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STABILITY AND BIFURCATION ANALYSIS OF VOLTERRA FUNCTIONAL EQUATIONS IN THE LIGHT OF SUNS AND STARS*

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Abstract. We show that the perturbation theory for dual semigroups (sun-star-calculus) that has proved useful for analyzing delay-differential equations is equally efficient for dealing with Volterra functional equations. In particular, we obtain both the stability and instability parts of the principle of linearized stability and the Hopf bifurcation theorem. Our results apply to situations in which the instability part has not been proved before. In applications to general physiologically structured populations even the stability part is new.

Key words. delay equations, dual semigroup, sun-star-calculus, Lipschitz perturbations, principle of linearized stability, center manifold, Hopf bifurcation, physiologically structured populations

AMS subject classifications. 39B82, 47D99, 92D25

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1. Introduction.

Delay equations are rules for extending (in one direction) a function that is a priori defined on an interval. Usually, as in the books [23, 40], one considers delay *differential* equations of the type

$$\dot{x}(t) = F(x_t), \quad t \geq 0, \tag{1.1}$$

where, for some given $h > 0$,

$$x_t(\theta) := x(t + \theta) \tag{1.2}$$

for $\theta \in [-h, 0]$. Here, in contrast, we consider functional equations of Volterra type, so the extension rule prescribes the value of the function itself, rather than that of its derivative, in terms of the history. We thus study initial value problems of the form

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

$$x_0(\theta) = \varphi(\theta), \quad \theta \in [-h, 0], \tag{IC}$$

with φ being a given function on $[-h, 0]$. The formula labels (DE), (IC) stand for delay equation and initial condition, respectively.

In [23], the main tool for analyzing the delay differential equation (1.1) is the perturbation theory for dual semigroups developed in [9, 10, 11, 12, 20], which under appropriate assumptions transforms the Cauchy problem (1.1) and (IC) into an abstract *semilinear* problem. This theory has proved to be equally efficient for treating

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age-structured population models; see [9, 11] and various exercises in [23]. The aim of this paper is to show in detail that the same theory applies to functional equations of Volterra type (DE), the only difference being the choice of the underlying function space.

To give a feeling for the problems involved, we make a few formal manipulations. Let

$$u(t,\theta) := x_t(\theta), \quad t \geq 0, \ -h \leq \theta \leq 0. \tag{1.3}$$

The problem (DE), (IC) is equivalent to the following PDE with boundary and initial conditions:

$$\frac{\partial u}{\partial t} - \frac{\partial u}{\partial \theta} = 0, \quad t > 0, \ -h \leq \theta \leq 0, \tag{1.4}$$

$$u(t,0) = F(u(t,\cdot)), \quad t \geq 0, \tag{1.5}$$

$$u(0,\theta) = \varphi(\theta), \quad -h \leq \theta \leq 0. \tag{1.6}$$

If $F = 0$, the problem reduces to an elementary linear problem. Its solution semigroup $T_0 = \{T_0(t)\}_{t\geq 0}$ is simply translation to the left with extension by zero:

$$(T_0(t)\varphi)(\theta) := \begin{cases} \varphi(t+\theta) & \text{for} \quad t+\theta \in [-h,0], \\ 0 & \text{for} \quad t+\theta > 0, \end{cases} \qquad t \geq 0, \ \theta \in [-h,0]. \tag{1.7}$$

Next we have to specify the state space (history space) on which the semigroup T_0 acts. The continuous functions will not do, because as can be seen from (1.7), $C[-h,0]$ is not invariant under T_0. A natural choice is $X = L^1[-h,0]$. With this choice of state space, the generator A_0 of T_0 is differentiation with the zero boundary condition entering into the domain of definition:

$$\mathcal{D}(A_0) = \{\varphi \in X : \varphi \in AC, \ \varphi(0) = 0\}, \tag{1.8}$$

$$A_0\varphi = \varphi', \tag{1.9}$$

where the notation $\varphi \in AC$ means that φ is absolutely continuous [2, p. 11].

The nonlinear problem (1.4)–(1.6) with $F \neq 0$ can now be written as the abstract Cauchy problem

$$\frac{du(t)}{dt} = A(u(t))u(t), \quad t > 0, \tag{1.10}$$

$$u(0) = \varphi \tag{1.11}$$

for $u(t) := u(t,\cdot) = x_t$, where the action of $A(u(t))$ is still differentiation, but the domain depends on the solution itself in a nonlinear way:

$$\mathcal{D}(A(u(t))) = \{\varphi \in X : \varphi \in AC, \varphi(0) = F(u(t))\}. \tag{1.12}$$

So the problem is *quasi-linear* and hence notoriously difficult [49]. A small trick, however, turns the quasi-linear problem into a *semilinear* one, that is, a problem in which the nonlinearity appears as an additive and relatively bounded perturbation of the linear operator A_0. Next we explain how this is done.

The space $L^1[-h,0]$ can be embedded into $\mathrm{NBV}(-h,0]$, the space of functions of bounded variation on $(-h,0]$ normalized to be zero at zero and continuous from the right, by integration $j : L^1[-h,0] \to \mathrm{NBV}(-h,0]$,

$$(j\varphi)(\theta) := -\int_\theta^0 \varphi(\tau)d\tau, \quad \theta \in (-h,0]. \tag{1.13}$$

The image of $L^1[-h,0]$ in $\mathrm{NBV}(-h,0]$ under j consists of all functions absolutely continuous on $[-h,0]$ and vanishing at 0 [46, sections IX. 2–4].

Integrating (1.4) from θ to 0 and taking the boundary condition (1.5) into account, one obtains the semilinear problem

$$\frac{d}{dt} ju(t) = A_0^{\odot *} ju(t) + F(u(t))H, \quad t > 0, \tag{1.14}$$

$$u(0) = \varphi, \tag{1.15}$$

where the operator $A_0^{\odot *}$ is differentiation on $\mathrm{NBV}(-h,0]$ with appropriate domain of definition (the $\odot *$-notation will be explained in section 2) and H is a Heaviside function defined by

$$H(\theta) := \begin{cases} -1 & \text{for} \quad \theta \in (-h,0), \\ 0 & \text{for} \quad \theta = 0. \end{cases} \tag{1.16}$$

The price one has to pay for the transformation of the quasi-linear problem into a semilinear one is that, while the unknown $u(t) = x_t$ belongs to $L^1[-h,0]$, the range of the perturbation lies in the bigger space $\mathrm{NBV}(-h,0]$ and actually outside $j\left(L^1[-h,0]\right)$ (note that $H \in \mathrm{NBV}(-h,0]$, but because of the discontinuity in 0 it is not absolutely continuous). The perturbation theory mentioned above was designed especially to have a general framework for such problems.

A key step is to replace the Cauchy problem (1.14) and (1.15) by an abstract integral equation of the variation-of-constants type, which is obtained from (1.14) and (1.15) by formal integration. The main point is that, in fact, this abstract integral equation is equivalent to the original problem (DE), (IC), while at the same time, it allows us to prove linearized stability and other properties in a standard manner. As these proofs are provided in detail in [23], we can concentrate here on the equivalence. Note, however, that in the present paper we shall always explicitly express the embedding operator j, while in [23] it is often suppressed with the understanding that one can identify X and $X^{\odot\odot}$ once and for all.

The mathematics of age-structured populations mentioned above has been extensively treated, for instance, in the books [17, 56]. Our main motivation comes from the theory of general physiologically structured populations [24, 25, 27, 45]. Individuals are distinguished from one another by their i-state (i for individual), which belongs to a measurable space Ω. The population state (p-state) is a measure m on Ω giving the distribution of i-states. Deterministic structured population models are defined in terms of ingredients prescribing i-state specific survival, reproduction, and i-state development, given the course of the *environmental condition* (or *input*) $I(t)$ and a feedback mechanism, which often is of the form

$$I(t) = \int_\Omega \gamma(\xi) m(t)(d\xi). \tag{1.17}$$

From the basic ingredients one can calculate the quantities $\mathcal{F}_{I_{|[t-a,t]}}(\xi,\omega)$ and $\lambda_{I_{|[t-a,t]}}(\xi,\omega)$ with the following interpretations: Let I be a given function of time, let $\xi \in \Omega$, and let ω be a measurable subset of Ω. Then we have the following.

- $\mathcal{F}_{I_{|[t-a,t]}}(\xi,\omega)$ is the probability that an individual who was born at time $t-a$ with i-state ξ is still alive at time t (when it has age a) and then has i-state in ω.
- $\lambda_{I_{|[t-a,t]}}(\xi,\omega)$ is the rate at which an individual who was born at time $t-a$ with i-state ξ produces offspring with state-at-birth in ω at time t (when it has age a).

The subscripts $I_{|[t-a,t]}$ of $\mathcal{F}$ and λ indicate that the quantities depend on the restriction of I to the interval $[t-a,t]$; that is, they depend only on the values of I during the lifetime of the individual in question.

Let $b(t)(\omega)$ denote the rate at which individuals are born with i-state in ω at time t. Assuming a maximal life span h, bookkeeping gives

$$b(t)(\omega) = \int_0^h \int_\Omega b(t-a)(d\xi)\lambda_{I_{|[t-a,t]}}(\xi,\omega)da, \tag{1.18}$$

$$m(t)(\omega) = \int_0^h \int_\Omega b(t-a)(d\xi)\mathcal{F}_{I_{|[t-a,t]}}(\xi,\omega)da. \tag{1.19}$$

Thus in this generality one has an abstract variant of (DE).

Often there is but one possible state-at-birth. Or, in particular when dealing with several interacting populations, there may be a finite number of possible states-at-birth. In such cases one may limit ω in (1.18) to points chosen from a finite set. If, in addition, $I(t)$ in (1.17) has only finitely many components, we can condense the essential information concerning the population problem into a finite dimensional equation (DE). Indeed, combining (1.18) and (1.19) with the feedback law (1.17), one finds that the value

$$x(t) = \begin{pmatrix} b(t) \\ I(t) \end{pmatrix} \tag{1.20}$$

is a nonlinear function of the history of x on $[t-h,t]$; that is, x satisfies a delay equation of the form (DE), with F being a function from $L^1\big([-h,0],\mathbf{R}^N\big)$ to $\mathbf{R}^N$ for some integer $N \geq 2$.

The population dynamical applications also motivate our choice of $L^1\left([-h,0],\mathbf{R}^N\right)$ as the history space. The components of b are *rates* at which individuals are born with certain i-states. While rates may be unbounded, *numbers* of individuals (integrals of rates) must remain finite.

The idea to use the history of I is new. The fact that in this manner we can use perturbation theory for dual semigroups to treat *general* physiologically structured population models, and not just age-structured models, triggered the writing of this paper. In a companion paper, to be written jointly with J. A. J. Metz, we shall elaborate in detail how the results of the present paper apply to population models.

In the present paper we shall consider only the case of finite delay. The reason is that in this case the semigroup defined by (1.7) has a desirable property called sun-reflexivity, which is lost in the case of infinite delay. However, our results can easily be extended to also encompass the case of infinite delay. In section 6 we briefly indicate how this can be done.

In this paper we follow a top-down approach. We start in section 2 by presenting the abstract perturbation theory for dual semigroups and then we formulate the principle of linearized stability which says that, under appropriate assumptions, local (in)stability of a steady state is completely determined by the spectral properties of the generator of the linearized semigroup. Under the extra assumption of finite dimensional range of the nonlinear perturbation G, we derive a characteristic equation, the roots of which are the spectral values of the generator of the linearized semigroup. We then give results on the stable, unstable, and center manifolds and on Hopf bifurcation. The results of section 2 are either known or slight modifications of known results. In section 3 we then specialize to the system (DE), (IC) and the associated unperturbed semigroup T_0 defined by (1.7) and verify that the assumptions made in section 2 indeed hold true. Models of structured populations often lead to delay equations coupled with delay differential equations. In section 4 we therefore consider such coupled systems. In section 5 we illustrate our theoretical results by two examples from population dynamics. We conclude in section 6 by relating our results to results by other authors and by discussing directions for future work.

2. Lipschitz perturbations in the sun-reflexive case.

We start by briefly recalling the basic facts about dual semigroups. The books [4, 42, 47] are good general references, as are Chapter III and Appendix II of [23]. The theory of nonlinear Lipschitz continuous perturbations of generators of dual semigroups was first introduced in [11], where the principle of linearized stability was proved following [19]. The treatment of the stable, unstable, and center manifolds and of Hopf bifurcation follows [23].

2.1. Sun-reflexive dual semigroups.

Let X be a real Banach space and $T_0 := \{T_0(t)\}_{t\geq 0}$ be a strongly continuous (i.e., the orbit $t \mapsto T_0(t)\varphi$ is continuous with respect to the norm topology on X for all initial values $\varphi \in X$) semigroup of bounded linear operators on X with infinitesimal generator A_0. Then $T_0^* := \{T_0^*(t)\}_{t\geq 0}$, where $T_0^*(t) : X^* \to X^*$ is the adjoint of $T_0(t)$, is a semigroup on the dual space X^* of X. T_0^* is called the *adjoint* or *dual* semigroup of T_0. If X is not reflexive, then T^* need not be strongly continuous. All one can say in general is that the orbits are continuous with respect to the weak* topology of X. At the level of generators this is reflected in the fact that the adjoint A_0^* of A_0 need not have dense domain and that A_0^* is the weak*-generator of T_0^*.

The maximal invariant subspace of X^* on which T_0^* is strongly continuous is denoted by $X^\odot$, that is,

$$X^\odot := \left\{\varphi^* \in X^* : \lim_{t\downarrow 0} \|T_0^*(t)\varphi^* - \varphi^*\| = 0\right\}. \tag{2.1}$$

Note that this so-called sun-subspace depends on the dynamical system one considers on the original space. It is known that

$$X^\odot = \overline{D(A_0^*)}, \tag{2.2}$$

where the bar denotes closure with respect to the norm topology of X^*. The operators $T_0^*(t)$, $t \geq 0$, leave $X^\odot$ invariant, and the restriction $T_0^\odot(t) := T_0^*(t)|_{X^\odot}$ of T_0^* to $X^\odot$ is a strongly continuous semigroup and its generator $A_0^\odot$ is the part of A_0^* in $X^\odot$; that is,

$$\mathcal{D}(A_0^\odot) := \{\varphi^\odot \in \mathcal{D}(A_0^*) :\ A_0^*\varphi^\odot \in X^\odot\}, \tag{2.3}$$

$$A_0^\odot\varphi^\odot := A_0^*\varphi^\odot. \tag{2.4}$$

We now have on $X^{\odot}$ exactly the same situation as we had on X at the outset. So in self-explanatory notation we obtain $X^{\odot *}$, $T_0^{\odot *}$, $A_0^{\odot *}$ and $X^{\odot\odot}$, $T_0^{\odot\odot}$, $A_0^{\odot\odot}$.

As usual, we denote the duality pairing between a Banach space X and its normed dual X^* by $\langle \cdot, \cdot \rangle$; that is, for $\varphi \in X$, $\varphi^* \in X^*$ we write $\langle \varphi, \varphi^* \rangle$ instead of $\varphi^*(\varphi)$. The formula

$$\langle \varphi^{\odot}, j\varphi \rangle = \langle \varphi, \varphi^{\odot} \rangle, \quad \varphi \in X, \ \varphi^{\odot} \in X^{\odot} \tag{2.5}$$

defines an embedding j of X into $X^{\odot *}$, the range of which lies in $X^{\odot\odot}$. Moreover, one has $T_0^{\odot *}(t)j = jT_0(t)$ for $t \geq 0$.

DEFINITION 2.1. *A Banach space X is called* sun-reflexive *with respect to the strongly continuous linear semigroup T_0 if*

$$j(X) = X^{\odot\odot}.$$

From now on we shall always assume that X is sun-reflexive with respect to the unperturbed semigroup T_0.

2.2. Lipschitz perturbations and the nonlinear semigroup. Let $G : X \to X^{\odot *}$ be a nonlinear operator. The initial value problem

$$\frac{dju}{dt}(t) = A_0^{\odot *} ju(t) + G(u(t)), \quad t > 0, \tag{2.6}$$

$$u(0) = \varphi, \tag{2.7}$$

where u is an X-valued function, can be formally integrated to yield the abstract integral equation

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

but we have to verify that the integral does indeed belong to $j(X)$.

The integral in (AIE) is to be interpreted in the weak*-sense. More precisely, if Z is a Banach space and $f : [a,b] \to Z^*$ is weakly*-continuous, then $\int_a^b f(t)dt$ is defined as the continuous linear functional on Z which takes $z \in Z$ to $\int_a^b \langle z, f(t) \rangle dt$. Note that $\int_a^b f(t)dt$ is an element of Z^*. For weak* integrals of the form

$$v(t) = \int_0^t T_0^{\odot *}(t-s)f(s)ds,$$

we have the following desirable result.

PROPOSITION 2.2 (see [9, Theorem 3.2]). *If f is weakly*-continuous, then v is weakly*-continuous with values in $X^{\odot *}$. If f is norm continuous, then v is norm continuous as well and takes values in $X^{\odot\odot}$.*

We now consider (AIE). If G is globally Lipschitz continuous, then standard contraction mapping arguments yield existence and uniqueness of a solution $u(\cdot\,;\varphi) : \mathbf{R}_+ \to X$ of (AIE) for every $\varphi \in X$. The formula

$$\Sigma(t)\varphi := u(t;\varphi), \quad t \geq 0, \ \varphi \in X, \tag{2.8}$$

defines a strongly continuous nonlinear semigroup Σ on X. The generator of Σ, which we denote by C, is defined exactly as in the linear case: Its domain $\mathcal{D}(C)$ is the set of all $\varphi \in X$ for which the limit $\lim_{t\downarrow 0}(\Sigma(t)\varphi - \varphi)/t$ exists in the norm topology of X and $C\varphi$ is equal to this limit. The weak* generator $C^\times$ of Σ is defined as follows: $\varphi \in X$ belongs to $\mathcal{D}(C^\times)$ if $(j\Sigma(t)\varphi - j\varphi)/t$ converges to some $\varphi^{\odot *} \in X^{\odot *}$ as $t \downarrow 0$ and in this case $C^\times\varphi = \varphi^{\odot *}$.

Theorem 2.3 (see [11, Theorems 3.2–3.6]).

