\odot}(0), \quad \varphi^{\odot} \in X^{\odot}. \tag{2.6}$$

The adjoint δ^* of δ maps Y^{**} into $X^{\odot *}$. By restricting δ^* to Y (using the canonical embedding of a Banach space into its second dual) we obtain a linear mapping $\ell : Y \to X^{\odot *}$. Explicitly, it is defined via

$$\left\langle \varphi^{\odot}, \ell y \right\rangle = \left\langle y, \varphi^{\odot}(0) \right\rangle, \quad y \in Y, \quad \varphi^{\odot} \in X^{\odot}. \tag{2.7}$$

Obviously, ℓ is an isometric isomorphism of Y onto a closed subspace of $X^{\odot *}$.

Lemma 2.2. *For every $y \in Y$ and $\varphi^{\odot} \in X^{\odot}$ one has*

$$\left\langle T_0^{\odot *}(t)\ell y, \varphi^{\odot} \right\rangle = \left\langle y, \varphi^{\odot}(t) \right\rangle, \quad t \geq 0.$$

Proof. $\left\langle T_0^{\odot *}(t)\ell y, \varphi^{\odot} \right\rangle = \left\langle \ell y, T_0^{\odot}(t)\varphi^{\odot} \right\rangle = \left\langle y, \left(T_0^{\odot}(t)\varphi^{\odot}\right)(0) \right\rangle = \langle y, \varphi^{\odot}(t) \rangle.$ □

Lemma 2.3. *Let $h : \mathbf{R}_+ \to Y$ be a continuous function. Then, for every $\varphi^{\odot} \in X^{\odot}$ one has*

$$\left\langle \int_0^t T_0^{\odot *}(t-\tau)\ell h(\tau)\, d\tau, \varphi^{\odot} \right\rangle = \int_0^t \left\langle h(t-\tau), \varphi^{\odot}(\tau) \right\rangle d\tau, \quad t \geq 0.$$

Proof. Using Lemma 2.2 one gets

$$\left\langle \int_0^t T_0^{\odot *}(t-\tau)\ell h(\tau)\, d\tau, \varphi^{\odot} \right\rangle = \int_0^t \left\langle T_0^{\odot *}(t-\tau)\ell h(\tau), \varphi^{\odot} \right\rangle d\tau =$$

$$\int_0^t \left\langle \ell h(\tau), T_0^{\odot}(t-\tau)\varphi^{\odot} \right\rangle d\tau = \int_0^t \left\langle h(\tau), \varphi^{\odot}(t-\tau) \right\rangle d\tau$$

$$\int_0^t \left\langle h(t-\tau), \varphi^{\odot}(\tau) \right\rangle d\tau.$$ □

As a corollary, we get the result alluded to in the introduction: the convolution integral $\int_0^t T_0^{\odot *}(t-\tau) f(\tau)\, d\tau$ belongs to $j(X)$, whenever $f : \mathbf{R}_+ \to X^{\odot *}$ is continuous with values in $\ell(Y)$.

Corollary 2.4. *Let $h : \mathbf{R}_+ \to Y$ be a continuous function and define $\varphi \in X = L^1(\mathbf{R}_-; Y)$ by*

$$\varphi(\theta) = \begin{cases} h(t+\theta) & -t \leq \theta \leq 0, \\ 0, & -\infty < \theta < -t. \end{cases} \tag{2.8}$$

Then

$$\int_0^t T_0^{\odot *}(t-\tau)\ell h(\tau)\,d\tau = j\varphi. \tag{2.9}$$

In particular, $\int_0^t T_0^{\odot *}(t-\tau)\ell h(\tau)\,d\tau \in j(X)$ *and*

$$\left\| j^{-1}\left(\int_0^t T_0^{\odot *}(t-\tau)\ell h(\tau)\,d\tau\right)\right\|_1 \le \frac{1}{\varrho}\left(1-e^{-\varrho t}\right)\sup_{0\le\tau\le t}\|h(\tau)\|, \quad t\ge 0. \tag{2.10}$$

(If $\varrho = 0$*, the factor* $\left(1-e^{-\varrho t}\right)/\varrho$ *has to be interpreted as the limiting value* t*.)*

