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Boundedness, global existence and continuous dependence for nonlinear dynamical systems describing physiologically structured populations

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Abstract

The paper is aimed as a contribution to the general theory of nonlinear infinite dimensional dynamical systems describing interacting physiologically structured populations. We carry out continuation of local solutions to maximal solutions in a functional analytic setting. For maximal solutions we establish global existence via exponential boundedness and by a contraction argument, adapted to derive uniform existence time. Moreover, within the setting of dual Banach spaces, we derive results on continuous dependence with respect to time and initial state.

To achieve generality the paper is organized top down, in the way that we first treat abstract nonlinear dynamical systems under very few but rather strong hypotheses and thereafter work our way down towards verifiable assumptions in terms of more basic biological modelling ingredients that guarantee that the high level hypotheses hold.

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1. Introduction

1.1. Aims

The main aim of this paper is to present several new results concerning the general theory of nonlinear physiologically structured population models. Traditionally, see e.g. [30,24] and the references in both, the dynamics of such populations are described by partial differential equations (PDE), but more recently, see [10,12] by constructing next state operators, which define a nonlinear semigroup. Following the second approach, we here extend the local constructions of [10], give conditions for the existence of global solutions in terms of exponential bounds and establish continuity properties. For steady-state analysis for structured populations, see [11] (general structured populations), [15,16] (application to a cannibalism model) and for numerical approaches see [2–4,8,20].

An essential tool for constructing local next state operators is the so-called *method of interaction variables*, which consists basically in splitting a quasilinear problem into a linear problem and (coupled to that) a fixed point problem. After having outlined this method, we start by establishing a linear theory, which has a biological interpretation by itself: it describes the population dynamics, when conditions are such that interactions can be ignored. In particular, we illustrate how the mathematical theory of adjoint semigroups provides a natural framework for the investigation of continuity properties. More generally, the motivation for the use of duality is the combination of a general and natural population state space and a convenient space, the space of continuous functions vanishing at infinity, to work with. We present examples of semigroups representing a population evolution that are the “not strongly continuous adjoint” of a strongly continuous semigroup. In view of the coupling to a fixed point problem, the central object in our linear theory is a linear semigroup, which is not parametrized by time, but more generally by functions of time, which we call *inputs*. In this setting, we generalize the well-known fact, that the adjoint semigroup of a strongly continuous semigroup is continuous in the weak* topology, see [14] or [6], to semigroups with infinite dimensional parameters. In the classic [19, Section 10.10] treats aspects of n -parameter semigroups, but does not contain duality results.

Coming to the nonlinear problem, we find that continuous dependence can quickly be deduced from the corresponding properties of the linear problem. Moreover we demonstrate how, at an abstract level, under very few assumptions a fairly general local construction can be extended to maximal time intervals, such that one gets a *nonlinear semiflow*. Once established, the semiflow properties provide a framework for investigating global existence and qualitative behaviour.

From a mathematical point of view, the closest kin to the dynamical systems considered here are generated by differential equations with state-dependent delay. In fact we are dealing with “translation along orbits of ordinary differential equation” semigroups provided with nonlocal boundary conditions. The special feature is that both, the direction of the orbits and the speed of translation incorporate nonlinearities (it is this property that prevents us from applying the theory developed by Marcus and Mizel [23]). Our hope is that in the long run the kind of tools and results developed

for equations with state-dependent delay (see [22,29,5] and the references given there) can be extended to the present more general class of dynamical systems (a side-aim of the present paper is to draw the attention of the “delay” community to this class of models and the mathematical problems they pose).

Our notion of “input” yields a linear skew-product flow when inputs are defined for all time (see e.g. [27] and the references given there). So one might say that we construct a nonlinear dynamical system by providing a linear skew-product flow with a constraint that specifies the “parameter” part of the flow in terms of the dynamics on the state space. We are not aware of any other examples of such a situation but are curious whether there are any!

1.2. Background and motivation from structured populations

To motivate the treatment of nonlinearities with interaction variables, we consider the PDE

$$\begin{aligned} \frac{\partial}{\partial t} n(t, x) + \frac{\partial}{\partial x} g(x, n(t, \cdot)) n(t, x) &= -\mu(x, n(t, \cdot)) n(t, x), \\ g(x_b, n(t, \cdot)) n(t, x_b) &= \int_{x_b}^{x_m} \beta(x, n(t, \cdot)) n(t, x) dx, \\ n(0, x) &= n_0(x), \end{aligned}$$

which describes the development of a population structured by individual body size. Here, x denotes the size of the individual and $n(t, x)$ the density of individuals having size x at time t . By g , μ and β we denote the individual rates of growth, death and reproduction, respectively, which are allowed to depend on individual size and population density. Finally, x_b and x_m denote size at birth and maximum size and $n_0(x)$ an initial population density.

In the one species case, the dependence on $n(t, \cdot)$ may reflect cannibalistic interactions, see [7,10], but the PDE can via vector notation easily be extended to multispecies models, see e.g. [25].

Note, that if the structuring variable x models an individuals age instead of its size, growth means ageing, hence g equals one and the PDE is semilinear, when viewed in the framework of dual semigroups and perturbation theory [9]. In the case of size structure, however, the growth rate g is in general density dependent and the PDE is no longer semilinear but quasilinear. For such problems, it seems hard to derive perturbation results, since generators cannot be defined in a manner analogous to the semilinear case.