(a) *$j\left(\mathcal{D}(C^\times)\right) = \mathcal{D}(A_0^{\odot *})$ and $C^\times\varphi = A_0^{\odot *}j\varphi + G(\varphi)$.*

(b) *C is the part of $C^\times$ in X, that is,*

$$\mathcal{D}(C) = \left\{\varphi \in X : \varphi \in \mathcal{D}(C^\times),\ C^\times\varphi \in j(X)\right\},$$

$$C\varphi = j^{-1}\left(C^\times\varphi\right).$$

(c) *If $\varphi \in \mathcal{D}(C)$ and if G is continuously Fréchet differentiable, then $t \mapsto u(t;\varphi) = \Sigma(t)\varphi$ is continuously differentiable and*

$$\frac{d}{dt}u(t;\varphi) = j^{-1}\left(A_0^{\odot *}ju(t;\varphi) + G(u(t;\varphi))\right).$$

2.3. Linearization around a steady state. In what follows we assume that the nonlinear operator $G : X \to X^{\odot *}$ is continuously Fréchet differentiable.

Assume that $\overline{\varphi} \in X$ is a steady state of the nonlinear dynamical system; that is,

$$\Sigma(t)\overline{\varphi} = \overline{\varphi} \tag{2.9}$$

for all $t \geq 0$. Equivalently, $j\overline{\varphi} \in \mathcal{D}(A_0^{\odot *})$ and

$$A_0^{\odot *}j\overline{\varphi} + G(\overline{\varphi}) = 0; \tag{2.10}$$

cf. Theorem 2.3(c). Because $G : X \to X^{\odot *}$ is Fréchet differentiable at $\overline{\varphi}$, its Fréchet derivative $B := G'(\overline{\varphi})$ is a bounded linear operator from X to $X^{\odot *}$. Formal linearization of (AIE) yields the following linear abstract integral equation:

$$T(t)\varphi = T_0(t)\varphi + j^{-1}\left(\int_0^t T_0^{\odot *}(t-\tau)BT(\tau)\varphi d\tau\right). \tag{LAIE}$$

For such equations the following result is known.

Theorem 2.4 (see [9]). *The linear abstract integral equation* (LAIE) *uniquely defines a strongly continuous semigroup $T = \{T(t)\}_{t\geq 0}$ of bounded linear operators with generator A given by*

$$\mathcal{D}(A) = \{\varphi \in X : j\varphi \in \mathcal{D}(A_0^{\odot *}), A_0^{\odot *}j\varphi + B\varphi \in j(X)\},$$

$$A\varphi = j^{-1}(A_0^{\odot *}j\varphi + B\varphi).$$

That the formal linearization yields the desired result is the content of the following theorem.

Theorem 2.5 (see [11]). *Let* (2.9) *hold and assume that the nonlinear operator $G : X \to X^{\odot *}$ 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

$$\mathcal{D}(A) = \{\varphi \in X : j\varphi \in \mathcal{D}(A_0^{\odot *}), A_0^{\odot *}j\varphi + G'(\overline{\varphi})\varphi \in j(X)\},$$

$$A\varphi = j^{-1}(A_0^{\odot *}j\varphi + G'(\overline{\varphi})\varphi).$$

Moreover, for every $\varphi \in X$, $T(t)\varphi$ is the unique solution of (LAIE) *with $B = G'(\overline{\varphi})$.*

2.4. Eventual compactness and spectral analysis of the linearized semigroup. In subsection 2.6 we shall deal with criteria for the stability of a steady state. As is well known from the theory of ordinary differential equations (ODEs), *spectral analysis* of the linearized system is a most efficient tool for investigating stability. Therefore we shall in this subsection analyze the spectrum of the generator A of the semigroup T defined by (LAIE).

Our original nonlinear problem is meaningful only for *real* Banach spaces, whereas spectral analysis requires complex scalars. We therefore have to complexify X before doing spectral analysis. In the infinite dimensional case and, in particular, in our sun-star-framework, this is not a trivial task. We shall, however, omit the details because they can all be found in [23, section III.7].

As usual, we denote the resolvent set and the spectrum of a linear operator L by $\varrho(L)$ and $\sigma(L)$, respectively. The point spectrum of L, that is, the set of eigenvalues of L, is denoted by $P\sigma(L)$. The identity operator is denoted by E (to follow the tradition of Hilbert [14, formula (8), p. 5] and to avoid confusion with the input I of (1.17)), and Laplace transformation is denoted by $\widehat{\ }$:

$$\widehat{f}(\lambda) = \int_0^\infty e^{-\lambda t} f(t)dt. \tag{2.12}$$

$R(\lambda, L)$ denotes the *resolvent operator* of L:

$$R(\lambda, L) := (\lambda E - L)^{-1}, \quad \lambda \in \varrho(L). \tag{2.13}$$

Recall that $\lambda \mapsto R(\lambda, L)$ is a holomorphic operator-valued function on $\varrho(L)$. As for complex valued functions, an operator-valued function is *entire* if it is holomorphic in the whole complex plane.

The *growth bound* $\omega_0(T)$ of a semigroup T is defined by

$$\omega_0(T) = \inf\{\omega \in \mathbf{R} : \exists M_\omega \geq 1 \text{ such that } \|T(t)\| \leq M_\omega e^{\omega t} \text{ for all } t \geq 0\},$$

and the *spectral bound* $s(A)$ of its generator A is defined by

$$s(A) = \sup\{\operatorname{Re}\lambda : \lambda \in \sigma(A)\}.$$

One has $\sigma(A) = \sigma(A^*) = \sigma(A^\odot) = \sigma(A^{\odot *})$, $s(A) = s(A^*) = s(A^\odot) = s(A^{\odot *})$, and $\omega_0(T) = \omega_0(T^*) = \omega_0(T^\odot) = \omega_0(T^{\odot *})$ [26, Proposition 2.18, p. 262].

We start by characterizing the part of the point spectrum which belongs to $\varrho(A_0)$.

PROPOSITION 2.6. *Let A be the generator of the semigroup T defined by* (LAIE); *cf. Theorem 2.4. Then $\lambda \in \varrho(A_0)$ is an eigenvalue of A if and only if 1 is an eigenvalue of $j^{-1}R(\lambda, A_0^{\odot *})B$ and the corresponding eigenvectors are the same.*

Proof. Let $\psi \in X$. Using Theorem 2.4 we see that in the following sequence of identities, each implies both the preceding and the next one:

$$j^{-1}R(\lambda, A_0^{\odot *})B\psi = \psi,$$

$$j\psi \in \mathcal{D}(A_0^{\odot *}) \quad \text{and} \quad B\psi = \left(\lambda E - A_0^{\odot *}\right) j\psi,$$

$$j\psi \in \mathcal{D}(A_0^{\odot *}) \quad \text{and} \quad A_0^{\odot *} j\psi + B\psi = \lambda j\psi,$$

$$j\psi \in \mathcal{D}(A_0^{\odot *}) \quad \text{and} \quad j^{-1}\left(A_0^{\odot *} j\psi + B\psi\right) = \lambda\psi,$$

$$\psi \in \mathcal{D}(A) \quad \text{and} \quad A\psi = \lambda\psi. \qquad \square$$

If the semigroup T is *eventually compact*, that is, if the operators $T(t)$ are compact for all t greater than some $t_0 \geq 0$, then spectral analysis becomes as easy as one can possibly expect from an infinite dimensional system.

THEOREM 2.7. *Let A generate an eventually compact C_0-semigroup T on the Banach space X. Then*

$$\sigma(A) = P\sigma(A),$$

$$s(A) = \omega_0(T),$$

and every $\lambda \in \sigma(A)$ is a pole of the resolvent $R(\lambda, A)$ of finite algebraic multiplicity. Every right half-plane $\{\lambda \in \mathbf{C} : \alpha \leq \operatorname{Re}\lambda\}$ $(-\infty < \alpha)$ contains at most finitely many eigenvalues of A.

For a proof of this well-known result, see, e.g., [2, Theorem 2.1, p. 209].

Next we give a criterion for the eventual compactness of the perturbed semigroup which is easy to check and which applies to all our applications.

THEOREM 2.8. *Let T_0 be an eventually compact C_0-semigroup and let $B : X \to X^{\odot *}$ be compact. Then the C_0-semigroup T defined by* (LAIE) *is eventually compact.*

The corresponding result for the case in which B maps X into X is known [26, Proposition 1.14, p. 166], but Theorem 2.8 does not seem to have been stated in the literature yet. We therefore give a complete proof in the appendix.

2.5. Perturbations with finite dimensional range. If, as in the case of the delay problem (DE), (IC), the nonlinear perturbation G has finite dimensional range in $X^{\odot *}$, much of the analysis becomes considerably simpler, in fact, essentially finite dimensional. We therefore have a closer look at this special case. So let $G : X \to X^{\odot *}$ have the form

$$G(\varphi) = \sum_{i=1}^{N} F_i(\varphi) r_i^{\odot *}, \quad \varphi \in X, \tag{2.14}$$

where $F = (F_1, F_2, \ldots, F_N)$ is a mapping from X to $\mathbf{R}^N$ and $\{r_1^{\odot *}, r_2^{\odot *}, \ldots, r_N^{\odot *}\}$ is a linearly independent set in $X^{\odot *}$.

Note. In what follows we shall use the letter j both as a summation index and, as before, to denote the canonical embedding of X into $X^{\odot *}$, sometimes even in the same formula. This should not lead to any misunderstanding.

Clearly G is Fréchet differentiable at $\overline{\varphi}$ if and only if F is Fréchet differentiable at $\overline{\varphi}$, which is the case if and only if all the components F_i are Fréchet differentiable at $\overline{\varphi}$. So when G is Fréchet differentiable at $\overline{\varphi}$, there exist elements $r_1^*, r_2^*, \ldots, r_N^*$ of X^* such that the derivative $G'(\overline{\varphi})$ is the linear operator $B : X \to X^{\odot *}$ given by

$$B\varphi = \sum_{i=1}^{N} \langle \varphi, r_i^* \rangle r_i^{\odot *}, \quad \varphi \in X. \tag{2.15}$$

In order to exploit the finite dimensional structure of the perturbation we define

$$r_i(\lambda) = j^{-1} R(\lambda, A_0^{\odot *}) r_i^{\odot *}, \quad \lambda \in \varrho(A_0), \tag{2.16}$$

$$r_i^{\odot}(\lambda) = R(\lambda, A_0^*) r_i^*, \quad \lambda \in \varrho(A_0), \tag{2.17}$$

and let $M(\lambda)$ be the matrix with entries

$$M_{ij}(\lambda) = \langle r_j(\lambda), r_i^* \rangle, \quad \lambda \in \varrho(A_0). \tag{2.18}$$

Note that the matrix-valued function M is defined in $\varrho(A_0)$ only. When the real part of λ is greater than the growth bound of T_0, we can express $r_i(\lambda)$ and $r_i^{\odot}(\lambda)$ using the Laplace transform representation of the resolvent [26, Theorem 1.10, p. 55]:

$$r_i(\lambda) = j^{-1} \int_0^\infty e^{-\lambda t} T_0^{\odot *}(t) r_i^{\odot *} dt, \quad \operatorname{Re} \lambda > \omega_0(T_0), \tag{2.19}$$

$$r_i^{\odot}(\lambda) = \int_0^\infty e^{-\lambda t} T_0^*(t) r_i^* dt, \quad \operatorname{Re} \lambda > \omega_0(T_0). \tag{2.20}$$

We start with a few lemmas.

LEMMA 2.9. *Let M be the matrix-valued function defined by* (2.18). *Then*

$$M_{ij}(\lambda) = \left\langle r_i^{\odot}(\lambda), r_j^{\odot *} \right\rangle, \quad \lambda \in \varrho(A_0). \tag{2.21}$$

Proof. We first prove the claim for $\operatorname{Re} \lambda > \omega_0(T_0)$ using the representations (2.19) and (2.20). If $r_i^* \in X^{\odot}$, the equality of the right-hand sides of (2.18) and (2.21) is clear from the definition of the weak*-integral. Next we approximate r_i^* by

$$\varphi_s^{\odot} = \frac{1}{s} \int_0^s T_0^*(\tau) r_i^* d\tau, \quad s > 0.$$

It follows from Proposition 2.2 (just interchange the roles of X and $X^{\odot}$) that $\varphi_s^{\odot} \in X^{\odot}$ for all $s > 0$. By the observation made above, one has

$$\left\langle j^{-1} \int_0^\infty e^{-\lambda t} T_0^{\odot *}(t) r_i^{\odot *} dt, \varphi_s^{\odot} \right\rangle = \left\langle \int_0^\infty e^{-\lambda t} T_0^{\odot}(t) \varphi_s^{\odot} dt, r_i^{\odot *} \right\rangle \tag{2.22}$$

for all $s > 0$. A straightforward calculation (see the proof of Lemma 2.17 in [23, p. 61] for a very similar case) shows that the left-hand side of (2.22) converges to (2.18) and that the right-hand side of (2.22) converges to the right-hand side of (2.21). This proves the assertion for the case $\operatorname{Re} \lambda > \omega_0(T_0)$. The general case follows from the resolvent identity. ∎

When B has finite dimensional range we get a more detailed description of the point spectrum of A than we do in Proposition 2.6.

LEMMA 2.10. *Let A be the generator of the semigroup T defined by* (LAIE) *and assume that B has the form* (2.15). *If $\lambda \in \varrho(A_0)$ and $\psi \in X$, then*

$$A\psi = \lambda \psi \tag{2.23}$$

if and only if

$$\psi = \sum_{i=1}^N c_i r_i(\lambda), \tag{2.24}$$

where the coefficients c_i are the components of a vector c satisfying

$$M(\lambda) c = c \tag{2.25}$$

and $M(\lambda)$ is the matrix defined by (2.18).

Proof. By Proposition 2.6, $A\psi = \psi$ if and only if

$$j^{-1}R(\lambda, A_0^{\odot *})B\psi = \psi. \tag{2.26}$$

Because the vectors $r_1^{\odot *}, r_2^{\odot *}, \ldots, r_N^{\odot *}$ are linearly independent and $j^{-1}R(\lambda, A_0^{\odot *})$ is one-to-one, the definition (2.16) shows that also the vectors $r_1(\lambda), r_2(\lambda), \ldots, r_N(\lambda)$ are linearly independent. Equation (2.26) shows that ψ belongs to the subspace spanned by the vectors $r_i(\lambda)$, $i = 1, 2, \ldots, N$; that is, ψ is of the form (2.24). Substituting (2.24) into (2.26), one obtains (2.25). ∎

The following dual version of Lemma 2.10 is proved analogously.

LEMMA 2.11. *Let A be the generator of the semigroup T defined by* (LAIE) *and assume that B has the form* (2.15). *If $\lambda \in \varrho(A_0)$ and $\psi^\odot \in X^\odot$, then*

$$A^*\psi^\odot = \lambda\psi^\odot \tag{2.27}$$

if and only if

$$\psi^\odot = \sum_{i=1}^{N} d_i r_i^\odot(\lambda), \tag{2.28}$$

where the coefficients d_i are the components of a row vector d satisfying

$$dM(\lambda) = d \tag{2.29}$$

and $M(\lambda)$ is the matrix defined by (2.18).

LEMMA 2.12. *The mapping $\lambda \mapsto \langle r_j(\lambda), r_i^*\rangle$ is holomorphic in $\varrho(A_0)$ and*

$$\frac{d}{d\lambda}\langle r_j(\lambda), r_i^*\rangle = -\left\langle r_j(\lambda), r_i^\odot(\lambda)\right\rangle, \quad \lambda \in \varrho(A_0). \tag{2.30}$$

Proof. Using the resolvent identity, one finds that

$$\begin{aligned}\frac{1}{\lambda - \mu}\left(\langle r_j(\lambda), r_i^*\rangle - \langle r_j(\mu), r_i^*\rangle\right) &= -\left\langle j^{-1}R(\lambda, A_0^{\odot *})R(\mu, A_0^{\odot *})r_j^{\odot *}, r_i^*\right\rangle \\ &= -\left\langle j^{-1}R(\mu, A_0^{\odot *})r_j^{\odot *}, R(\lambda, A_0^*)r_i^*\right\rangle \\ &= -\left\langle r_j(\mu), r_i^\odot(\lambda)\right\rangle,\end{aligned}$$

which proves the assertion. ∎

As a direct consequence of the three preceding lemmas we obtain the following result.

COROLLARY 2.13. *The matrix-valued function $\lambda \mapsto M(\lambda)$ is holomorphic in $\varrho(A_0)$, and if λ is an eigenvalue of A with eigenvector ψ and adjoint eigenvector $\psi^\odot$, then*

$$\left\langle \psi, \psi^\odot\right\rangle = -dM'(\lambda)c, \quad \lambda \in \varrho(A_0), \tag{2.31}$$

where c and d are as described in Lemmas 2.10 *and* 2.11, *respectively.*

Corollary 2.13 provides a convenient criterion for the simplicity of an eigenvalue, which we shall use in the context of the Hopf bifurcation theorem to be treated in subsection 2.8. In the present subsection we shall show that when B has finite dimensional range, there exists a so-called characteristic equation, the roots of which are the eigenvalues of the generator of the perturbed semigroup. It turns out that the order of λ as a root of the characteristic equation equals the algebraic multiplicity of λ as an eigenvalue of A. An easy way to show this is to use the theory of Weinstein–Aronszajn determinants; see [43, section IV.6] for an account of the general theory and [22] for an application to perturbed dual semigroups. Before we can present the Weinstein–Aronszajn formula we have to define the multiplicity functions for closed operators and meromorphic functions.