Proof. For each $\varphi^{\odot} \in X^{\odot}$ we have by the definition of φ and Lemma 2.3:

$$\begin{aligned}\left\langle \varphi, \varphi^{\odot}\right\rangle &= \int_{-\infty}^0 \left\langle \varphi(\theta), \varphi^{\odot}(-\theta)\right\rangle\,d\theta = \int_{-t}^0 \left\langle h(t+\theta), \varphi^{\odot}(-\theta)\right\rangle\,d\theta \\ \int_0^t \left\langle h(t-\theta), \varphi^{\odot}(\theta)\right\rangle\,d\theta &= \left\langle \int_0^t T_0^{\odot *}(t-\tau)\ell h(\tau)\,d\tau, \varphi^{\odot}\right\rangle.\end{aligned}$$

The definition (1.1) of the embedding $j : X \to X^{\odot *}$ now yields (2.9). The estimate (2.10) follows readily:

$$\begin{aligned}&\left\| j^{-1}\left(\int_0^t T_0^{\odot *}(t-\tau)\ell h(\tau)\,d\tau\right)\right\|_1 = \|\varphi\|_1 = \int_{-\infty}^0 e^{\rho\theta}\|\varphi(\theta)\|\,d\theta = \\ &\int_{-t}^0 e^{\varrho\theta}\|h(t+\theta)\|\,d\theta = e^{-\varrho t}\int_0^t e^{\varrho\tau}\|h(\tau)\|\,d\tau \le \frac{1}{\varrho}\left(1-e^{-\varrho t}\right)\sup_{0\le\tau\le t}\|h(\tau)\|.\end{aligned}$$ □

Theorem 2.5. *Let* $F : X \to Y$ *be Lipschitz continuous. Then the abstract integral equation*

$$u(t) = T_0(t)\varphi + j^{-1}\left(\int_0^t T_0^{\odot *}(t-s)G(u(s))ds\right), \tag{AIE}$$

with T_0 *defined by* (2.2) *and* $G = \ell \circ F$*, has a unique solution on* $[0,\infty)$*.*

Proof. With Corollary 2.4 at hand, the proof is identical to the proof of the corresponding result in the sun-reflexive case [5, 8]. □

Next we consider steady states of the dynamical system $\Sigma(t)$ induced by (AIE) by declaring $\Sigma(t)\varphi$ to be the solution $u(t)$ of (AIE). We now realize why we have to use *weighted* L^1-spaces: Without a weight, nonzero constant functions on an infinite interval do not belong to L^1. Linearization around a steady state works exactly as in the sun-reflexive case [5]:

Theorem 2.6. *Let* $\Sigma(t)\overline{\varphi} = \overline{\varphi}$ *and assume that the nonlinear operator* $F : X \to Y$ *is continuously Fréchet differentiable. Then for every* $t > 0$ *the nonlinear operator* $\Sigma(t)$ *is Fréchet differentiable at* $\overline{\varphi}$*. Its Fréchet derivative*

$$T(t) = (D\Sigma(t))(\overline{\varphi}) \tag{2.11}$$

defines a strongly continuous semigroup of bounded linear operators with generator A given by

$$\begin{aligned}\mathcal{D}(A) &= \{\varphi \in X : j\varphi \in \mathcal{D}(A_0^{\odot *}), A_0^{\odot *} j\varphi + \ell F'(\overline{\varphi})\varphi \in j(X)\},\\ A\varphi &= j^{-1}(A_0^{\odot *} j\varphi + \ell F'(\overline{\varphi})\varphi).\end{aligned}$$

Moreover, for every $\varphi \in X$, $T(t)\varphi$ is the unique solution of the linear abstract integral equation

$$T(t)\varphi = T_0(t)\varphi + j^{-1}\left(\int_0^t T_0^{\odot *}(t-s)\ell F'(\overline{\varphi})T(s)\varphi ds\right). \qquad \text{(LAIE)}$$

The proofs of the principle of linearized stability, the centre manifold theorem and the Hopf bifurcation theorem depend essentially on the linearization described in Theorem 2.6.

3. Delay equations as abstract integral equations

We consider the initial value problem

$$x(t) = F(x_t), \quad t > 0 \qquad \text{(DE)}$$

$$x_0(\theta) = \varphi(\theta), \quad \theta \in (-\infty, 0], \qquad \text{(IC)}$$

consisting of a delay equation (DE) specifying the rule for extending the unknown function x from the history given by (IC). Here the unknown function x takes values in a Banach space Y and x_t denotes for each $t \geq 0$ the translated function defined by

$$x_t(\theta) := x(t+\theta), \quad -\infty < t \leq 0. \qquad (3.1)$$

As state space (history space) we choose the space $X = L^1(\mathbf{R}_-; Y)$ of Bochner integrable (with respect to the weight function $\theta \mapsto e^{\rho\theta}$) functions on $\mathbf{R}_-$, see Section 2. We therefore assume that F maps X into Y and that the initial value φ belongs to X. In this section we show that the problem (DE) & (IC) is equivalent to (AIE) with $G = \ell \circ F$ and T_0 defined by (2.2). We shall always assume that T_0 and G are chosen in this way.

An application of Corollary 2.4 to the function $h = F \circ u$ for a continuous function $u : \mathbf{R}_+ \to X$ immediately gives the following result:

Lemma 3.1.

$$\left(j^{-1}\int_0^t T_0^{\odot *}(t-s)\ell F(u(s))ds\right)(\theta) = \begin{cases} F(u(t+\theta)), & -t \leq \theta \leq 0,\\ 0, & -\infty < \theta < -t.\end{cases}$$

We are now ready to state and prove the equivalence of (DE) & (IC) and (AIE).

Theorem 3.2. *Let $\varphi \in X = L^1(\mathbf{R}_-; Y)$ be given.*

(a) *Suppose that $x \in L^1_{\text{loc}}((-\infty,\infty); Y)$ satisfies* (DE) *&* (IC)*. Then the function $u : [0,\infty) \to X$ defined by $u(t) := x_t$ is continuous and satisfies* (AIE).

(b) *If $u : [0,\infty) \to X$ is continuous and satisfies* (AIE)*, then the function x defined by*

$$x(t) := \begin{cases} \varphi(t) & \text{for } -\infty < t < 0, \\ u(t)(0) & \text{for } t \geq 0 \end{cases} \tag{3.2}$$

is an element of $L^1_{\text{loc}}((-\infty,\infty); Y)$ and satisfies (DE) *&* (IC).

Proof. (a) The continuity of $u(t) = x_t$ follows from the continuity of translation in L^1. Fix $t \geq 0$. By the definition of T_0 one has for $-t \leq \theta \leq 0$

$$u(t)(\theta) - (T_0(t)\varphi)(\theta) = x(t+\theta) - 0 = F(x_{t+\theta}) = F(u(t+\theta))$$

and for $-\infty < \theta < -t$

$$u(t)(\theta) - (T_0(t)\varphi)(\theta) = x(t+\theta) - \varphi(t+\theta) = \varphi(t+\theta) - \varphi(t+\theta) = 0$$

Lemma 3.1 shows that in both cases $u(t)(\theta) - (T_0(t)\varphi)(\theta)$ equals $\left(j^{-1}\int_0^t T_0^{\odot *}(t-s)\ell F(u(s))ds\right)(\theta)$ and thus u satisfies (AIE).

(b) Lemma 3.1 shows that for $t > 0$,

$$\begin{aligned} x(t) &= u(t)(0) = (T_0(t)\varphi)(0) + \left(j^{-1}\int_0^t T_0^{\odot *}(t-s)\ell F(u(s))ds\right)(0) \\ &= F(u(t)). \end{aligned} \tag{3.3}$$

It thus remains to be shown that $u(t) = x_t$. For $-t < \theta \leq 0$, (3.3) gives

$$x_t(\theta) = x(t+\theta) = u(t+\theta)(0) = F(u(t+\theta)) = u(t)(\theta)$$

and for $-\infty < \theta < -t$, Lemma 3.1 gives

$$x_t(\theta) = x(t+\theta) = \varphi(t+\theta) = (T_0(t)\varphi)(\theta) = u(t)(\theta)$$

so indeed $u(t) = x_t$. □

4. A model involving cannibalistic behaviour

Consider a population structured by the size of individuals. We assume that individuals eat their conspecifics and that this cannibalistic behaviour is modelled through the *attack rate* $\alpha(\xi,\eta)$, which is the rate at which individuals of size η kill and eat individuals of size ξ. Usually the victim of cannibalism is smaller than the attacker, so $a(\xi,\eta)$ should be zero for $\xi > \eta$, but we will make no explicit use of this assumption in what follows. We assume that all individuals are born with the same size ξ_b.