Let L be a closed operator in a Banach space. For every isolated point λ of $\sigma(L)$ we denote the spectral projection onto the corresponding generalized eigenspace by P_λ. The *multiplicity function* $\widetilde{\nu}(\lambda, L)$ of L is defined as

$$\widetilde{\nu}(\lambda, L) = \begin{cases} 0 & \text{if } \lambda \in \varrho(L), \\ \dim \mathcal{R}(P_\lambda) & \text{if } \lambda \text{ is an isolated point of } \sigma(L), \\ \infty & \text{in all other cases.} \end{cases} \tag{2.32}$$

The multiplicity function of a (numerical) meromorphic function f is defined as

$$\nu(\lambda, f) = \begin{cases} k & \text{if } \lambda \text{ is a zero of order } k \text{ of } f, \\ -k & \text{if } \lambda \text{ is a pole of order } k \text{ of } f, \\ 0 & \text{otherwise.} \end{cases} \tag{2.33}$$

THEOREM 2.14 (Weinstein–Aronszajn formula). *Let A be the generator of the semigroup T defined by* (LAIE), *assume that B has the form* (2.15), *and let $M(\lambda)$ be the matrix-valued function defined in* (2.18). *Then*

$$\widetilde{\nu}(\lambda, A) = \widetilde{\nu}(\lambda, A_0) + \nu\left(\lambda, \det\left(E - M(\lambda)\right)\right). \tag{2.34}$$

Proof. Because B has finite dimensional range one can unambiguously define the so-called Weinstein–Aronszajn determinant $\det\left(E - BR\left(\lambda, A_0^{\odot *}\right)\right)$ as the determinant of the restriction of $E - BR\left(\lambda, A_0^{\odot *}\right)$ to $\mathcal{R}(B)$. The definition of M together with Lemma 2.9 shows that

$$\det\left(E - BR\left(\lambda, A_0^{\odot *}\right)\right) = \det\left(E - M(\lambda)\right).$$

The Weinstein–Aronszajn formula [43, Theorem IV.6.2] now yields

$$\widetilde{\nu}(\lambda, A^{\odot *}) = \widetilde{\nu}(\lambda, A_0^{\odot *}) + \nu\left(\lambda, \det\left(E - M(\lambda)\right)\right). \tag{2.35}$$

But A_0 (resp., A) is the part of $A_0^{\odot *}$ (resp., $A^{\odot *}$) in $j(X)$, and hence it follows from [26, Lemma 1.15, p. 245 and Proposition 2.17, p. 261] that

$$\widetilde{\nu}(\lambda, A_0^{\odot *}) = \widetilde{\nu}(\lambda, A_0),$$

$$\widetilde{\nu}(\lambda, A^{\odot *}) = \widetilde{\nu}(\lambda, A),$$

from which the conclusion (2.34) follows. ∎

We are now ready to prove the following theorem.

THEOREM 2.15. *Let A be the generator of the semigroup T defined by* (LAIE). *Suppose that B has the form* (2.15) *and let M be the corresponding matrix-valued function defined by* (2.18). *Then $\lambda \in \varrho(A_0)$ is in $\sigma(A)$ if and only if*

$$\det(E - M(\lambda)) = 0, \tag{2.36}$$

where E denotes the $N \times N$ identity matrix. Moreover, when this is the case, λ belongs to $P\sigma(A)$ and the algebraic multiplicity of λ equals the order of λ as a root of (2.36).

In particular, if $\sigma(A_0) = \emptyset$, then

$$\sigma(A) = P\sigma(A) = \{\lambda \in \mathbf{C} : \det(E - M(\lambda)) = 0\}. \tag{2.37}$$

Proof. Taking the Laplace transform of (LAIE), one obtains

$$R(\lambda, A) = R(\lambda, A_0) + j^{-1} R(\lambda, A_0^{\odot *}) B R(\lambda, A)$$

or

$$\left(E - j^{-1} R(\lambda, A_0^{\odot *}) B\right) R(\lambda, A) = R(\lambda, A_0). \tag{2.38}$$

From (2.38) we deduce that if $\lambda \in \varrho(A_0)$, then $\lambda \in \sigma(A)$ if and only if

$$E - j^{-1} R(\lambda, A_0^{\odot *}) B$$

is not invertible. But because $j^{-1} R(\lambda, A_0^{\odot *}) B$ is a bounded linear operator $X \to X$ with finite dimensional range, this is the case if and only if 1 is an eigenvalue of $j^{-1} R(\lambda, A_0^{\odot *}) B$. According to Proposition 2.6, this in turn is equivalent to λ being an eigenvalue of A, which by Lemma 2.10 is equivalent to 1 being an eigenvalue of $M(\lambda)$. This shows that $\lambda \in \sigma(A)$ if and only if λ is a root of (2.36) and that then $\lambda \in P\sigma(A)$.

Since $\widetilde{\nu}(\lambda, A_0)$ is zero, the assertion concerning the multiplicity of λ follows from Theorem 2.14.

The final assertion is obvious, because if $\sigma(A_0)$ is empty, then the basic assumption $\lambda \in \varrho(A_0)$ is automatically satisfied. $\square$

Equation (2.36) is called the *characteristic equation*.

Remark 2.16. It was shown in [9, Lemma 5.1] that there exists a matrix-valued function $k \in L^\infty_{\text{loc}}(\mathbf{R}_+, \mathbf{R}^{N \times N})$ such that

$$\left\langle j^{-1} \left(\int_0^t T_0^{\odot *}(t-\tau) r_j^{\odot *} \eta(\tau) d\tau \right), r_i^* \right\rangle = \int_0^t k_{ij}(t-\tau) \eta(\tau) d\tau$$

for all $\eta \in L^1_{\text{loc}}(\mathbf{R}_+)$. From this it follows easily that

$$\widehat{k}(\lambda) = M(\lambda), \quad \lambda \in \varrho(A_0),$$

where M is the matrix-valued function defined by (2.18). The characteristic equation can thus be rewritten as

$$\det\left(E - \widehat{k}(\lambda)\right) = 0. \tag{2.39}$$

In subsection 3.4 we shall compute the matrix k explicitly in the concrete case connected to (DE).

Using properties of the Laplace transform and holomorphic functions (in particular, the Riemann–Lebesgue lemma and the fact that the zeros of holomorphic functions have no limit points) it is possible to prove directly (in the case $\sigma(A_0) = \emptyset$) that there are only finitely many eigenvalues in each right half-plane. But because we obtain this result from Theorem 2.7 in all our applications, we have refrained from stating it in Theorem 2.15.

As the proof of Theorem 2.15 shows, the existence of a characteristic equation depends on two facts: the analyticity in the whole complex plane of the resolvent of the generator A_0 of the unperturbed semigroup and the finite dimensionality of the range of the perturbation. We shall later encounter applications where $R(\lambda, A_0)$ has a simple pole at the origin. Anticipating this situation, we next show that the corresponding singularity of $R(\lambda, A)$ is removable and that we still get a characteristic equation.

THEOREM 2.17. *Let B be given by* (2.15) *and assume that*

$$R(\lambda, A_0^{\odot *}) = \frac{1}{\lambda} P H_1(\lambda) + (E - P) H_2(\lambda), \tag{2.40}$$

where $P : X^{\odot *} \to X^{\odot *}$ is a projection with finite dimensional range in $j(X)$, H_1 and H_2 are entire functions with values in $\mathcal{L}(X^{\odot *})$, and the range of $H_2(\lambda)$ is in $j(X)$. Then $\sigma(A) = P\sigma(A)$, and there exists an entire matrix-valued function Δ such that $\lambda \in \sigma(A)$ if and only if

$$\det \Delta(\lambda) = 0. \tag{2.41}$$

Proof. The assumption (2.40) implies that

$$j^{-1} R(\lambda, A_0^{\odot *}) B = \left(E - j^{-1} P j + \frac{1}{\lambda} j^{-1} P j \right) K(\lambda) \tag{2.42}$$

for the entire function K defined by

$$K(\lambda)\varphi = \sum_{i=1}^{N} \langle \varphi, r_i^* \rangle \, j^{-1} \left(P H_1(\lambda) + (E - P) H_2(\lambda) \right) r_i^{\odot *}$$

with values in the subspace of finite rank operators of $\mathcal{L}(X)$. It follows (cf. (2.38)) that

$$\begin{aligned} &\left(E - \left(E - j^{-1} P j + \frac{1}{\lambda} j^{-1} P j \right) K(\lambda) \right) R(\lambda, A) \\ &\qquad = j^{-1} \left(\frac{1}{\lambda} P H_1(\lambda) + (E - P) H_2(\lambda) \right) j. \end{aligned} \tag{2.43}$$

If one multiplies (2.43) by $E - j^{-1} P j + \lambda j^{-1} P j$, one obtains

$$(E - j^{-1} P j + \lambda j^{-1} P j - K(\lambda)) R(\lambda, A) = j^{-1} \left(P H_1(\lambda) + (E - P) H_2(\lambda) \right) j. \tag{2.44}$$

Because the right-hand side of (2.44) is entire, $R(\lambda, A)$ is holomorphic everywhere except at the points where $(E - j^{-1} P j + \lambda j^{-1} P j - K(\lambda))$ is not invertible. Because $j^{-1} P j - \lambda j^{-1} P j + K(\lambda)$ has finite dimensional range and is everywhere holomorphic, it follows as in the proof of Theorem 2.15 that there is an entire matrix $\Delta(\lambda)$ such that $(E - j^{-1} P j + \lambda j^{-1} P j - K(\lambda))$ is not invertible if and only if $\Delta(\lambda)$ is not invertible, that is, if and only if (2.41) holds. $\square$

2.6. Linearized stability. Recall that a steady state $\overline{\varphi}$ of Σ is (locally) *stable* if for every $\varepsilon > 0$ there exists a $\delta > 0$ such that

$$\|\Sigma(t)\varphi - \overline{\varphi}\| \leq \varepsilon \quad \text{for all } t \geq 0$$

whenever $\|\varphi - \overline{\varphi}\| \leq \delta$. If $\overline{\varphi}$ is not stable, it is *unstable*. It is (locally) *exponentially stable* if there exist numbers $\delta > 0,\ K > 0,\ \alpha > 0$ such that

$$\|\Sigma(t)\varphi - \overline{\varphi}\| \leq K e^{-\alpha t}, \quad t \geq 0,$$

for all φ with $\|\varphi - \overline{\varphi}\| \leq \delta$.

The next result is called the *principle of linearized stability*. It has two parts. The first states that if the growth bound of the linearized semigroup is negative, then the steady state is exponentially stable. The second part states that if the generator of the linearized semigroup has at least one eigenvalue of finite multiplicity with positive real part, then the steady state is not stable.

THEOREM 2.18 (see [19], [11, Theorems 4.2 and 4.3], [23, Corollary 5.12]). *Let Σ be a strongly continuous nonlinear semigroup. Let $\overline{\varphi}$ be a steady state of Σ and assume that for each $t \geq 0$, $\Sigma(t)$ has a (uniform) Fréchet derivative $T(t)$ at $\overline{\varphi}$. Let A be the infinitesimal generator of T. Assume further that X admits a decomposition*

$$X = X_- \oplus X_+$$

into two $T(t)$-invariant subspaces X_- and X_+ such that

(i) *X_+ is finite dimensional,*

(ii) *the restriction of $T(t)$ to X_- converges exponentially to 0 as $t \to \infty$.*

Then $\overline{\varphi}$ is

(a) *(locally) exponentially stable if* $\operatorname{Re}\lambda < 0$ *for all $\lambda \in \sigma(A\big|_{X_+})$,*

(b) *unstable if there exists a $\lambda \in \sigma(A\big|_{X_+})$ with* $\operatorname{Re}\lambda > 0$.

Note that if $\omega_0(T) < 0$, then (i) and (ii) are satisfied with X_+ equal to the trivial subspace $\{0\}$, and hence $\overline{\varphi}$ is exponentially stable because $\sigma(A\big|_{X_+})$ is empty.

Theorem 2.5 shows that the differentiability assumption of Theorem 2.18 is indeed satisfied for the semigroup Σ generated by the abstract integral equation (AIE).

When applied to the nonlinear semigroup Σ generated by the abstract integral equation (AIE), Theorem 2.18 becomes particularly simple to apply if T_0 is eventually compact and $G'(\overline{\varphi})$ is compact (in particular if G has finite dimensional range). Indeed, Theorem 2.7 immediately implies the following corollary.

COROLLARY 2.19. *Assume that $G : X \to X^{\odot *}$ is continuously Fréchet differentiable. Let Σ be the nonlinear semigroup "generated" by* (AIE) *(i.e., defined through* (2.8)*) and let A be the generator of the linearized semigroup T as in Theorem* 2.5. *Let $\overline{\varphi}$ be a steady state of Σ.*

If T_0 is eventually compact and if $G'(\overline{\varphi})$ is compact, then $\overline{\varphi}$ is locally exponentially stable if all $\lambda \in \sigma(A)$ have real part less than zero, whereas if there exists at least one $\lambda \in \sigma(A)$ with positive real part, then $\overline{\varphi}$ is unstable.

Proof. By Theorem 2.8 T is eventually compact, and hence the growth bound equals the spectral bound (Theorem 2.7). Thus, if all $\lambda \in \sigma(A) = P\sigma(A)$ have negative real part, then $\omega_0(T) < 0$ and, as noted after Theorem 2.18, $\overline{\varphi}$ is exponentially stable. If there exists an eigenvalue with positive real part, there exist finitely many eigenvalues with positive real part, and they all have generalized eigenspaces of finite dimension (Theorem 2.7). Therefore there exists a decomposition as in Theorem 2.18

with X_+ finite dimensional and a $\lambda \in \sigma(A\big|_{X_+})$ with $\operatorname{Re}\lambda > 0$. An application of Theorem 2.18 completes the proof. ∎

We close this section by applying a version of the argument principle [52, Theorem 10.43(a)], also known as Nyquist's theorem, to derive a very convenient criterion for the (in)stability of steady states in the case where the perturbation has finite dimensional range and we have a characteristic equation. Nyquist's theorem states that if the matrix-valued function k belongs to $L^1(\mathbf{R}_+)$ and satisfies $\det\big(E - \widehat{k}(i\omega)\big) \neq 0$ for all $\omega \in \mathbf{R}$, then the number of zeros of $\det\big(E - \widehat{k}(\lambda)\big)$ in the open right half-plane $\operatorname{Re}\lambda > 0$, counted according to their multiplicities, equals the index $\operatorname{Ind}_\Gamma(0)$ of the curve $\Gamma : \omega \mapsto \det\big(E - \widehat{k}(i\omega)\big)$, where ω runs from $+\infty$ to $-\infty$ [29, Theorem 6.3, p. 61]. Recall the geometrical interpretation of the index $\operatorname{Ind}_\Gamma(0)$: it is the number of times the curve Γ winds counterclockwise around the origin as ω runs from $+\infty$ to $-\infty$.

COROLLARY 2.20. *Assume in addition to the hypotheses of Corollary* 2.19 *that* T_0 *is nilpotent and that* G *has finite dimensional range. Let* $M(\lambda) = \widehat{k}(\lambda)$ *be the matrix-valued function as defined by* (2.18) *and Remark* 2.16 *and let* Γ *be the curve defined above. If the characteristic equation* (2.39) *has no roots on the imaginary axis, then* $\overline{\varphi}$ *is exponentially stable if* $\operatorname{Ind}_\Gamma(0) = 0$ *and unstable if* $\operatorname{Ind}_\Gamma(0) > 0$.

Proof. The nilpotency of T_0 implies that k has compact support and hence (being locally L^∞) belongs to $L^1(\mathbf{R}_+)$. The conclusion now follows from Nyquist's theorem. ∎

The assumption that T_0 is nilpotent is much stronger than is actually needed, but it is a convenient assumption that is satisfied in many applications (including structured populations with a maximum individual life span). The key point is that when we extend the argument principle from integration along closed curves to integration along the imaginary axis, we need to control the behavior of the integrand at infinity. The assumption $k \in L^1$ makes the Riemann–Lebesgue lemma valid and gives an easy estimate of the behavior at infinity.

The stability criterion of Corollary 2.20 is easy to implement numerically and even graphically. By the Riemann–Lebesgue lemma, $\widehat{k}(i\omega)$ tends to 0 as $\omega \to \pm\infty$, and hence $\det\big(E - \widehat{k}(i\omega)\big)$ tends to 1 as $\omega \to \pm\infty$. Choose ω_0 so large that $\det\big(E - \widehat{k}(i\omega_0)\big)$ is close to 1 for $|\omega| > \omega_0$ and plot $\det\big(E - \widehat{k}(i\omega)\big)$ as ω runs from $+i\omega_0$ to $-i\omega_0$. If the plotted curve does not wind around the origin, then $\overline{\varphi}$ is exponentially stable; otherwise it is unstable. If the curve passes through the origin, the test does not give any information.

2.7. The unstable, stable, and center manifolds. It is possible to give a more detailed description of the behavior near an unstable steady state. For the linearized semigroup, one has, provided that the characteristic equation has no roots on the imaginary axis, a direct sum spectral decomposition into a finite dimensional unstable subspace X_+ and an infinite dimensional stable subspace X_-. On X_+ one can go backwards in time. As a matter of fact, X_+ is *characterized* by the property that the orbit through a point in X_+ can be extended in the negative time-direction to $-\infty$ and that the α-limit set equals $\{0\}$. Similarly, X_- consists of precisely those points that have $\{0\}$ as ω-limit set. A general orbit shows saddle-point behavior: It may come close to 0 but will eventually move far away and, if it can be extended in the negative time-direction, it will also move far away in that direction.

One can construct a finite dimensional local unstable manifold $\mathcal{W}_u$ as the graph of a smooth function from X_+ to X_-, shifted to $\overline{\varphi}$. The manifold $\mathcal{W}_u$ is invariant, and the tangent space at $\overline{\varphi}$ is exactly X_+. Moreover, an orbit starting in a sufficiently small ball around $\overline{\varphi}$ can be extended to $t = -\infty$ with α-limit set equal to $\{\overline{\varphi}\}$ if and only if it starts (and hence remains) in $\mathcal{W}_u$. We refer to [23, Chapter VIII] for precise formulations (see in particular Theorems 4.4 and 4.7 and Corollary 4.11). Similarly, one can construct and characterize the local stable manifold $\mathcal{W}_s$ [23, Chapter VIII, Theorem 6.1].

If A does have a spectrum on the imaginary axis, the spectral decomposition involves a third component X_0, which in the setting of Theorem 2.15 or Theorem 2.17 is finite dimensional. The orbits of the linearized semigroup that start in X_0 are characterized by the fact that they grow at most polynomially as $t \to \pm\infty$ (note that in X_0 orbits can be extended to $t = -\infty$). As this characterization is more difficult to work with, the construction of the corresponding center manifold for the nonlinear semigroup (and the proof of its smoothness) is much more involved. Moreover, modification of the nonlinearity outside a small ball around $\overline{\varphi}$ plays a role in the construction and as a consequence the center manifold is not unique (yet it will contain all solutions which are defined for all times and remain inside the small ball for all times). We refer to [23, Chapter IX] for detailed formulations and proofs that apply verbatim to the setting of Theorem 2.15 or Theorem 2.17.