Cannibalism leads to an extra mortality in the population. If $n(t,\cdot)$ denotes the density of the size-distribution of the population at time t, then the extra size-specific mortality rate due to cannibalism at time t is

$$M(t,\xi) = \int_{\xi_b}^{\infty} \alpha(\xi,\eta) n(t,\eta) d\eta. \tag{4.1}$$

Let $c(\eta)$ be the energetic value of an individual of size η. Then the extra energy intake due to cannibalism per unit of time of an individual of size ξ is

$$E(t,\xi) = \int_{\xi_b}^{\infty} c(\eta)\alpha(\eta,\xi) n(t,\eta) d\eta. \tag{4.2}$$

We assume that E is channelled into growth and affects "ordinary" mortality, that is, mortality not due to cannibalism but due, e.g., to starvation. The traditional PDE formulation then takes the form of the boundary value problem

$$\begin{aligned} &\frac{\partial}{\partial t} n(t,\xi) + \frac{\partial}{\partial \xi}\left(g(\xi, E(t,\xi)) n(t,\xi)\right) = \\ &-\left(\mu(\xi, E(t,\xi)) + M(t,\xi)\right) n(t,\xi), \quad \xi > \xi_b \\ &g(\xi_b, E(t,\xi_b)) n(t,\xi_b) = \int_{\xi_b}^{\infty} \beta(\xi) n(t,\xi) d\xi, \end{aligned} \tag{4.3}$$

where $\beta(\xi)$ is the size-specific fecundity. If some of the extra energy intake is also channelled into reproduction, then β depends also on $E(t,\xi)$. Nothing essential would change in the sequel, only the notation would be more cumbersome.

Next we want to write the model as a delay equation (DE) for the unknown

$$x(t) = \begin{pmatrix} b(t) \\ I(t) \end{pmatrix},$$

where $b(t)$ is the population birth rate and $I(t)$ is some conveniently chosen interaction variable. To this end, let $I^1(t,a)$ be the total per capita death rate and let $I^2(t,a)$ be the individual growth rate of an individual of age a at time t:

$$I^1(t,a) = \mu(\xi, E(t,\xi)) + M(t,\xi), \tag{4.4}$$

$$I^2(t,a) = g(\xi, E(t,\xi)). \tag{4.5}$$

Note that we use superscripts as indices because subscripts are reserved for translation, cf. (3.1).

We emphasize that *age* does not occur in the original model formulation and that Eqs. (4.4) and (4.5) are meaningless as they stand. So for the time being we *assume* that $I^1(t,a)$ and $I^2(t,a)$ are given. More precisely, we consider the mappings $t \mapsto I^1(t,\cdot)$ and $t \mapsto I^2(t,\cdot)$ as mappings from $\mathbf{R}_-$ to $C(\mathbf{R}_+)$, the Banach space of bounded continuous scalar-valued functions on $\mathbf{R}_+$. Later, when we close the feedback loop, we shall see how the original ingredients, given in terms of size, transform into quantities defined in terms of age.

Consider an individual of age a at time t. It was born at time $t-a$. By definition, it has grown according to

$$\begin{aligned} \frac{d\xi}{d\tau} &= I^2(t-a+\tau,\tau), \quad 0<\tau\le a, &(4.6)\\ \xi(0) &= \xi_b. &(4.7)\end{aligned}$$

The solution evaluated at $\tau=a$ gives the size of the individual at time t:

$$\xi(a)=\xi_b+\int_0^a I^2(t-a+\tau,\tau)d\tau=\xi_b+\int_0^a I_t^2(\tau-a,\tau)d\tau=:X^2\left(I_t^2\right)(a). \quad (4.8)$$

Notice that the size of an individual of age a at time t is an *affine* (that is, constant plus linear) mapping X^2 of $L^1(\mathbf{R}_-;C(\mathbf{R}_+))$ into $C(\mathbf{R}_+)$.

The probability that an individual that was born at time $t-a$ survives to age a, given the history of I, is

$$e^{-\int_0^a I^1(t-a+\tau,\tau)d\tau}=e^{-X^1\left(I_t^1\right)(a)},$$

where, in analogy with the definition of X^2, we have defined the linear mapping $X^1: L^1(\mathbf{R}_-;C(\mathbf{R}_+))\to C(\mathbf{R}_+)$ by

$$X^1\left(I_t^1\right)(a):=\int_0^a I_t^1(\tau-a,\tau)d\tau.$$

Therefore the birth rate

$$b(t):=g(\xi_b,E(t,\xi_b))n(t,\xi_b)$$

satisfies the renewal equation

$$b(t)=\int_0^a \beta\left(X^2\left(I_t^2\right)(a)\right)e^{-X^1\left(I_t^1\right)(a)}b_t(-a)da. \quad (4.9)$$

Alternatively and equivalently, the renewal equation (4.9) could have been obtained from the boundary condition in (4.3) by the change $\xi=X^2\left(I_t^2\right)(a)$ of variables. Similarly, we get from (4.1) and (4.2), respectively:

$$M(t,\xi)=\int_0^\infty \alpha\left(\xi,X^2\left(I_t^2\right)(a)\right)e^{-X^1\left(I_t^1\right)(a)}b_t(-a)da \quad (4.10)$$

and

$$E(t,\xi)=\int_0^\infty c\left(X^2\left(I_t^2\right)(a)\right)\alpha\left(X^2\left(I_t^2\right)(a),\xi\right)e^{-X^1\left(I_t^1\right)(a)}b_t(-a)da. \quad (4.11)$$

We now substitute (4.8), (4.10) and (4.11) into (4.4) and (4.5) and obtain

$$I^1(t,a) = \mu\Big(X^2\big(I_t^2\big)(a), \int_0^\infty c\big(X^2\big(I_t^2\big)(\tau)\big)\,\alpha\big(X^2\big(I_t^2\big)(\tau), X^2\big(I_t^2\big)(a)\big)\,e^{-X^1\left(I_t^1\right)(\tau)}b_t(-\tau)d\tau\Big) + \int_0^\infty \alpha\big(X^2\big(I_t^2\big)(a), X^2\big(I_t^2\big)(\tau)\big)\,e^{-X^1\left(I_t^1\right)(\tau)}b_t(-\tau)d\tau \tag{4.12}$$

$$I^2(t,a) = g\Big(X^2\big(I_t^2\big)(a), \int_0^\infty c\big(X^2\big(I_t^2\big)(\tau)\big)\,\alpha\big(X^2\big(I_t^2\big)(\tau), X^2\big(I_t^2\big)(a)\big)\,e^{-X^1\left(I_t^1\right)(\tau)}b_t(-\tau)d\tau\Big) \tag{4.13}$$

Equations (4.9), (4.12) and (4.13) form a delay equation (DE) for the unknown

$$x(t) = \begin{pmatrix} b(t) \\ I^1(t) \\ I^2(t) \end{pmatrix},$$

with $F : L^1(\mathbf{R}_-; Y) \to Y$ and $Y = \mathbf{R} \times C(\mathbf{R}_+) \times C(\mathbf{R}_+)$. The function F is of course defined by declaring

$$F \begin{pmatrix} b_t \\ I_t^1 \\ I_t^2 \end{pmatrix} (a)$$

to be the vector with the right-hand sides of (4.9), (4.12) and (4.13) as components.

The formulation of the principle of linearized stability, the centre manifold theorem and the Hopf bifurcation theorem involves the linearization described in Theorem 2.6 as well as the location of the spectrum of the generator of the linearized semigroup. Linearization is possible only if F is continuously Fréchet differentiable. It is a pleasant fact that F is indeed continuously differentiable under very natural conditions.