A situation of particular interest is the case that the nonlinear semigroup depends on a parameter and that for a specific value of this parameter, the characteristic equation (2.39) has a pair of simple roots on the imaginary axis (note that since the kernel k takes on real values, $\widehat{k}(-i\omega) = \overline{\widehat{k}(i\omega)}$, and hence complex roots of (2.39) occur in conjugate pairs). Under some further mild genericity conditions one then finds periodic orbits for nearby parameter values. Chapter X of [23] gives a detailed treatment of this so-called Hopf bifurcation in the setting of exactly the abstract integral equation (AIE) that we consider here. We present the main result in the next subsection and at the end of subsection 3.4 we shall briefly indicate how to obtain a corollary for Volterra functional equations.

2.8. Hopf bifurcation. In this subsection we consider Hopf bifurcation under the assumption that the nonlinear perturbation $G : X \to X^{\odot *}$ has finite dimensional range, which does *not* depend on the bifurcation parameter θ. So G is of the form

$$G(\varphi, \theta) = \sum_{i=1}^{N} F_i(\varphi, \theta) r_i^{\odot *}, \tag{2.45}$$

and its derivative with respect to φ at 0 is

$$B(\theta)\varphi = \sum_{i=1}^{N} \langle \varphi, r_i^*(\theta) \rangle \, r_i^{\odot *}. \tag{2.46}$$

Note carefully that now the vector r_i^* depends on the bifurcation parameter θ, as do the vector $r_i^{\odot}(\lambda)$ and the matrix $M(\lambda)$ introduced in (2.17) and (2.18), respectively:

$$M_{ij}(\lambda, \theta) = \langle r_j(\lambda), r_i^*(\theta) \rangle = \left\langle r_i^{\odot}(\lambda, \theta), r_j^{\odot *} \right\rangle. \tag{2.47}$$

In order to have Hopf bifurcation, we need to make sure that a conjugate pair $\pm i\omega_0$ of simple eigenvalues crosses the imaginary axis with positive speed as the bifurcation parameter θ passes some value θ_0. (Note: The real number ω_0 used in this subsection has of course nothing to do with the growth bound of a semigroup. We use the same symbol to denote two unrelated numbers because in both cases the usage conforms with common practice. No confusion is expected to arise.)

The simplicity of the eigenvalues is, by Corollary 2.13 and Theorem 2.15, ensured by the condition

$$\left\langle \psi(\theta_0), \psi^{\odot}(\theta_0) \right\rangle = -d(\theta_0) \frac{\partial M}{\partial \lambda}(i\omega_0, \theta_0) c(\theta_0) \neq 0. \tag{2.48}$$

The condition of crossing the imaginary axis with positive speed means more precisely that

$$\operatorname{Re} \lambda'(\theta_0) \neq 0, \tag{2.49}$$

where $\lambda(\theta)$ is a branch of eigenvalues through $i\omega_0$ at $\theta = \theta_0$. To derive a verifiable form of this condition, let $c(\theta)$ and $d(\theta)$ be the right and left eigenvectors, respectively, of $M(\lambda, \theta)$ normalized by

$$|c(\theta)| = \sum_{i=1}^{N} |c_i(\theta)| = 1, \tag{2.50}$$

$$d(\theta)c(\theta) = 1. \tag{2.51}$$

Differentiating the equation

$$d(\theta)M(\lambda, \theta)c(\theta) = 1$$

implicitly with respect to θ, one obtains

$$\frac{d}{d\theta}\left(d(\theta)c(\theta)\right) + d(\theta)\frac{\partial M}{\partial \theta} c(\theta) + d(\theta)\frac{\partial M}{\partial \lambda} c(\theta)\lambda'(\theta) = 0. \tag{2.52}$$

It now follows from (2.51) and Corollary 2.13 that

$$d(\theta)\frac{\partial M}{\partial \theta}(\lambda(\theta), \theta)c(\theta) = \left\langle \psi(\theta), \psi^{\odot}(\theta) \right\rangle \lambda'(\theta). \tag{2.53}$$

From (2.48) and (2.53) we deduce that (2.49) holds if and only if

$$\operatorname{Re} d(\theta_0)\frac{\partial M}{\partial \theta}(i\omega_0, \theta_0)c(\theta_0) \neq 0. \tag{2.54}$$

We are now ready to formulate the Hopf bifurcation theorem.

THEOREM 2.21 (Hopf bifurcation theorem, [23, Theorem 2.6, p. 290]). *Consider the abstract integral equation*

$$u(t) = T_0(t-s)u(s) + j^{-1}\int_s^t T_0^{\odot *}(t-\tau)G(u(\tau), \theta)d\tau, \quad -\infty < s \leq t < \infty, \tag{AIE}$$

and assume that the following hold:

(H1) $G(\varphi, \theta) = \sum_{i=1}^{N} F_i(\varphi, \theta) r_i^{\odot *}$, $F : X \times \mathbf{R} \to \mathbf{R}^N$ *is* C^k, $k \geq 2$.
(H2) $F(0, \theta) = 0$ *for all* θ.
(H3) $D_1 G(0, \theta) = B(\theta)$ *with* $B(\theta)$ *defined by* (2.46). *The corresponding matrix* $M(\lambda, \theta)$ *has for* $\lambda = \pm i\omega_0$, $\theta = \theta_0$, *eigenvalue* 1 *with right eigenvector* $c(\theta_0)$ *and left eigenvector* $d(\theta_0)$ *and* $d(\theta_0)\frac{\partial}{\partial \lambda}M(i\omega_0, \theta_0)c(\theta_0) \neq 0$. *For* $\theta = \theta_0$, *no root of the characteristic equation* $\det(E - M(\lambda)) = 0$ *other than* $\lambda = \pm i\omega_0$ *belongs to* $i\omega_0\mathbf{Z}$.

(H4) $\operatorname{Re} d(\theta_0)\frac{\partial}{\partial\theta}M(i\omega_0,\theta_0)c(\theta_0) \neq 0$.

There exist C^{k-1} functions $\varepsilon \mapsto \widetilde{\theta}(\varepsilon)$, $\varepsilon \mapsto \widetilde{\psi}(\varepsilon)$, and $\varepsilon \mapsto \widetilde{\omega}(\varepsilon)$ with values in $\mathbf{R}$, X, and $\mathbf{R}$, respectively, defined for ε sufficiently small, such that the solution of (AIE) *with $u(0) = \widetilde{\psi}(\varepsilon)$ is $2\pi/\widetilde{\omega}(\varepsilon)$ periodic. Moreover, $\widetilde{\theta}$ and $\widetilde{\omega}$ are even functions, $\widetilde{\theta}(0) = \theta_0$, $\widetilde{\omega}(0) = \omega_0$, $\widetilde{\psi}(-\varepsilon) = \widetilde{\psi}(\varepsilon + \frac{\pi}{\widetilde{\omega}(\varepsilon)})$. If $u(t)$ is any small periodic solution of* (AIE) *for θ close to θ_0 and period close to $2\pi/\omega_0$, then necessarily $\theta = \widetilde{\theta}(\varepsilon)$ for some ε and there exists $\sigma \in [0, 2\pi/\widetilde{\omega}(\varepsilon))$ such that $u(\sigma) = \widetilde{\psi}(\varepsilon)$. If for $\theta = \theta_0$ all roots λ of the characteristic equation*

$$\det(E - M(\lambda,\theta_0)) = 0$$

other than $\pm i\omega_0$ lie in the left half-plane and $\operatorname{Re} d(\theta_0)\frac{\partial}{\partial\theta}M(i\omega_0,\theta_0)c(\theta_0) < 0$, then the periodic solution is, for ε sufficiently small, asymptotically stable with asymptotic phase if $\widetilde{\theta}(\varepsilon) > \theta_0$ and unstable if $\widetilde{\theta}(\varepsilon) < \theta_0$.

Remark 2.22. In order to determine the direction of the bifurcation one has to compute the second derivative of $\widetilde{\theta}$. How this is done is explained in [23, section X.3].

3. Volterra functional equations.

3.1. Unperturbed semigroup for systems of delay equations. We let h denote a positive real number and N a positive integer. $X = L^1\left([-h,0];\mathbf{R}^N\right)$ is the space of all (equivalence classes of) $\mathbf{R}^N$-valued measurable functions φ defined and absolutely integrable on $[-h,0]$ (i.e., each component φ_i, $i = 1,2,\ldots,N$, is absolutely integrable) with norm

$$\|\varphi\|_1 := \sum_{i=1}^{N} \|\varphi_i\|_1. \tag{3.1}$$

The dual space X^* of $X = L^1\left([-h,0];\mathbf{R}^N\right)$ is represented by $L^\infty\left([0,h];\mathbf{R}^N\right)$, that is, the space of (equivalence classes of) $\mathbf{R}^N$-valued essentially bounded measurable functions g with norm

$$\|g\|_\infty := \max_{1\le i\le N} \|g_i\|_\infty \tag{3.2}$$

via the duality pairing

$$\langle \varphi, g\rangle = \sum_{i=1}^{N}\int_{-h}^{0} \varphi_i(\theta)g_i(-\theta)d\theta, \quad \varphi \in X,\ g \in X^*. \tag{3.3}$$

In order to apply the general linear theory summarized in section 2, we take X as above and consider the strongly continuous semigroup T_0 defined by (1.7):

$$(T_0(t)\varphi)(\theta) := \begin{cases} \varphi(t+\theta) & \text{for } \quad t+\theta \in [-h,0], \\ 0 & \text{for } \quad t+\theta > 0, \end{cases} \quad \varphi \in X,\, t \ge 0,\, \theta \in [-h,0]. \tag{3.4}$$

Note that T_0 is nilpotent ($T_0(t) = 0$ for $t > h$). In particular, T_0 is eventually compact.

Remark 3.1. The explicit formula (3.4) makes it clear that equivalence classes are mapped to equivalence classes, such that $T_0(t)$ is indeed an operator mapping X into X. In line with common praxis, we will be sloppy when it comes to distinguishing elements of L^1, namely equivalence classes, from their representatives. It is, however, important to note that an equivalence class is by definition absolutely continuous if it contains an absolutely continuous function (that is, a function all the components of which are absolutely continuous). We shall always use this absolutely continuous function to represent an absolutely continuous equivalence class. As in the introduction we shall use the notation $\varphi \in AC$ to indicate that φ is absolutely continuous.

The following characterization of the generator of T_0 is well known, at least in the case of scalar-valued functions [2, p. 11]. As the vector-valued case is not more difficult, we present it without proof.

PROPOSITION 3.2. *The generator A_0 of T_0 is given by*

$$\mathcal{D}(A_0) = \{\varphi \in X : \varphi \in AC,\ \varphi(0) = 0\},$$
$$A_0\varphi = \varphi'.$$

Our next task is to characterize $X^{\odot *}$ and $T_0^{\odot *}$ and prove sun-reflexivity of X with respect to T_0 so that we can give a precise meaning to the abstract integral equation (AIE) for the specific application we are considering. This is a rather straightforward exercise. In the case of scalar-valued functions it is essentially carried out in [9], the only difference being the way in which the spaces X^*, $X^\odot$, $X^{\odot *}$ are represented. Because the smoothness and boundary conditions entering into the domains of definition of the generators are defined componentwise, the vector-valued case does not present any extra difficulties [27, Chapter 3]. We shall therefore give only a brief sketch of the construction of $X^{\odot *}$ and $T_0^{\odot *}$ and a precise formulation of the result that we need.

With the chosen representation of X^*, the adjoint semigroup T_0^* is translation to the left with extension by zero. Translation is clearly *not* continuous in L^∞ (to see this, just consider translation of any discontinuous function). The maximal subspace on which T_0^* is strongly continuous is $X^\odot = C_0\left([0,h);\mathbf{R}^N\right)$, the space of all continuous $\mathbf{R}^N$-valued functions vanishing at h. This last condition derives, of course, from the extension by zero of the translated function.

By the Riesz representation theorem, the dual $X^{\odot *}$ can be represented by $\mathrm{NBV}((-h,0];\ \mathbf{R}^N)$, the space of all $\mathbf{R}^N$-valued functions f, all the components of which are of bounded variation, are continuous from the right, and vanish at 0. Note, in particular, that $f \in \mathrm{NBV}\big((-h,0];\mathbf{R}^N\big)$ does *not* have a jump in $-h$ and that this is indicated by the half-open interval $(-h,0]$ of definition of f. The duality pairing between $X^\odot = C_0\big([0,h);\mathbf{R}^N\big)$ and $X^{\odot *} = \mathrm{NBV}\big((-h,0];\mathbf{R}^N\big)$ is given by the sum of Riemann–Stieltjes integrals

$$\langle g, f\rangle = \sum_{i=1}^{N} \int_{-h}^{0} g_i(-\theta) f_i(d\theta), \quad g \in X^\odot,\ f \in X^{\odot *}, \tag{3.5}$$

and the norm on $X^{\odot *}$ by

$$\|f\|_{\mathrm{NBV}} := \sum_{i=1}^{N} \|f_i\|_{\mathrm{NBV}}, \tag{3.6}$$

where on the right-hand side $\|f_i\|_{\mathrm{NBV}}$ denotes the total variation of f_i.

The semigroup $T_0^{\odot *}$ is again translation to the left with extension by zero and it is not strongly continuous on $X^{\odot *}$. It is strongly continuous precisely on $X^{\odot\odot} = \{f \in X^{\odot *} : f \in AC\}$ [4, 9]. By the definition (2.5) of the canonical injection j :

$X \to X^{\odot *}$ and the definitions (3.3) and (3.5) of the pairings between our particular representations of X and $X^{\odot}$ and $X^{\odot}$ and $X^{\odot *}$, one obtains

$$\sum_{i=1}^{N} \int_{-h}^{0} g_i(-\theta)(j\varphi)_i(d\theta) = \langle g, j\varphi\rangle = \langle \varphi, g\rangle = \sum_{i=1}^{N} \int_{-h}^{0} \varphi_i(\theta) g_i(-\theta) d\theta,$$

from which it follows that $(j\varphi)' = \varphi$ or, equivalently,

$$j(\varphi)(\theta) = -\int_{\theta}^{0} \varphi(\tau)d\tau, \quad \theta \in (-h, 0]. \tag{3.7}$$

Now it is well known [52, Theorem 8.18] that a function of bounded variation is absolutely continuous if and only if it is the primitive of an L^1-function. Thus $j(X) = X^{\odot\odot}$; that is, X is sun-reflexive. We formulate the main conclusions as the following proposition.

PROPOSITION 3.3. *The space* $X = L^1\left([-h, 0]; \mathbf{R}^N\right)$ *is sun-reflexive with respect to the strongly continuous semigroup* T_0 *of bounded linear operators defined by* (3.4). *For* $\psi \in X^{\odot *} = \mathrm{NBV}((-h, 0]; \mathbf{R}^N)$, $t \geq 0$, *and* $\theta \in [-h, 0]$ *one has*

$$(T_0^{\odot *}(t)\psi)(\theta) = \begin{cases} \psi(t+\theta) & \text{for} \quad t+\theta \in [-h, 0), \\ 0 & \text{for} \quad t+\theta \geq 0. \end{cases} \tag{3.8}$$

The generator $A_0^{\odot *}$ *of* $T_0^{\odot *}$ *is given by*

$$\mathcal{D}(A_0^{\odot *}) = \{\varphi \in X^{\odot *} : \ \varphi(\theta) = \int_{\theta}^{0} \psi(\alpha) d\alpha \text{ for all } \theta \in [-h, 0]$$

$$\text{and some } \psi \in X^{\odot *}\}, \tag{3.9}$$

$$A_0^{\odot *}\varphi = -\psi \tag{3.10}$$

or, in shorthand notation, $A_0^{\odot *}\varphi = \varphi'$.

As a corollary to Proposition 3.3 we get a formula for the resolvent of $A_0^{\odot *}$ which we state for later use.

COROLLARY 3.4. *For* $f \in X^{\odot *} = \mathrm{NBV}((-h, 0]; \mathbf{R}^N)$ *and* $\lambda \in \mathbf{C}$ *we have*

$$\left(j^{-1} R\left(\lambda, A_0^{\odot *}\right) f\right)(\theta) = \int_{\theta}^{0} e^{\lambda(\theta-\tau)} f(d\tau), \quad \theta \in [-h, 0].$$

Proof. By definition, $R\left(\lambda, A_0^{\odot *}\right) f$ is the unique element $\varphi \in \mathcal{D}(A_0^{\odot *})$ which satisfies the equation

$$(\lambda E - A_0^{\odot *})\varphi = f. \tag{3.11}$$

By Proposition 3.3 there exists a $\psi \in X^{\odot *}$ such that

$$\varphi(\theta) = \int_{\theta}^{0} \psi(\alpha) d\alpha, \quad \theta \in [-h, 0], \tag{3.12}$$

and

$$A_0^{\odot *}\varphi = -\psi. \tag{3.13}$$

Equation (3.11) therefore becomes

$$\lambda \int_\theta^0 \psi(\alpha) d\alpha + \psi(\theta) = f(\theta), \quad \theta \in [-h, 0], \tag{3.14}$$

which has the unique solution

$$\psi(\theta) = -\int_\theta^0 e^{\lambda(\theta-\tau)} f(d\tau), \quad \theta \in [-h, 0]. \tag{3.15}$$

The inverse of the canonical injection j defined by (3.7) is clearly differentiation. Therefore

$$j^{-1} R\left(\lambda, A_0^{\odot *}\right) f = j^{-1}\varphi = \varphi' = -\psi. \tag{3.16}$$

The assertion now follows from (3.15) and (3.16). $\square$

3.2. The perturbed problem. In this subsection we show that with a specific choice of perturbation $G : X \to X^{\odot *}$, the perturbed problem, which, as we have shown in section 2, amounts to the abstract integral equation (AIE), is equivalent to the originally given delay equation (DE) and initial condition (IC). To this end, we let $F : X \to \mathbf{R}^N$ be a nonlinear mapping and define $G : X \to X^{\odot *}$ by

$$G(\varphi) = \sum_{i=1}^N F_i(\varphi) H_i, \tag{3.17}$$

where F_i denotes the ith component of F for $i = 1, \ldots, N$ and H_i is defined by

$$H_i(\theta) := \begin{cases} e_i & \text{for} \quad \theta \in (-h, 0), \\ 0 & \text{for} \quad \theta = 0. \end{cases} \tag{3.18}$$

Here and in what follows $\{e_1, e_2, \ldots, e_N\}$ is the standard basis of $\mathbf{R}^N$. Notice that G has finite dimensional range spanned by $\{H_1, H_2, \ldots, H_N\}$ in $X^{\odot *}$.