Theorem 4.1. *Let g, β, μ, α and c have continuous partial derivatives with respect to all variables. Then the mapping $F : L^1(\mathbf{R}_-; Y) \to Y$ is continuously Fréchet differentiable.*

Proof. F is linear in b_t and hence continuously differentiable in b_t. As noted above, X^1 and X^2 are affine mappings, and hence continuously differentiable with values in the continuous functions. $X^1(I_t^1)$ and $X^2(I_t^2)$ appear everywhere as arguments of continuously differentiable mappings. Because the Nemytskiĭ operator $N_g : f \mapsto g \circ f$ is continuously differentiable from C to C if g is continuously differentiable, the conclusion follows. □

5. Conclusions

The reformulation of delay differential equations [8] and delay equations [12] as abstract integral equations has proven to be useful because standard results from the theory of ordinary differential equations such as linearized (in)stability and Hopf bifurcation can easily be extended to this class of problems using the so-called sun-star calculus of adjoint semigroups. In the references mentioned above, the analysis was restricted to the case of delay (differential) equations with finite delay and unknowns taking values in finite-dimensional spaces. The reason is that in this case the state space is sun-reflexive with respect to the unperturbed semigroup and standard results concerning adjoint semigroups show that the abstract integral equation makes sense and has a unique solution. In this paper we have shown that the assumption of sun-reflexivity can be relaxed. Indeed, we have shown that the abstract integral equation (AIE) is well posed if the nonlinear operator G is restricted to take on values in a certain subspace of $X^{\odot *}$. This is a very natural approach because when the delay is infinite, one cannot give an easy representation of $X^{\odot *}$, so one is anyhow forced to define the operator G as taking values in a subspace that can be given a representation.

The natural state space is the space $X = L^1(\mathbf{R}_-; Y)$ of suitably weighted Bochner integrable functions. One cannot work with continuous functions because they are not invariant under the unperturbed semigroup, which is translation and extension by zero. A weight is needed to have nonzero steady states in the state space. In applications to population problems, the components of the unknown are typically *rates*, which integrated over a finite time interval yield finite numbers. So L^1 (and not, e.g., L^p) is the right state space.

From certain points of view the space L^1 is not particularly nice. One complication is that the Nemytskiĭ (or substitution) operator $N_g : f \mapsto g \circ f$ is differentiable in L^1 if and only if g is affine, that is, a constant plus a linear map [17]. This appears to be a severe restriction, at least when the space Y is chosen in what at first thought seems the most natural way. For instance, in [12] the principle of linearized stability for the well-known Gurtin-MacCamy model

$$b(t) = \int_0^\infty \beta(a, N(t)) e^{-\int_0^a \mu(N(t-a+\tau,\tau)d\tau} b(t-a)da, \tag{5.1}$$

$$N(t) = \int_0^\infty e^{-\int_0^a \mu(N(t-a+\tau,\tau)d\tau} b(t-a)da \tag{5.2}$$

with one-dimensional interaction variable N, could be established only if the per capita death rate μ was affine: $\mu(a, N) = \mu_0(a) + \mu_1(N)$. This is somewhat unsatisfactory because the principle of linearized stability has been proven in much greater generality in [19, 20].

But in the present paper we allow for infinite-dimensional Y and hence the Gurtin-MacCamy model (5.1) & (5.2) can be rewritten using the infinite-dimensional interaction variable

$$I(t, a) = \mu(a, N(t))$$

as

$$b(t) = \int_0^\infty \beta\left(a, \int_0^\infty e^{-\int_0^\sigma I_t(\tau-\sigma,\tau)d\tau} b_t(-\sigma)d\sigma\right) e^{-\int_0^a I_t(\tau-a,\tau)d\tau} b_t(-a)da, \tag{5.3}$$

$$I(t,a) = \mu\left(\int_0^\infty e^{-\int_0^\sigma I_t(\tau-\sigma,\tau)d\tau} b_t(-\sigma)d\sigma, a\right). \tag{5.4}$$

If β and μ are continuously differentiable, then the right-hand sides of (5.3) and (5.4) are continuously differentiable in I_t as compositions of continuously differentiable mappings on C and affine mappings $L^1 \to C$. For the Gurtin-MacCamy model the shift from one-dimensional to infinite-dimensional interaction variable, just to make the abstract framework functioning, may seem artificial because the problem can be, and has been, solved by other means. But for the cannibalism model treated in Section 4, in which the more obvious candidates for interaction variables, viz. $M(t,x)$ and $E(t,x)$, already are infinite dimensional, the choice of $I^1(t,a)$ and $I^2(t,a)$ as interaction variables is very natural.

The setting of this paper with an infinite-dimensional Y also allows for infinitely many states at birth in contrast to the assumption of only finitely many states at birth made in [12].

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