Next we compute the weak* integral in (AIE) when G is defined through (3.17) and (3.18).

LEMMA 3.5. *Let T_0 be the strongly continuous semigroup defined by* (3.4). *Then for every $\eta \in L^1_{\text{loc}}(\mathbf{R}_+)$ and $t \geq 0$ one has*

$$\left(\int_0^t T_0^{\odot *}(t-\tau)\eta(\tau) H_i d\tau \right)(\theta) = -e_i \int_{t+\max\{-t,\theta\}}^t \eta(\sigma) d\sigma, \quad \theta \in (-h, 0].$$

Proof. First notice that for $0 \leq s < h$ one has

$$\left(T_0^{\odot *}(s) H_i\right)(\theta) = \begin{cases} -e_i & \text{for} \quad -h \leq \theta < -s, \\ 0 & \text{for} \quad -s \leq \theta \leq 0. \end{cases} \tag{3.19}$$

The NBV function $T_0^{\odot *}(s) H_i$ thus has a unit jump at $\theta = -s$, and hence

$$\left\langle T_0^{\odot *}(t) H_i, g \right\rangle = \int_{-h}^0 g(-\theta) \left(T_0^{\odot *}(s) H_i\right)(d\theta) = g_i(s) \tag{3.20}$$

for any continuous g. It follows that for $0 \leq t \leq h$

$$\left\langle \int_0^t T_0^{\odot *}(t-s)\eta(s)H_i ds, g \right\rangle = \int_0^t \eta(s)g_i(t-s)ds$$

$$= \int_{-t}^0 \eta(t+s)g_i(-s)ds = \langle y, g\rangle ,$$

where y is the absolutely continuous NBV function defined by

$$y(\theta) = \begin{cases} -\int_{t+\theta}^t \eta(s)ds & \text{for} \quad \theta \leq 0 \leq 0, \\ -\int_0^t \eta(s)ds & \text{for} \quad -h \leq \theta < -t, \end{cases} \tag{3.21}$$

and the conclusion follows. □

Applying this result to $\eta(t) = F_i(u(t))$, we get the following corollary.

COROLLARY 3.6. *Let T_0 be the strongly continuous semigroup defined by* (3.4) *and let $G : X \to X^{\odot *}$ be defined by* (3.17) *and* (3.18). *If $u : [0, t) \to X$ is continuous, then*

$$\left(\int_0^t T_0^{\odot *}(t-s)G(u(s))ds\right)(\theta) = -\int_{t+\max\{-t,\theta\}}^t F(u(s))ds \tag{3.22}$$

for all $\theta \in [-h, 0]$.

Proof. Using Lemma 3.5, one computes

$$\left(\int_0^t T_0^{\odot *}(t-s)G(u(s))ds\right)(\theta) = \sum_{i=1}^N \left(\int_0^t T_0^{\odot *}(t-s)F_i(u(s))H_i ds\right)(\theta)$$

$$= -\sum_{i=1}^N e_i \int_{t+\max\{-t,\theta\}}^t F_i(u(s))ds = -\int_{t+\max\{-t,\theta\}}^t F(u(s))ds. \qquad \square$$

We are now ready to prove equivalence of solutions of the abstract integral equation

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

and the delay problem

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

$$x_0(\theta) = \varphi(\theta), \quad \theta \in [-h, 0]. \tag{IC}$$

For ease of formulation we consider global solutions, i.e., solutions defined for all future times. It should, however, be evident that one can formulate and prove an analogous result concerning local solutions.

THEOREM 3.7. *Let $\varphi \in X = L^1\left([-h, 0]; \mathbf{R}^N\right)$ be given.*

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

(b) *Suppose that there is a continuous map* $u : [0,\infty) \to X$ *that satisfies* (AIE). *Then the function* x *defined as*

$$x(t) := \begin{cases} \varphi(t) & \text{for} \quad t \in [-h, 0), \\ u(t)(0) & \text{for} \quad t \geq 0 \end{cases} \tag{3.23}$$

is an element of $L^1_{\mathrm{loc}}\left([-h,\infty);\mathbf{R}^N\right)$ *and satisfies* (DE) *and* (IC).

Proof. (a) First, note that the continuity assertion follows from the fact that translation is continuous in L^1. Then, by (DE) and (IC) we get

$$u(t)(\theta) - (T_0(t)\varphi)(\theta) = \begin{cases} 0 & \text{for} \quad t+\theta \in [-h,0), \\ x(t+\theta) & \text{for} \quad t+\theta \geq 0 \end{cases} \tag{3.24}$$

$$= \begin{cases} 0 \\ F(x_{t+\theta}) \end{cases} = \begin{cases} 0 & \text{for} \quad t+\theta \in [-h,0), \\ F(u(t+\theta)) & \text{for} \quad t+\theta \geq 0. \end{cases}$$

On the other hand, by Corollary 3.6 one gets

$$j^{-1}\left(\int_0^t T_0^{\odot *}(t-s)G(u(s))ds\right)(\theta) = \begin{cases} 0 & \text{for} \quad t+\theta \in [-h,0), \\ F(u(t+\theta)) & \text{for} \quad t+\theta \geq 0, \end{cases}$$

which equals (3.24), and therefore (AIE) holds.

(b) Suppose now that u satisfies (AIE). Then by Corollary 3.6 for $t \geq 0$ one has

$$\begin{aligned} x(t) = u(t)(0) &= j^{-1}\left(\int_0^t T_0^{\odot *}(t-s)G(u(s))ds\right)(0) \\ &= -\frac{d}{da}\int_{t+\max\{-t,a\}}^t F(u(s))ds|_{a=0} \\ &= F(u(t)). \end{aligned} \tag{3.25}$$

Hence it remains to be shown that $u(t) = x_t$. Using (AIE), Corollary 3.6, and (3.25), one computes for $\theta \in [-h, 0]$ that

$$u(t)(\theta) = \begin{cases} \varphi(t+\theta) & \text{for} \quad t+\theta \in [-h,0), \\ j^{-1}\left(\int_0^t T_0^{\odot *}(t-s)G(u(s))ds\right)(\theta) & \text{for} \quad t+\theta \geq 0 \end{cases}$$

$$= \begin{cases} \varphi(t+\theta) & \text{for} \quad t+\theta \in [-h,0), \\ j^{-1}\left(\int_{t+\max\{-t,\cdot\}}^t F(u(s))ds\right)(\theta) & \text{for} \quad t+\theta \geq 0 \end{cases}$$

$$= \begin{cases} \varphi(t+\theta) & \text{for} \quad t+\theta \in [-h,0), \\ F(u(t+\theta)) & \text{for} \quad t+\theta \geq 0. \end{cases}$$

Thus one has $u(t) = x_t$, and (b) is also proved. ∎

As is clear from the results of section 2, the abstract integral equation approach is ideal for deriving results concerning the qualitative behavior of solutions, such as stability and bifurcation. On the other hand, for proving regularity of solutions it is usually easier to attack the problem (DE) and (IC) directly. This is shown in the proof of the next theorem (which is not the sharpest possible result; indeed, the conclusion holds even if F is only locally Lipschitz, but then the proof is a bit more technical).

One of the advantages of the equivalence result of Theorem 3.7 is that we can freely choose between the abstract and the concrete, according to our needs.

THEOREM 3.8. *Let $F : L^1\left([-h,0];\mathbf{R}^N\right) \to \mathbf{R}^N$ be globally Lipschitz continuous. Then the unique solution $x : [-h,\infty) \to \mathbf{R}^N$ of* (DE), (IC) *with $\varphi \in L^1\left([-h,0];\mathbf{R}^N\right)$ is continuous in $[0,\infty)$.*

Proof. Let $\varphi \in L^1\left([-h,0];\mathbf{R}^N\right)$ and $\ell > 0$. Define

$$Z = \left\{y \in C\left([0,\ell];\mathbf{R}^N\right) : y(0) = F(\varphi)\right\}.$$

Then Z is a closed subset of the Banach space $C\left([0,\ell];\mathbf{R}^N\right)$ and thus a complete metric space. Define for each $y \in Z$ the function $\Phi(y)$ on $[0,\ell]$ by

$$\left(\Phi y\right)(t) = F(z_t^y), \quad 0 \le t \le \ell,$$

where z^y is the function defined by

$$z^y(\tau) = \begin{cases} \varphi(\tau) & \text{for} \quad -h \le \tau < 0, \\ y(\tau) & \text{for} \quad \le \tau \le \ell \end{cases}$$

and z_t^y is the translate of z^y as in (1.2). Clearly z^y belongs to L^1. Because translation is continuous when regarded as a mapping from an interval to L^1 and F is continuous on L^1, it follows that Φy is continuous. Moreover, $\left(\Phi y\right)(0) = F(z_0^y) = F(\varphi)$, and hence Φy belongs to Z. Next we show that Φ is a contraction on Z for ℓ sufficiently small. Because F is globally Lipschitz continuous we have for y_1, $y_2 \in Z$

$$\begin{aligned} \left|\left(\Phi y_1\right)(t) - \left(\Phi y_2\right)(t)\right| &= \left|F\left(z_t^{y_1}\right) - F\left(z_t^{y_2}\right)\right| \\ &\le L\left\|z_t^{y_1} - z_t^{y_2}\right\|_{L^1([-h,0];\mathbf{R}^N)} \\ &\le L\int_0^\ell \left|y_1(\tau) - y_2(\tau)\right|\,d\tau. \end{aligned}$$

Hence Φ has, for ℓ sufficiently small, a unique fixed point. The fixed point is obviously a solution of (DE) and (IC). This proves the assertion. ∎

The present way to associate a dynamical system with a Volterra integral equation is dual to the way studied in [21], where, of course, "dual" is precisely defined only in the linear case. The advantage of the present approach is that we also cover autonomous nonlinear problems that are *not* of convolution type, while [21] is restricted to convolution equations (see subsection 3.5 below).

3.3. Steady states. In this subsection we characterize the steady states of the nonlinear semigroup Σ generated by the abstract integral equation (AIE) in terms of constant solutions of (DE) and (IC).

THEOREM 3.9. (a) *Suppose $\overline{\varphi}$ is a steady state of Σ. Then $\overline{\varphi}$ is a constant function*

$$\overline{\varphi}(\theta) = \overline{x}, \quad \theta \in [-h,0], \tag{3.26}$$

and

$$\overline{x} = F\left(\overline{\varphi}\right). \tag{3.27}$$

(b) *Conversely, if the constant function $\overline{\varphi}$ given by* (3.26) *satisfies* (3.27)*, then it is a steady state of Σ.*

Proof. (a) Let $\overline{\varphi}$ be a steady state of Σ, i.e., $\Sigma(t)\overline{\varphi} = \overline{\varphi}$ for all $t \geq 0$. From (AIE) we then get

$$\overline{\varphi} = T_0(t)\overline{\varphi} + j^{-1}\left(\int_0^t T_0^{\odot *}(t-\tau)G(\overline{\varphi})d\tau\right), \quad t \geq 0.$$

Because $T_0(t) = 0$ for $t > h$, it follows that

$$j\overline{\varphi} = \int_0^t T_0^{\odot *}(t-\tau)G(\overline{\varphi})d\tau = \sum_{i=1}^N \int_0^t T_0^{\odot *}(\tau)H_i F_i(\overline{\varphi})d\tau.$$

Using Lemma 3.5 we then deduce that for $t > h$

$$(j\overline{\varphi}) = \sum_{i=1}^N -e_i \int_{t+\theta}^t F_i(\overline{\varphi})d\theta = \sum_{i=1}^N e_i \theta F_i(\overline{\varphi}).$$

But because j is integration, this means precisely that

$$\overline{\varphi}(\theta) = \sum_{i=1}^N e_i F_i(\overline{\varphi}) = F(\overline{\varphi}), \quad \theta \in [-h, 0];$$

that is, $\overline{\varphi}$ is a constant function and (3.27) holds.

The proof of (b) is similar. ∎

From the equivalence of (AIE) and (DE), (IC) (Theorem 3.7) it is clear that a function $\overline{\varphi}$ that takes the constant value $\overline{x} \in \mathbf{R}^N$ on $[-h, 0]$ is a steady state of Σ if and only if the constant function $x(t) = \overline{x},\ t \in [-h, \infty)$ is the solution of (DE), (IC).

Remark 3.10. In what follows we shall abuse notation and denote both the constant function $\overline{\varphi}$ on $[-h, 0]$ and the corresponding constant function on $[-h, \infty)$ by the same symbol as the constant value they take, viz. $\overline{x}$.

Because the constant solutions of (DE), (IC) are steady states of the dynamical system Σ, we have well-defined notions of stability at our disposal. It follows immediately from Theorem 3.8 that the constant solution $\overline{x}$ of (DE), (IC) is (locally) stable if and only if for every $\varepsilon > 0$ there exists a $\delta > 0$ such that

$$\int_{-h}^0 |x(t) - \overline{x}|dt \leq \delta \quad \Rightarrow \quad |x(t) - \overline{x}| \leq \varepsilon \text{ for all } t > 0$$

and (locally) *exponentially stable* if there exist numbers $\delta > 0,\ K > 0,\ \alpha > 0$ such that

$$\int_{-h}^0 |x(t) - \overline{x}|dt \leq \delta \quad \Rightarrow \quad |x(t) - \overline{x}| \leq K e^{-\alpha t} \text{ for all } t > 0.$$

3.4. The characteristic equation. In section 2.5 we showed that whenever $\sigma(A_0)$ is empty (in particular, when T_0 is nilpotent) and the perturbation has finite dimensional range, the spectrum $\sigma(A)$ of the perturbed generator consists entirely of eigenvalues and there exists a characteristic equation

$$\det(E - M(\lambda)) = 0,$$

the roots of which are exactly the eigenvalues. The characteristic equation contains all the information about asymptotic behavior, Hopf bifurcation, etc. In this section we identify the matrix $M(\lambda)$ for the special case in which the unperturbed semigroup T_0 is given by (3.4) and the perturbation G is of the form (3.17).

If G is differentiable at $\overline{\varphi}$, there exist functions $k_{ij} \in L^\infty([0,h];\mathbf{R})$ such that

$$G'(\overline{\varphi})\varphi = \sum_{i=1}^N \left(\sum_{j=1}^N \int_{-h}^0 k_{ij}(-\theta)\varphi_j(\theta)d\theta \right) H_i.$$

$B = G'(\overline{\varphi})$ is thus of the form (2.15), with $r_i^{\odot *} = H_i$ and $r_i^* = k_i = \{k_{ij}\}_{j=1}^N$. Corollary 3.4 now yields

$$\begin{aligned}(r_j(\lambda))(\theta) &= \left(j^{-1}R(\lambda, A_0^{\odot *})H_j\right)(\theta) \\ &= \int_\theta^0 e^{\lambda(\theta-\tau)}H_j(d\tau) = e^{\lambda\theta}e_j, \quad \theta \in [-h,0],\end{aligned} \tag{3.28}$$

and hence

$$M_{ij}(\lambda) = \langle r_j(\lambda), k_i \rangle = \int_{-h}^0 e^{\lambda\theta}k_{ij}(-\theta)d\theta = \int_0^h e^{-\lambda\theta}k_{ij}(\theta)d\theta = \widehat{k}_{ij}(\lambda).$$

Denoting the matrix with entries k_{ij} by k, the characteristic equation thus takes the form

$$\det\left(E - \widehat{k}(\lambda)\right) = 0. \tag{3.29}$$

The results of subsection 2.6 now tell us that if all the roots of the characteristic equation (3.29) have negative real part, then the steady state is exponentially stable, whereas it is unstable if at least one root has positive real part. Note that the hypotheses of Corollary 2.20 are fulfilled, so Nyquist's criterion for (in)stability is applicable. It is also a straightforward fill-in exercise to translate Theorem 2.21 into a result for delay equations (generalizing Theorem 11.1 in [21] to include equations which are not of convolution type, and being the analogue of Theorem X.2.7 in [23], which applies to delay differential equations).

3.5. Differentiability for three important classes of nonlinearity. In order to apply the general results on stability and bifurcation to the system (DE), (IC) we have to give conditions that ensure that the map $G : X \to X^{\odot *}$ is Fréchet differentiable with $X = L^1\left([-h,0];\mathbf{R}^N\right)$ and G of finite dimensional range given by (3.17) or, more generally, by (2.14). As noted in subsection 2.5, G is differentiable if and only if F is differentiable from $L^1\left([-h,0];\mathbf{R}^N\right)$ to $\mathbf{R}^N$. This leads us to have a closer look at differentiability criteria for functions from $L^1\left([-h,0];\mathbf{R}^N\right)$ to $\mathbf{R}^N$.

There is one obvious class of differentiable mappings from $L^1\left([-h,0];\mathbf{R}^N\right)$ to $\mathbf{R}^N$, consisting of those mappings of the form $\varphi \mapsto (g\circ\Lambda)\varphi$, where $\Lambda : L^1\left([-h,0];\mathbf{R}^N\right) \to \mathbf{R}^N$ is a bounded linear map and g is a smooth function from $\mathbf{R}^N$ to $\mathbf{R}^N$.

A map F that occurs frequently in applications is $F = \Lambda \circ N_g$, where Λ is a bounded linear map from $L^1\left([-h,0];\mathbf{R}^N\right)$ to $\mathbf{R}^N$ and N_g is the Nemytskiĭ operator induced by a smooth function $g : \mathbf{R}^N \to \mathbf{R}^N$ as follows:

$$(N_g(\varphi))(\theta) = g(\varphi(\theta)). \tag{3.30}$$

For instance, the nonlinear Volterra convolution equation

$$x(t) = \int_0^h k(s) g(x(t-s)) ds, \quad t > 0, \tag{3.31}$$

$$x(t) = \varphi(t), \quad -h \le t \le 0, \tag{3.32}$$

is of the form (DE), (IC) with $F = \Lambda \circ N_g$ and $\Lambda\varphi = \int_0^h k(\theta)\varphi(-\theta) d\theta$.

It may come as a surprise that the Nemytskiĭ operator from $L^1\left([-h,0];\mathbf{R}^N\right)$ to $L^1\left([-h,0];\mathbf{R}^N\right)$ generated by a differentiable, globally Lipschitz continuous function $g : \mathbf{R}^N \to \mathbf{R}^N$ is *not* Fréchet differentiable unless g is affine (a constant plus a linear operator), but in hindsight this is easy to understand. An indication of the reason is that in the formal Taylor series expansion

$$\begin{aligned}(N_g(\varphi))(\theta) &= g(\varphi(\theta)) \\ &= g(\overline{\varphi}(\theta)) + g'(\overline{\varphi}(\theta))(\overline{\varphi}(\theta) - \varphi(\theta)) + \frac{1}{2} g''(\overline{\varphi}(\theta))(\overline{\varphi}(\theta) - \varphi(\theta))^2 + \cdots\end{aligned} \tag{3.33}$$

around an element $\overline{\varphi} \in L^1$, the higher order terms contain powers of φ which need not belong to L^1. So showing that the higher order terms are small cannot be done in the standard way (and, in fact, cannot be done at all).

The above result may seem disastrous for our theory because it appears as if the important case of the nonlinear Volterra convolution equation (3.31) would not be covered by it. Fortunately, a simple transformation saves our bacon.

Consider the Volterra functional equation

$$x(t) = \Lambda N_g(x_t) \tag{3.34}$$

with initial condition

$$x_0 = \varphi. \tag{3.35}$$

Applying the function g to both sides of (3.34) and (3.35), one obtains

$$(g \circ x)(t) = g\left(\Lambda N_g(x_t)\right) \tag{3.36}$$

and

$$g(x_0) = g(\varphi). \tag{3.37}$$

But

$$(g \circ x)_t(\theta) = g(x(t+\theta)) = g(x_t(\theta)) = (N_g(x_t))(\theta),$$

that is,

$$(g \circ x)_t = N_g(x_t), \tag{3.38}$$

and hence (3.36) and (3.37) take the form

$$y(t) = (g \circ \Lambda)(y_t), \tag{3.39}$$

$$y_0 = \psi \tag{3.40}$$

with

$$y(t) = (g \circ x)(t), \tag{3.41}$$

$$\psi = g \circ \varphi. \tag{3.42}$$

But $g \circ \Lambda$ is differentiable, and thus our theory applies to the transformed problem (3.39), (3.40): A constant solution $\overline{y}$ of (3.39), (3.40) is exponentially stable if all the roots λ of the characteristic equation

$$\det\left(E - g'(\overline{x})\widehat{k}(\lambda)\right) = 0 \tag{3.43}$$

satisfy $\mathrm{Re}\lambda < 0$ and unstable if there exists at least one root with positive real part.

We recover the solution x of our original problem (3.34), (3.35), because (3.34), (3.41), and (3.38) together show that

$$x(t) = \Lambda y_t. \tag{3.44}$$

It remains to be shown that the stability properties of the transformed problem determine those of the original problem. For this the differentiability of g is irrelevant; we assume only global Lipschitz continuity as this guarantees that the Nemytskiĭ operator N_g maps L^1 into L^1.

THEOREM 3.11. *Let $\Lambda : L^1\left([-h,0];\mathbf{R}^N\right) \to \mathbf{R}^N$ be a bounded linear operator and let $g : \mathbf{R}^N \to \mathbf{R}^N$ be globally Lipschitz continuous with Lipschitz constant L. Let $\overline{x}$ be a constant solution of* (3.34), (3.35) *and let $\overline{y} = g(\overline{x})$ be the corresponding constant solution of* (3.39), (3.40). *Then the following hold:*

(a) *If $\overline{y}$ is [exponentially] stable, then so is $\overline{x}$.*

(b) *If $\overline{y}$ is unstable, then so is $\overline{x}$.*

Proof. The estimate

$$|x(t) - \overline{x}| = |\Lambda y_t - \Lambda g(\overline{x})| \leq \|\Lambda\| \|y_t - \overline{y}\|_1 \tag{3.45}$$

proves (a). Assume now that $\overline{x}$ is stable and let y be the solution of (3.39), (3.40). Define

$$x(t) = \Lambda y_t, \quad t \geq 0. \tag{3.46}$$

We know by Theorem 3.8 that y is continuous for $t \geq 0$; it follows that $x_h \in L^1\left([-h,0];\mathbf{R}^N\right)$. So, for $t \geq h$, y may be regarded as the solution of (3.39) with the initial condition (3.40) replaced by

$$y_h = g \circ x_h. \tag{3.47}$$

Because the mapping that takes ψ to y_t is a strongly continuous (nonlinear) semigroup, $\sup_{0 \leq t \leq h} \|y_t - \overline{y}\|_1$ can be made arbitrarily small by choosing $\|\psi - \overline{y}\|_1$ sufficiently small. Now (3.45) shows that $x_h - \overline{x}$ also can be made arbitrarily small.

Let $\varepsilon > 0$ be arbitrary. Because $\overline{x}$ is stable one can choose $\delta > 0$ such that $\|x_h - \overline{x}\| < \delta$ implies $|x(t) - \overline{x}| < \varepsilon / L$ for all $t > h$. It follows that

$$|y(t) - \overline{y}| = |g(x(t)) - g(\overline{x})| \leq L|x(t) - \overline{x}| < \varepsilon$$

for all $t > 0$ provided that $\|\psi - \overline{y}\|_1$ is sufficiently small, that is, $\overline{y}$ is stable. ∎

Note that if we linearize the nonlinear Volterra integral equation (3.31) in $\mathbf{R}^N$ (as opposed to linearizing $F : L^1 \to \mathbf{R}^N$ in the delay equation), we obtain

$$x(t) = \int_0^t k(s)g'(\overline{x})x(t-s)ds + G(x)(t), \tag{3.48}$$

where $G(x)(t)$ stands for the higher order terms. In the theory of Volterra integral equations [29] one associates the characteristic equation

$$\det\left(E - \widehat{k}(\lambda)g'(\overline{x})\right) = 0 \tag{3.49}$$

with (3.48). Clearly, (3.43) and (3.49) have exactly the same roots.

A third class of differentiable maps from $L^1\left([-h,0];\mathbf{R}^N\right)$ to $\mathbf{R}^N$ is obtained by composing a map from the space $C\left([0,\ell];\mathbf{R}^N\right)$ of continuous functions on some interval $[0,\ell]$ to $\mathbf{R}^N$ with a linear (or affine) map from $L^1\left([-h,0];\mathbf{R}^N\right)$ to $C\left([0,\ell];\mathbf{R}^N\right)$. The reason for this detour via $C\left([0,\ell];\mathbf{R}^N\right)$ is that, roughly speaking, it is much easier for a function to be differentiable if it is defined on $C\left([0,\ell];\mathbf{R}^N\right)$ than if it is defined on L^1. Indeed, the product of two continuous functions which are small in the supremum norm is continuous, and the supremum norm of the product is of quadratic order. In particular, the expansion (3.33) applied to a continuous function φ shows that the Nemytskiĭ operator is differentiable in $C\left([0,\ell];\mathbf{R}^N\right)$ and that

$$N_g'(\overline{\varphi}) = N_{g'}(\overline{\varphi}). \tag{3.50}$$

This observation is important in applications to, for instance, population dynamics. Let us illustrate it by an age-structured model of the type first studied in [30]. Assume that the age-specific per capita death rate depends on the present value $I(t)$ of the (one-dimensional) environmental condition in the following way:

$$\mu(a, I(t)) = \mu_0(a) + \mu_1(a)I(t) \tag{3.51}$$

(where μ_0 and μ_1 are nonnegative functions). Then the probability $\mathcal{F}(a;\varphi)$ that an individual that was born a time units ago is still alive, given the history φ of the environmental condition, is the solution of the ODE initial value problem

$$\frac{d}{d\alpha}\mathcal{F}(\alpha;\varphi) = -\mu(\alpha, \varphi(\alpha - a))\mathcal{F}(\alpha,\varphi), \tag{3.52}$$

$$\mathcal{F}(0) = 1 \tag{3.53}$$

at $\alpha = a$, that is,

$$\mathcal{F}(a;\varphi) = \exp\left(-\int_0^a \left(\mu_0(\alpha) + \mu_1(\alpha)\varphi(\alpha - a)\right) d\alpha\right). \tag{3.54}$$

The theory presented in this paper presupposes a maximum life span h. This is achieved by assuming that μ_0 has a nonintegrable singularity at h:

$$\int_0^h \mu_0(a)da = \infty,$$

because then the survival probability

$$\mathcal{F}_0(a) = \exp\left(-\int_0^a \mu_0(\alpha)d\alpha\right) \tag{3.55}$$

with respect to density-independent effects vanishes at h.

If $\beta(a, I(t))$ is the age-specific fecundity, then the integral equations (1.18), (1.19) combined with the feedback law (1.17) yield

$$b(t) = \int_0^h \beta(a, I(t))\mathcal{F}(a; I_t)b(t-a)da, \tag{3.56}$$

$$I(t) = \int_0^h \gamma(a)\mathcal{F}(a; I_t)b(t-a)da, \tag{3.57}$$

which is a delay equation of the type (DE). More specifically, we have

$$\begin{pmatrix} b(t) \\ I(t) \end{pmatrix} = F\begin{pmatrix} b_t \\ I_t \end{pmatrix} \tag{3.58}$$

with F given by

$$F\begin{pmatrix} \psi \\ \varphi \end{pmatrix} = \begin{pmatrix} \int_0^h \beta\left(a, \int_0^h \gamma(\alpha)\mathcal{F}(\alpha;\varphi)\psi(-\alpha)d\alpha\right)\mathcal{F}(a;\varphi)\psi(-a)da \\ \int_0^h \gamma(a)\mathcal{F}(a;\varphi)\psi(-a)da \end{pmatrix}. \tag{3.59}$$

F is a well-defined mapping from $L^1\left([-h,0];\mathbf{R}^2\right)$ to $\mathbf{R}^2$ if $\gamma\mathcal{F}_0 \in L^\infty[0,h]$ and $\beta(\cdot,\overline{I})\mathcal{F}_0 \in L^\infty[0,h]$ for all $\overline{I} \in \mathbf{R}$, and hence we make this assumption.

We want to show that F is differentiable. First notice that the argument of the exponential function in formula (3.54) is an affine map taking $\varphi \in L^1[-h,0]$ to $C[0,h]$. The mapping $\varphi \mapsto \mathcal{F}(\cdot;\varphi)$ is thus obtained by composing the Nemytskiĭ operator induced in $C[0,h]$ by the exponential function with an affine map. As we already saw, this map is Fréchet differentiable. For fixed ψ, the second component F_2 of F is now obtained by applying a continuous linear mapping to the differentiable map $\varphi \mapsto \mathcal{F}(\cdot;\varphi)$. Hence F_2 is differentiable in φ. Because F_2 is linear in ψ it is also differentiable in ψ. Because $F_2(\psi,\varphi)$ appears as the second argument of β in the expression for F_1, the chain rule implies that F_2 also is differentiable provided that $\beta : \mathbf{R}^2 \to \mathbf{R}$ is differentiable in its second argument.

The derivative of F can be computed explicitly. A straightforward but tedious computation yields F' at a steady state $(\overline{b}, \overline{I})$:

$$\left[F'\begin{pmatrix} \overline{b} \\ \overline{I} \end{pmatrix}\right]\begin{pmatrix} \psi \\ \varphi \end{pmatrix} = \int_0^h k(a)\begin{pmatrix} \psi \\ \varphi \end{pmatrix}(-a)da, \tag{3.60}$$

where k is a 2×2 matrix-valued function with entries

$$k_{11}(a) = \left(\gamma(a)\int_0^h \partial_2\beta(\tau,\overline{I})\mathcal{F}(\tau;\overline{I})d\tau\,\overline{b} + \beta(a,\overline{I})\right)\mathcal{F}(a;\overline{I}), \tag{3.61}$$

$$\begin{aligned} k_{12}(a) = &\int_0^h \partial_2\beta(\tau,\overline{I})\mathcal{F}(\tau;\overline{I})d\tau\,\overline{b}\,k_{22}(a) \\ &- \int_0^{h-a} \mu_1(\alpha)\beta(\alpha+a,\overline{I})\mathcal{F}(\alpha+a;\overline{I})d\alpha\,\overline{b}, \end{aligned} \tag{3.62}$$

$$k_{21}(a) = \gamma(a)\mathcal{F}(a;\overline{I}), \tag{3.63}$$

$$k_{22}(a) = -\int_0^{h-a} \mu_1(\alpha)\gamma(\alpha+a)\mathcal{F}(\alpha+a;\overline{I})d\alpha\,\overline{b}. \tag{3.64}$$

The characteristic equation is (3.29) with the matrix k defined by (3.61)–(3.64). It is easy to check that the resulting stability criterion is equivalent (as it should be) to the one given in [30] for $\gamma \equiv 1$ and in [32] and [50] for the general case.

The steady environmental condition $\overline{I}$ of a nontrivial equilibrium $(\bar{b}, \overline{I}) \neq (0,0)$ is a solution (there may be many) of the steady state condition

$$1 = \int_0^h \beta(a, \overline{I}) \mathcal{F}(a; \overline{I}) da. \tag{3.65}$$

Once $\overline{I}$ has been solved from (3.65), the corresponding steady birth rate is obtained from

$$\bar{b} = \frac{\overline{I}}{\int_0^h \gamma(a) \mathcal{F}(a; \overline{I}) da}. \tag{3.66}$$

On the other hand, for the population-free, or trivial, steady state $(\bar{b}, \overline{I}) = (0,0)$, the characteristic equation (3.29) reduces to the scalar equation

$$1 = \int_0^h e^{-\lambda a} \beta(a, 0) \mathcal{F}_0(a) da. \tag{3.67}$$

As a consequence, the population-free steady state is exponentially stable if

$$R_0 := \int_0^h \beta(a, 0) \mathcal{F}_0(a) da < 1$$

and unstable if

$$R_0 > 1.$$

In subsection 5.1 we shall elaborate on this a bit more in the context of a model for an age-structured population with cannibalistic behavior.

4. Volterra functional equations coupled with delay differential equations. In applications to structured population dynamics, one encounters models that take the form of a Volterra functional equation coupled with a delay differential equation [31, 32]. In this section we therefore briefly consider systems of the following type:

$$x(t) = F_1(x_t, y_t), \tag{4.1}$$

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

For the component x of the delay equation (4.1), we choose as before $X = L^1\left([-h, 0]; \mathbf{R}^N\right)$ as state space, whereas the natural state space for the component y of the delay differential equation (4.2) is $Y = C\left([-h, 0]; \mathbf{R}^M\right)$ (see [23]). We therefore have to assume that the mappings $F_1 : X \times Y \to \mathbf{R}^N$ and $F_2 : X \times Y \to \mathbf{R}^M$ are at least Lipschitz continuous. Equations (4.1) and (4.2) must, of course, be supplemented by initial conditions

$$x(\theta) = \varphi(\theta), \quad -h \leq \theta \leq 0, \tag{4.3}$$

$$y(\theta) = \psi(\theta), \quad -h \leq \theta \leq 0. \tag{4.4}$$

In section 3 we showed in detail how a Volterra functional equation could be written as a semilinear abstract integral equation. The same program has been carried out for delay differential equations in the book [23] (see also [40]). It is now an easy exercise to combine the two procedures for the coupled system (4.1)–(4.4).

Let T_{10} be the C_0-semigroup defined on X by (3.4) and define the C_0-semigroup T_{20} on Y by

$$(T_{20}(t)\psi)(\theta) := \left\{ \begin{array}{lll} \psi(t+\theta) & \text{for} & t+\theta \in [-h,0], \\ \psi(0) & \text{for} & t+\theta \geq 0, \end{array} \right. \quad \psi \in Y,\, t \geq 0,\, \theta \in [-h,0]. \tag{4.5}$$

The two semigroups T_{10} and T_{20} induce in an obvious way a semigroup T_0 on $X \times Y$:

$$T_0(t) = \begin{pmatrix} T_{10}(t) & 0 \\ 0 & T_{20}(t) \end{pmatrix}. \tag{4.6}$$

It was shown in [23] that $Y^{\odot *}$ has the representation $\mathbf{R}^M \times L^\infty\left([-h,0];\mathbf{R}^M\right)$ and that Y is $\odot$-reflexive with respect to T_{20}. Because X is $\odot$-reflexive with respect to T_{10}, as shown in section 3, it is plain that $X \times Y$ is $\odot$-reflexive with respect to T_0, that $(X \times Y)^{\odot *}$ is (isometrically isomorphic to) $X^{\odot *} \times Y^{\odot *}$, and that $j_{X\times Y}(X \times Y) = j_X(X) \times j_Y(Y)$ (here, of course, j_Z denotes the canonical embedding of Z into $Z^{\odot *}$). Note also that for $t > h$, the range of $T_{20}(t)$ lies in the subspace of Y consisting of the constant functions, which is finite dimensional. In particular, $T_{20}(t)$ is eventually compact. As T_{10} is nilpotent, the semigroup T_0 on $X \times Y$ is eventually compact.

The system (4.1)–(4.4) is equivalent to the abstract integral equation

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

where $G : X \times Y \to X^{\odot *} \times Y^{\odot *}$ is defined by

$$G(\varphi,\psi) = \sum_{i=1}^{N} F_{1i}(\varphi,\psi)\begin{pmatrix} r_i^{\odot *} \\ 0 \end{pmatrix} + \sum_{i=1}^{M} F_{2i}(\varphi,\psi)\begin{pmatrix} 0 \\ s_i^{\odot *} \end{pmatrix}. \tag{4.7}$$

Here $r_i^{\odot *} \in X^{\odot *}$ is the Heaviside function (3.18), and $s_i^{\odot *} = (f_i, 0) \in Y^{\odot *}$, where $\{f_1, f_2, \dots, f_M\}$ is the standard basis of $\mathbf{R}^M$ and 0 is the zero element of $L^\infty\left([-h,0];\mathbf{R}^M\right)$. We are now exactly in the situation described in section 2.5.

The resolvent $R\left(\lambda, A_{10}^{\odot *}\right)$ of $T_{10}^{\odot *}$ was calculated in Corollary 3.4 and the associated vector $r_i(\lambda)$ in (3.28). An analogous computation for $T_{20}^{\odot *}$ shows that $\sigma(A_{20}) = \sigma(A_{20}^{\odot *}) = \{0\}$ and that the resolvent of $A_{20}^{\odot *}$ is given by

$$\begin{aligned} &\left(R\left(\lambda, A_{20}^{\odot *}\right)(\alpha,\psi)\right)(\theta) \\ &= \frac{1}{\lambda}e^{\lambda\theta}\alpha + \int_\theta^0 e^{\lambda(\theta-\tau)}\psi(\tau)d\tau, \quad (\alpha,\psi) \in Y^{\odot *}, \quad \theta \in [-h,0]. \end{aligned} \tag{4.8}$$

In particular,

$$s_i(\lambda) := \left(j^{-1}R\left(\lambda, A_{20}^{\odot *}\right)s_i^{\odot *}\right)(\theta) = \frac{1}{\lambda}e^{\lambda\theta}f_i, \quad \theta \in [-h,0]. \tag{4.9}$$

If F is Fréchet differentiable, its derivative can be represented by the $(N+M) \times (N+M)$ matrix

$$\begin{pmatrix} k_{11} & m_{12} \\ k_{21} & m_{22} \end{pmatrix}, \tag{4.10}$$

where k_{11} and k_{21} are $N \times N$ (resp., $N \times M$) matrices of elements of $L^\infty([0,h]$ and m_{12} and m_{22} are $M \times N$ (resp., $M \times M$) matrices of elements in $NBV[0,h]$. The interpretation of (4.10) is that

$$F'(\overline{\varphi},\overline{\psi})\begin{pmatrix}\varphi\\ \psi\end{pmatrix} = \begin{pmatrix}\int_0^h k_{11}(\theta)\varphi(-\theta)d\theta + \int_0^h m_{12}(d\theta)\psi(-\theta)\\ \int_0^h k_{21}(\theta)\varphi(-\theta)d\theta + \int_0^h m_{22}(d\theta)\psi(-\theta)\end{pmatrix}. \tag{4.11}$$

Using the expressions (3.28) and (4.9) for $r_i(\lambda)$ and $s_i(\lambda)$, respectively, and the definition (2.18) of the matrix $M(\lambda)$, we deduce that

$$M(\lambda) = \begin{pmatrix}\widehat{k}_{11}(\lambda) & \frac{1}{\lambda}\widehat{dm}_{12}(\lambda)\\ \widehat{k}_{21}(\lambda) & \frac{1}{\lambda}\widehat{dm}_{22}(\lambda)\end{pmatrix}, \quad \lambda \neq 0, \tag{4.12}$$

where, as before, $\widehat{k}$ denotes the Laplace transform of k and $\widehat{dm}$ denotes the Laplace–Stieltjes transform of m,

$$\widehat{dm}(\lambda) = \int_0^h e^{-\lambda\theta}m(d\theta). \tag{4.13}$$

It now follows from Theorem 2.15 that $\lambda \neq 0$ is an eigenvalue of the generator of the linearized equation (LAIE) if and only if

$$\det(E - M(\lambda)) = 0 \tag{4.14}$$

and that the algebraic multiplicity of λ coincides with the order of λ as a root of (4.14). Clearly, for $\lambda \neq 0$, (4.14) is equivalent to

$$\det\left(\begin{pmatrix}E & 0\\ 0 & \lambda E\end{pmatrix} - \begin{pmatrix}\widehat{k}_{11}(\lambda) & \widehat{dm}_{12}(\lambda)\\ \widehat{k}_{21}(\lambda) & \widehat{dm}_{22}(\lambda)\end{pmatrix}\right) = 0. \tag{4.15}$$

As Theorem 2.17 shows that the singularity at $\lambda = 0$ is removable, we conclude that (4.15) is the characteristic equation for the (AIE) with T_0 and G as specified above.

5. Examples.

5.1. Cannibalistic interaction. Even though *size* is the more natural individual state variable used to describe cannibalistic interaction, we shall here use *age* as a substitute, while referring to [25, section 4.1] and [28] for size-structured models. We assume that individuals turn adult and start to reproduce upon reaching age $\overline{a}$. Furthermore, only adults practice cannibalism and their victims are juveniles. The vulnerability for intraspecific predation is defined by a function c of age, the support of which lies in $[0,\overline{a})$.

Let $\mathcal{F}_0(a)$ be the survival probability to at least age a with respect to causes of death other than cannibalism. Let $b(t)$ be the population birth rate at time t and $I_1(t)$ the total number of adults at time t. We assume that "standard" adult food (that is, food other than juveniles of their own kind) is available at a constant density and that an adult produces, from this food, offspring at a rate Z. Let $I_2(t)$ denote the rate at which an adult produces offspring at time t on the basis of the energy provided by its cannibalistic actions. Then, by definition,

$$b(t) = (Z + I_2(t))\, I_1(t), \tag{5.1}$$

$$I_1(t) = \int_{\overline{a}}^\infty b(t-a)\mathcal{F}_0(a)e^{-\int_0^a c(\alpha)I_1(t-a+\alpha)d\alpha}da. \tag{5.2}$$

To these equations we add

$$I_2(t) = \int_0^{\overline{a}} b(t-a)\mathcal{F}_0(a)e^{-\int_0^a c(\alpha)I_1(t-a+\alpha)d\alpha}c(a)E(a)da, \tag{5.3}$$

expressing that the (instantaneous) offspring yield resulting from the consumption of an individual of age a is given by $E(a)$.

The system (5.1)–(5.3) is of the form (3.54)–(3.57) (albeit with two instead of one interaction variable), and thus the arguments provided in section 3.5 establish that the system is a (DE) on L^1 with a C^1-map F. To guarantee that the maximum delay is finite, we assume that $\mathcal{F}_0$ drops to zero at a finite age h (or, equivalently, that the μ_0 of (3.55) has a nonintegrable singularity at h).

By elementary manipulations one can eliminate $\overline{I}_2$ and $\overline{b}$ from the equations for nontrivial steady states to arrive at a single equation

$$Z = \frac{e^{C\overline{I}_1}}{\int_{\overline{a}}^h \mathcal{F}_0(a)da}\left(1 - \overline{I}_1\int_0^{\overline{a}} c(a)E(a)\mathcal{F}_0(a)e^{-\overline{I}_1\int_0^a c(\alpha)d\alpha}da\right) \tag{5.4}$$

for the unknown $\overline{I}_1$. Here

$$C := \int_0^{\overline{a}} c(a)da. \tag{5.5}$$

Next we consider Z (thus, in essence, the density of the standard food) as a bifurcation parameter. The formula (5.4) is an explicit expression for Z as a function of $\overline{I}_1$. If we insert $\overline{I}_1 = 0$ at the right-hand side of (5.4), we obtain the critical value

$$Z_{\text{crit}} = \frac{1}{\int_{\overline{a}}^h \mathcal{F}_0(a)da} \tag{5.6}$$

such that newborn individuals, on average, produce exactly one offspring. In the absence of cannibalism (i.e., for $c \equiv 0$), a nontrivial steady state exists if and only if $Z > Z_{\text{crit}}$. By computing the derivative of Z with respect to $\overline{I}_1$ from (5.4) and evaluating at $\overline{I}_1 = 0$, one concludes that the condition

$$\int_0^{\overline{a}} (E(a)\mathcal{F}_0(a) - 1)\, c(a)da > 0 \tag{5.7}$$

guarantees that the bifurcation from the trivial steady state is subcritical in the sense that $\overline{I}_1$ is positive for values of Z slightly less than Z_{crit}. Thus if (5.7) holds, cannibalism allows the population to persist at levels of the standard food that are, by themselves, insufficient to sustain a consumer population. We refer once more to [25, section 4.1] and [28] for the biological interpretation and further elaborations.

A characteristic equation can now be derived as for the system (3.54)–(3.57) treated in section 3.5. The stability of the trivial steady state is governed by the position of the roots of

$$1 = Z\int_{\overline{a}}^h e^{-\lambda a}\mathcal{F}_0(a)\, da \tag{5.8}$$

in the complex plane. Hence the trivial solution is stable for $Z < Z_{\text{crit}}$ and unstable for $Z > Z_{\text{crit}}$. According to the principle of exchange of stability (see [15, 16, 44] and [3] for an application to population dynamics), the branch of positive steady states described by (5.4) is locally (i.e., for Z near Z_{crit}) stable if the bifurcation is supercritical and unstable if it is subcritical.

For the nontrivial steady states a detailed analysis of the global shape of the curve defined by (5.4) and the changes in the position of the roots of the associated characteristic equation along this curve requires a considerable effort and is beyond the scope of this paper. The point, however, is that the results of this paper allow one to derive conclusions about (in)stability and Hopf bifurcation from the appropriate information about these roots.

5.2. A structured metapopulation model. In this subsection we consider a metapopulation model first introduced in [33] and later modified and analyzed in [34, 35, 36, 37, 39, 41]. The model considers an infinite collection of identical patches that can support local populations. The structuring variable is the size x of a local population. Local populations may go extinct due to a catastrophe, but the vacated patch is immediately recolonized by migrants arriving from other patches. In PDE-formulation, the model is described by

$$\frac{\partial}{\partial t}n(t,x) + \frac{\partial}{\partial x}\left(f(x,D(t))n(t,x)\right) = -\mu(x)n(t,x), \quad t>0,\ x>0, \tag{5.9}$$

$$f(0,D(t))n(t,0) = \int_{\mathbf{R}_+} \mu(x)n(t,x)\,dx, \tag{5.10}$$

$$\frac{d}{dt}D(t) = -(\alpha+\nu)D(t) + \int_{\mathbf{R}_+} \gamma(x)n(t,x)\,dx, \quad t>0, \tag{5.11}$$

supplemented, of course, by appropriate initial conditions.

In (5.9)–(5.11), $n(t,\cdot)$ is the size-distribution of local populations at time t, and $D(t)$ is the density of dispersers at time t. $\gamma(x) = k(x)x$ is the emigration rate ($k(x)$ is the *per capita* emigration rate), α is the rate at which dispersers immigrate into a patch, and ν is the death rate during dispersal. $f(x,D)$ is the growth rate of a local population of size x when the density of dispersers is D. It is given by

$$f(x,D) = g(x) + \alpha D = r(x)x - k(x)x + \alpha D, \tag{5.12}$$

where $r(x)$ is the difference between the per capita birth and death rates when the local population size is x. Finally, $\mu(x)$ is the size-specific catastrophe rate of local populations.

Next we rewrite the equations (5.9)–(5.11) as a coupled system of the form (4.1)–(4.2). By the *age* of the local population of a patch we shall mean the time elapsed since the last catastrophe. Hence a local population of age a at time t had size zero at time $t-a$. The dynamics of such a local population is therefore described by the scalar ODE

$$\frac{d}{d\tau}x(\tau) = g(x(\tau)) + \alpha D_t(\tau - a), \quad 0<\tau\le a, \tag{5.13}$$

$$x(0) = 0. \tag{5.14}$$

For the solution of (5.13)–(5.14) we use the notation

$$x(\tau) = X(\tau, a, D_t), \quad 0\le\tau\le a. \tag{5.15}$$

The probability that a local population survives to age a, given the history of D, is

$$\mathcal{F}(a, D_t) = e^{-\int_0^a \mu(X(\tau,a,D_t))\,d\tau}. \tag{5.16}$$

The results formulated in this paper require a finite maximum life span. In the present model, this could be achieved by assuming that the catastrophe rate has a nonintegrable singularity at some finite local population size. However, in nature it is often the case that large local populations are much less prone to extinction than small ones, which experience a high risk of extinction due to demographic stochasticity. If this is the case, μ should rather be a decreasing function of local population size instead of blowing up. Also, exponentially distributed lifetimes (corresponding to constant catastrophe rates μ) occur frequently in applications. Fortunately, our theory carries over almost *verbatim* to the case of infinite delay (see section 6). In this example we shall therefore not make the assumption of a finite maximum life span. In particular, we shall allow the catastrophe rate μ to be constant.

We can now express the age-distribution

$$m(t, a) = f(X(a, a, D_t), D(t))n(t, X(a, a, D_t)) \tag{5.17}$$

of local populations in terms of the histories of the disperser density D and the birth rate

$$b(t) = f(0, D(t))n(t, 0) \tag{5.18}$$

of local populations as follows:

$$m(t, a) = b(t - a)\mathcal{F}(a, D_t) = b_t(-a)\mathcal{F}(a, D_t), \quad t \geq 0,\ 0 \leq a. \tag{5.19}$$

Equations (5.10) and (5.11) now yield the following system of a delay equation coupled with a delay differential equation:

$$b(t) = \int_0^\infty \mu(X(a, a, D_t))\mathcal{F}(a, D_t)b_t(-a)\, da, \tag{5.20}$$

$$\frac{d}{dt}D(t) = -(\alpha + \nu)D(t) + \int_0^\infty \gamma(X(a, a, D_t))\mathcal{F}(a, D_t)b_t(-a)\, da. \tag{5.21}$$

Here D plays the role of the environmental interaction variable. As we saw in section 4, the state space of b_t should be taken as L^1 and the space of D_t as C.

The steady state equation for (5.20), (5.21) is readily found. For constant functions b and D, (5.20) becomes an identity because

$$\int_0^\infty \mu(X(a, a, \overline{D}))\mathcal{F}(a, \overline{D})da = 1. \tag{5.22}$$

The identity (5.22) reflects the conservation of local populations: After a catastrophe, the patch is immediately recolonized. If we normalize the total amount of patches to 1, then

$$\overline{b} = \frac{1}{\int_0^\infty \mathcal{F}(a, \overline{D})da} \tag{5.23}$$

and the steady state condition becomes

$$\overline{D} = \frac{1}{\alpha+\nu} \cdot \frac{\int_0^\infty \gamma(X(a,a,\overline{D}))\mathcal{F}(a,\overline{D})da}{\int_0^\infty \mathcal{F}(a,\overline{D})da}. \tag{5.24}$$

The numerator on the right-hand side of (5.24) is the expected number of dispersers produced by a local population during its lifetime. When divided by the expected lifetime $\int_0^\infty \mathcal{F}(a,\overline{D})da$, it yields the average rate of dispersers produced by a patch, and when this rate is multiplied by the expected sojourn time $1/(\alpha+\nu)$ in the disperser pool, one gets the local population's contribution to the disperser pool. Equation (5.24) says that at equilibrium this contribution equals the steady disperser density (i.e., dispersers per patch).

In order to derive a characteristic equation and apply our theory, we have to show that the right-hand sides of (5.20) and (5.21) are differentiable in b_t and D_t. As they are linear in b_t, we only have to prove differentiability of $\varphi \mapsto X(\tau,a,\varphi)$ as a mapping on C. The differentiability of $\varphi \mapsto \mathcal{F}(a,\varphi)$ then follows immediately, and to obtain the desired result we only have to assume differentiability of the real functions μ and γ.

Assume that g is differentiable. Differentiating the integrated form of (5.13), (5.14),

$$X(\tau,a,\varphi) = \int_0^\tau g(X(\sigma,a,\varphi))\,d\sigma + \alpha\int_0^\tau \varphi(\sigma-a)\,d\sigma, \tag{5.25}$$

with respect to φ at $\overline{D}$, one obtains the linear equation

$$\frac{\partial}{\partial\varphi}X(\tau,a,\overline{D})\varphi = \int_0^\tau g'(X(\sigma,a,\overline{D}))\frac{\partial}{\partial\varphi}X(\sigma,a,\overline{D})\varphi\,d\sigma + \alpha\int_0^\tau \varphi(\sigma-a)\,d\sigma, \tag{5.26}$$

the solution of which is

$$\frac{\partial}{\partial\varphi}X(\tau,a,\overline{D})\varphi = \alpha\int_0^\tau e^{\int_\sigma^\tau g'(X(s,a,\overline{D}))\,ds}\varphi(\sigma-a)\,d\sigma. \tag{5.27}$$

Let us now assume that the catastrophe rate μ and the per capita emigration rate k are constant. The survival probability then becomes independent of φ: $\mathcal{F}(a) = \exp(-\mu a)$, and the equations (5.20), (5.21) simplify to

$$b(t) = \int_0^\infty \mu e^{-\mu a} b_t(-a)\,da, \tag{5.28}$$

$$\begin{aligned} \frac{d}{dt}D(t) &= -(\alpha+\nu)D(t) \\ &\quad + k\int_0^\infty X(a,a,D_t)e^{-\mu a}b_t(-a)\,da, \end{aligned} \tag{5.29}$$

while the steady state condition (5.24) simplifies to

$$\overline{D} = \frac{\mu k}{\alpha+\nu}\int_0^\infty X(a,a,\overline{D})e^{-\mu a}da. \tag{5.30}$$

We take the per capita emigration rate k as a bifurcation parameter. Note that $X(a,a,\overline{D})$, being the solution of $dx/da = r(x)x - kx + \alpha\overline{D}$, $x(0) = 0$, depends on k, so in general one cannot solve (5.30) explicitly for k as a function of $\overline{D}$.

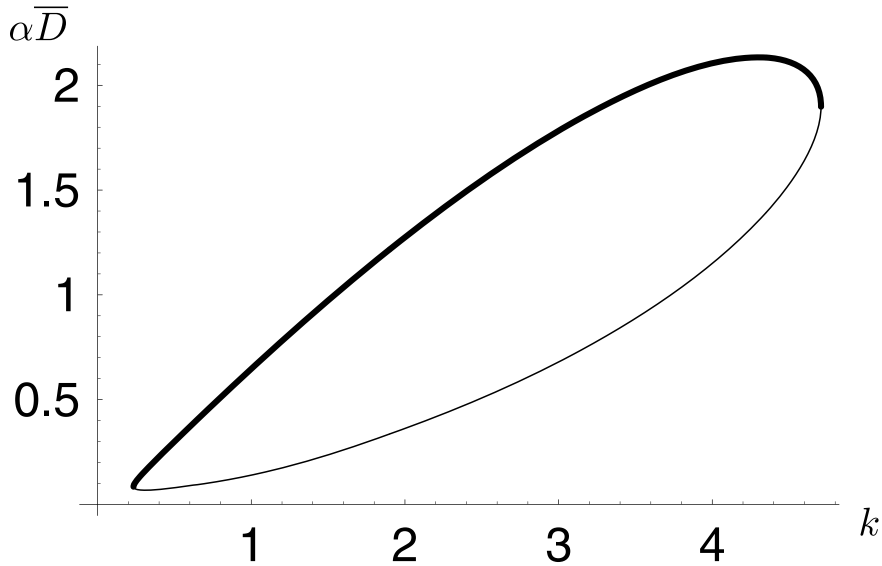

FIG. 1. *Equilibrium values for the immigration rate $\alpha\overline{D}$ in the case of an Allee effect with $f(x, D)$ given by* (5.32)*. Parameters: $\alpha = 0.5$, $\mu = 0.2$, $\nu = 0.1$, $H = 1$, $\beta = 18$, $c = 1$, $d = 8$.*

Next we assume that there is an *Allee effect*, that is, that small local populations have a negative intrinsic growth rate [1] and therefore cannot persist without a sufficiently large immigration rate. We model this by assuming that the per capita birth rate depends on the local population size x as

$$\frac{\beta x}{H + x} \tag{5.31}$$

for some positive constants β and H. For a discussion of the rationale for this choice and its biological interpretation we refer to [18, 38]. Furthermore, if we make the standard assumption of density-dependent death rate as in the logistic equation, we end up with

$$f(x, D) = \left(\frac{\beta x}{H + x} - c - dx \right) x - kx + \alpha D \tag{5.32}$$

for some positive constants c and d.

It is clear that with the choice (5.32), the curve defined by (5.30) in the $k\overline{D}$-plane does not touch the axis $\overline{D} = 0$. As a matter of fact, as shown in [39], equation (5.30) defines a closed curve like the one depicted in Figure 1, at least for some choices of parameter values. As seen in Figure 1, there is a saddle-node bifurcation at $k \approx 0.2$ and another one at $k \approx 4.9$. In contrast to the situation with the transcritical bifurcation treated in subsection 5.1, we cannot allude here to the principle of exchange of stability to determine which of the two branches is stable and which is not. That information has to be deduced from the characteristic equation, which we now derive.

The linearized version of (5.28), (5.29) is

$$\psi(t) = \int_0^\infty \mu e^{-\mu a} \psi(t - a)\, da, \tag{5.33}$$

$$\frac{d}{dt}\varphi(t) = -(\alpha+\nu)\varphi(t) + k\int_0^\infty Y(a,\overline{D})\psi(t-a)\,da$$
$$+ \alpha k \int_0^\infty Z(a,\overline{D})\varphi(t-a)\,da, \tag{5.34}$$

where

$$Y(a,\overline{D}) = X(a,a,\overline{D})e^{-\mu a}, \tag{5.35}$$

$$Z(a,\overline{D}) = \mu\int_a^\infty e^{\int_{\sigma-a}^{\sigma} g'(X(\tau,\sigma,\overline{D}))d\tau} e^{-\mu\sigma}\,d\sigma. \tag{5.36}$$

Taking the Laplace transform of (5.33), (5.34), one obtains

$$\widehat{\psi}(\lambda) = \frac{\mu}{\mu+\lambda}\widehat{\psi}(\lambda), \tag{5.37}$$

$$\lambda\widehat{\varphi}(\lambda) - \varphi(0) = -(\alpha+\nu)\widehat{\varphi}(\lambda) + k\widehat{Y}(\lambda,\overline{D})\widehat{\psi}(\lambda) + \alpha k\widehat{Z}(\lambda,\overline{D})\widehat{\varphi}(\lambda). \tag{5.38}$$

Hence the characteristic equation is

$$\det\begin{pmatrix} 1-\frac{\mu}{\mu+\lambda} & 0 \\ -k\widehat{Y}(\lambda,\overline{D}) & \lambda+\alpha+\nu-\alpha k\widehat{Z}(\lambda,\overline{D}) \end{pmatrix} = 0. \tag{5.39}$$

$\lambda = 0$ is always a root of (5.39). The reason is the indeterminacy of $\overline{b}$ explained above. The situation is analogous to the simple ODE SIS-model of mathematical epidemiology. If one treats the SIS model as a two-dimensional ODE, zero is an eigenvalue, which disappears after the substitution $S = N - I$ (N is the total population). Similarly, in our case the stability of the steady state is determined by the location in the complex plane of the roots of the equation

$$\lambda+\alpha+\nu-\alpha k\widehat{Z}(\lambda,\overline{D}) = 0. \tag{5.40}$$

For $\lambda \neq -(\alpha+\nu)$, (5.40) is equivalent to

$$1 - \alpha k\frac{\widehat{Z}(\lambda,\overline{D})}{\lambda+\alpha+\nu} = 0, \tag{5.41}$$

and to this equation we can apply Nyquist's criterion (Corollary 2.20). The (numerical) results show that the upper branch (the thick line in Figure 1) is stable, while the lower branch (thin line) is unstable.

6. Discussion. The principle of linearized stability and the Hopf bifurcation theorem are among the fundamental results of the theory of ODEs. In the past three decades they have been generalized in various ways to infinite dimensional dynamical systems. In this paper we have used perturbation theory of adjoint semigroups (sun-star-calculus) to prove the principle of linearized stability and the Hopf bifurcation theorem for Volterra functional equations. The sun-star-framework made it possible to treat fully nonlinear functional equations as semilinear problems by transforming the original equation into an abstract integral equation of variation-of-constants type.

The transformation of the fully nonlinear problem into a seminlinear problem was made possible by extending the originally given state space. The idea that one should extend the state space when dealing with Hopf bifurcation for delay differential equations was introduced by Chow and Mallet-Paret in 1977 in a pioneering paper [7]. The sun-star-framework provides a functional analytic elaboration of this idea.

The principle of linearized stability consists of two parts. The first part concerns stability and says that if all roots of the so-called characteristic equation associated with a steady state have negative real part, then the steady state is exponentially stable. The second part states that if at least one characteristic root has positive real part, then the steady state is unstable.

The proof of the stability part of the principle of linearized stability is relatively simple as it uses only standard estimates and Gronwall's inequality, and therefore this part can be rather easily generalized from the ODE setting to infinite dimensional systems. In contrast, the proof of the instability part is geometric in nature and is even in the finite dimensional case much more difficult than the proof of the stability part. As a consequence, infinite dimensional generalizations of the instability part are comparatively rare in the literature. In many cases authors hint that the instability part is valid, but without giving a formal proof.

In the important paper [19], Desch and Schappacher proved both the stability and instability parts of the principle of linearized stability for nonlinear perturbations of generators of strongly continuous semigroups. Following their proof, Clément et al. [11] proved both parts within the context of adjoint semigroups and Thieme [53] within the framework of integrated semigroups. In the book [23] sun-star-calculus was systematically used for stability and bifurcation analysis of delay differential equations.

Our main motivation comes from structured population dynamics. In their seminal paper [30], Gurtin and MacCamy proved the stability part of the principle of linearized stability for age-structured populations but passed the instability part with silence. The same applies to most of the papers published in the early 1980s (e.g., [31, 32]). In the first comprehensive book [56] on the mathematical theory of age-structured population dynamics, Webb treated both the stability and instability parts using semigroup methods. Finally, in a somewhat neglected paper [50], Prüß proved both the stability and instability parts in a very general setting of several interacting age-structured populations.

When one moves from age-structured models to general physiologically structured models, even results on stability become rare. Tucker and Zimmermann [55] proved the stability part for a class of models, which, however, did not allow for a finite number of states-at-birth. Calsina and Saldaña [5] 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. They also gave sufficient conditions for conditional convergence to a steady state. Here conditional convergence means that the size distribution converges to a steady distribution in L^1, given that the total population converges.

There is also a vast literature on the stability of Volterra integral equations

$$x(t) = \int_0^t k(s)x(t-s)ds + G(x)(t); \tag{6.1}$$

see [29] and the references and historical remarks therein. These results are usually based on a classical theorem of Paley and Wiener [48] or generalizations thereof. In its basic form, the Paley–Wiener theorem says that if the kernel k belongs to $L^1(\mathbf{R}_+)$, then its resolvent kernel r is in $L^1(\mathbf{R}_+)$ if the characteristic equation

$$\det\left(E - \widehat{k}(\lambda)\right) = 0 \tag{6.2}$$

has no roots in the closed half-plane $\{\lambda \in \mathbf{C} : \mathrm{Re}\lambda \geq 0\}$. Using the fact that the solution x of (6.1) satisfies

$$x(t) = G(x)(t) + \int_0^t r(t-s)G(x)(s)ds, \tag{6.3}$$

it is easy to show that if $G(x)$ is of higher order, then the zero solution of (6.1) is stable. If (6.2) has no roots in $\{\lambda \in \mathbf{C} : \mathrm{Re}\lambda \geq -\varepsilon\}$ for some $\varepsilon > 0$ (this is the case, for instance, if k has compact support), then 0 is exponentially stable. So the stability part of the principle of linearized stability is well known for Volterra integral equations. On the other hand, a clear statement of the instability part seems to be lacking in the literature (however, see [21]). In section 3.5 we showed that our general theory applies to equations of the type (6.1) (at least if k has compact support), and hence it provides the instability part of the principle of linearized stability for Volterra integral equations.

In some respects the theory presented in this paper is not general enough. It does not, for instance, encompass all population dynamical applications that we want to consider. First of all, we have made the assumption of a finite delay h. In applications to population dynamics this corresponds to the assumption of a maximum individual life span. Although true in nature, it disregards the (mathematically) important case of exponentially distributed lifetimes. However, this is not a serious defect. The assumption was made to have sun-reflexivity, which simplified analysis for the following reason: For a norm continuous function $f : [0,\infty) \to X^{\odot *}$, the weak*- integral

$$\int_0^t T_0^{\odot *}(t-\sigma)f(\sigma)d\sigma \tag{6.4}$$

takes values in $X^{\odot\odot}$ (Proposition 2.2). The key advantage of assuming sun-reflexivity is that then the integral automatically takes values in $j(X)$, so that we can apply j^{-1} to obtain an element of X. If, by lack of compactness, we do not have sun-reflexivity, it may still be the case that this integral takes values in $j(X)$ if we restrict f to take values in a certain subspace of $X^{\odot *}$. For (nonlinear) perturbation operators taking values in such a subspace, the complete machinery retains its strength and all the results carry through. We intend to elaborate on this very useful remark in detail in a separate publication, with two motivating examples: infinite delay and a continuum of birth states.

Secondly, the unknown $x(t)$, which in population dynamical applications is a vector consisting of the components of the birth rate and the environmental interaction variables, is a vector in $\mathbf{R}^N$. There are important applications, for instance, models of size-dependent cannibalism [8], which require an infinite dimensional environmental condition. Prüß [50] treated an age-structured model, and Calsina and Saldaña [6] a size-structured model with an infinite dimensional environmental condition by other means, but it is unclear how the results of the present paper could be extended to cover that situation.

Thirdly, because the Nemytskiĭ operator from $L^1([-h,0];\mathbf{R}^N)$ to $L^1([-h,0];\mathbf{R}^N)$ generated by a smooth function $g : \mathbf{R}^N \to \mathbf{R}^N$ is Fréchet differentiable if and only if g is affine, we have to assume in applications to population dynamics that, for instance, the death rate is of the form $\mu(\xi, I) = \mu_0(\xi) + \mu_1(\xi)I$, where ξ is the individual state variable and I the interaction variable. Interestingly, this affine form, which corresponds to mass action interaction, is biologically the most relevant. In the future we shall investigate this aspect in detail in collaboration with J. A. J. Metz.

Appendix. Proof of Theorem 2.8. In this appendix we prove that if T_0 is eventually compact and if the perturbation $B : X \to X^{\odot *}$ is a compact operator, then the semigroup T defined by (LAIE) is eventually compact. This does not seem to have been stated in the literature yet. Clément et al. [13] proved the eventual compactness of the perturbed semigroup under the slightly weaker assumption that $R(\lambda, A_0^{\odot *})B$ is compact, but in addition to that they needed the assumption that

$$t \mapsto \int_0^t T_0^{\odot *}(t-\tau) B T(\tau) d\tau$$

is eventually uniformly continuous (that is, continuous from $[t_0, \infty)$ to $\mathcal{L}(X)$ equipped with the uniform operator topology, for some t_0).

The corresponding result for the case in which B maps X into X is known [26, Proposition 1.14, p. 166]. Without the compactness assumption on B the statement is false [26, Example 1.15, p. 166]. Therefore, the task in Exercise 2.5 of [23, p. 57] is impossible.

The proof in [26] is rather opaque, as it is based on statements like "without loss of generality ... we may ... assume that [X] is $C[0, 1]$" [26, p. 525]. The proof provided here, which also covers the case in which the range of B lies in X, is more straightforward as it depends only on basic properties of semigroups and integrals.

Note. After we had finished this paper, Horst Thieme pointed out to us that Theorem 2.8 is an easy consequence of [54, Theorem 3], which he proved using the theory of integrated semigroups.

PROPOSITION A.1. *Let $B : X \to X^{\odot *}$ be compact. Then $j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau$ is a compact operator from X to X.*

Proof. By Schauder's theorem, $B^* : X^{\odot **} \to X^*$ is compact, and hence so is its "restriction" to $X^\odot$. Because the composition of a compact operator and a bounded operator is compact, it follows that $B^* \int_0^t T_0^\odot(\tau) d\tau : X^\odot \to X^*$ is compact. Using Schauder's theorem once more, we conclude that

$$\left(\left(B^* \int_0^t T_0^\odot(\tau) d\tau \right)^* \right)\Big|_X = j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau$$

is compact, as asserted. $\square$

Let V be a subset of a Banach space. In what follows, $\overline{\text{con}}\, V$ denotes the closed convex hull of V, that is, the smallest closed convex set that contains V. Without any specifications, closedness refers to the norm topology. When other topologies are considered, the topology is indicated by a subscript. For instance, if $V \subset X^*$, then $\overline{\text{con}}_{\sigma(X^*, X)}\, V$ is the smallest weakly* closed convex set that contains V.

The closed ball of radius r with center at x is denoted by $U(x, r)$.

THEOREM A.2. *Let $B : X \to X^{\odot *}$ be compact. Then $j^{-1} \int_0^t T_0^{\odot *}(\tau) B T(t - \tau) d\tau$ is a compact operator from X to X.*

Proof. Because T is a strongly continuous semigroup on X, the function $y : \tau \mapsto T(t - \tau)x$ is continuous from $[0, t]$ to X, and its range belongs to $U(0, M)$ for all $x \in U(0, 1)$ for some $M \geq 1$. Because $j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau$ is compact,

$$j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau (U(0, M))$$

is relatively compact, and hence

$$\overline{\text{con}}\, j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau (U(0, M))$$

is compact [51, Theorem 3.25, p. 72]. The proof is therefore completed if we can show that

$$j^{-1} \int_0^t T_0^{\odot *}(\tau) B T(t-\tau) x d\tau \in t\, \overline{\text{con}}\, j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau (U(0, M)).$$

This last statement is proved in the next lemmas. ◻

Lemma A.3. *Let $t \mapsto x^*(t)$ be a weakly* continuous function from $[a, b]$ to X^*. Then*

$$\int_a^b x^*(t) dt \in (b-a)\, \overline{\text{con}}_{\sigma(X^*, X)}\, x^*([a, b]).$$

Proof. First note that by the uniform boundedness principle a weakly* continuous function is norm bounded on compact intervals. By the definition of the weak* integral, one has that $\int_a^b x^*(t) dt$ belongs to the ball

$$U\left(0, (b-a) \sup_{a \le t \le b} \|x^*(t)\|\right),$$

which is weakly* compact by the Banach–Alaoglu theorem. Clearly $x^*([a, b]) \subset U\left(0, \sup_{a \le t \le b} \|x^*(t)\|\right)$, which is convex and weakly* compact. Hence

$$\overline{\text{con}}_{\sigma(X^*, X)}\, x^*([a, b])$$

is weakly* compact. Theorem 3.27 of [51] now implies the assertion. ◻

Lemma A.4. *Let $y : [0, t] \to X$ be continuous. Then*

$$x_0 := j^{-1} \int_0^t T_0^{\odot *}(\tau) B y(t-\tau) d\tau \in t\, \overline{\text{con}}\, j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau\, y([0, t]).$$

Proof. Because $j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau$ is a compact operator from X to X (Proposition A.1), the set $V := j^{-1} \int_0^t T_0^{\odot *}(\tau) B d\tau\, y([0, t])$ is relatively compact in X, and hence $t\, \overline{\text{con}}\, V$ is compact [51, Theorem 3.25, p. 72]. It follows that $t\, \overline{\text{con}}\, j(V) = j(t\, \overline{\text{con}}\, V)$ is compact in $X^{\odot *}$. Because $\sigma(X^{\odot *}, X^{\odot})$ is weaker than the norm topology of $X^{\odot *}$, the set $t\, \overline{\text{con}}\, j(V)$ is also $\sigma(X^{\odot *}, X^{\odot})$-compact.

Suppose x_0 does *not* belong to $t\, \overline{\text{con}}\, V$ or, equivalently, $j x_0 \notin t\, \overline{\text{con}}\, j(V)$. A version of the Hahn–Banach theorem [51, Theorem 3.4, p. 58] then implies that there exist $x^{\odot} \in X^{\odot}$ and $\gamma \in \mathbf{R}$ such that

$$\operatorname{Re} \langle x^{\odot}, j x_0 \rangle < \gamma < \operatorname{Re} \langle x^{\odot}, x^{\odot *} \rangle \quad \text{for all } x^{\odot *} \in t\, \overline{\text{con}}\, j(V).$$

So

$$\left\{ x^{\odot *} \in X^{\odot *} : \operatorname{Re} \langle x^{\odot}, x^{\odot *} - j x_0 \rangle < \gamma \right\}$$

is a $\sigma(X^{\odot *}, X^{\odot})$-neighborhood of $j x_0$ which does *not* intersect $t\, \overline{\text{con}}\, j(V)$. Hence $j x_0 \notin t\, \overline{\text{con}}_{\sigma(X^{\odot *}, X^{\odot})}\, j(V)$. But this contradicts Lemma A.3. ◻

Theorem 2.8 is now an immediate corollary of Theorem A.2.

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