We now outline how the system can be treated with the help of interaction variables. The proper definitions will be given in Section 2 when we follow the “constructive” approach. Let us denote by $I(t)$ a so-called input at time t . Think of an input as a variable that has a certain influence on the individuals: a first example is the food concentration that is experienced by an individual, because it influences its growth, maintenance and reproduction. A second example is the predation pressure an individual experiences,

because it influences its mortality. When taking both into account, $I(t)$ becomes a two component function. The crucial modelling task is, as we will now illustrate, to define inputs in such a way that if they are known, individuals are independent from one another and the resulting population system is linear. So one should define inputs such that the density dependences incorporated in g , μ and β can be replaced by inputs. In the often encountered case where a density dependence i occurs via a dependence on

$$\int \gamma_i(x)n(t, x) dx,$$

i.e., via some function γ_i weighing the influence of individuals on the basis of their state, one defines

$$I_i(t) := \int \gamma_i(x)n(t, x) dx.$$

Then the PDE can be rewritten as a combination of a linear system

$$\begin{aligned} \frac{\partial}{\partial t}n(t, x) + \frac{\partial}{\partial x}g(x, I_1(t))n(t, x) &= -\mu(x, I_2(t))n(t, x), \\ g(x_b, I_1(t))n(t, x_b) &= \int_{x_b}^{x_m} \beta(x, I_1(t))n(t, x) dx, \\ n(0, x) &= n_0(x) \end{aligned}$$

and a feedback law (in vector notation)

$$I(t) = \int \gamma(x)n(t, x) dx. \tag{1.1}$$

Suppose for now, that we have solved the linear system by constructing a linear operator T_I (e.g. acting on L^1) with the interpretation that

$$T_{\rho(t)I}n \tag{1.2}$$

represents the population state which has evolved from an initial state n under an input I after t time units (here by $\rho(t)$ we denote the restriction operator which will be properly defined later). Next, replace n in (1.1) by (1.2) to obtain the equation

$$I(t) := \int \gamma(y)(T_{\rho(t)I}n)(y) dy, \tag{1.3}$$

which, after dropping the assumption that I is given, we interpret as a fixed point equation for I . Suppose that (1.3) has a unique solution I_n , depending on the initial

state n , then $I_n(t)$ is the input value, the population produces for its individuals at time t if it is left to its own devices. Hence, by substituting I_n into (1.2) we obtain a nonlinear operator

$$T_{\rho(t)I_n}n, \tag{1.4}$$

representing the population state after time t .

One of the objectives of this paper is to study boundedness and continuity properties of (1.4). The construction suggests to first derive such properties for (1.2) and so we shall do so.

1.3. Structure of the paper

The paper employs three levels of (decreasing) generality. At each level, we first work on a linear theory and then draw conclusions for the nonlinear problem, which makes up for the $3 \times 2 = 6$, Sections 2–7.

In Section 2 we state the hypotheses concerning the existence of a family of linear operators with input having the semigroup property and subsequently show boundedness in the operator norm. The fact that, for fixed finite time, this boundedness is for a large class of models uniform with respect to the input, allows to transfer boundedness very quickly to the nonlinear system, see Section 3.7. Next, we establish for the linear system continuous dependence on the initial value and, via duality, on the input, both of which are used for proving for the nonlinear system continuous dependence on the initial value. Again via duality, we finally give conditions for continuous dependence of the linear system on time, a property that can also be transferred quickly to the nonlinear system, see Section 3.9.

In Section 3 we start by explaining how via a fixed point assumption a local nonlinear solution is constructed. With this construction we proceed as is usual in dynamical systems in that we establish the existence and uniqueness of a global solution via local and maximal unique extension and exponential boundedness (“no blow up”). Once we have a global solution, we conclude Section 3 by showing the earlier mentioned continuity properties for the nonlinear system.

In Sections 4 and 5 we let the abstract systems of Sections 2 and 3 represent the state evolution of a structured population. The individuals are characterized by two so-called kernels that specify survival probabilities and offspring production. Subsequently we work out conditions for these kernels such that the assumptions made in Sections 2 and 3 hold.

In Sections 6 and 7 we verify these conditions for the case of deterministic individual development and to do so construct the kernels in terms of vital functions.

In our presentation we employ a theory orientated top down approach, but in Section 8 we summarize the results in a more user friendly manner by applying them to a size structured population with deterministic individual growth.

We distinguish explicitly between hypotheses and assumptions. The assumptions are assumed to hold throughout the remaining part of the exposition, whereas the hypotheses

are operative throughout the treatment of the level and will be further elaborated in the subsequent level.

The idea for this top down approach is taken from [10]. In spite of this, we try to stay as complementary to [10] as possible, in the way that we establish new results for existing models and with only as much overlap as is necessary to keep the exposition self-contained. We therefore aim for and hope that the presentation is comprehensive and fruitful also for readers not familiar with the earlier paper.

2. Linear dynamical systems with input

2.1. Existence and semigroup property

Take a set Y , of which we will think as the population state space. Acting on Y is a family of operators $\{T_t\}$ that, unlike “ordinary” semigroups see e.g. [14], is not parametrized by time, but more generally by functions of time, which we call *inputs* and shall mostly denote by I .

Let E be some Banach space and let $Z \subset E$, then the inputs are assumed to be elements of $C_s := C([0, s], Z)$ for some $s > 0$, where $C([0, s], E)$ denotes the Banach space of continuous functions equipped with the sup-norm.

Remark 2.1. In this paper we assume inputs to be continuous functions of time (defined on closed intervals). This has some advantages relative to the slightly different setting of [10]. The price we pay is that some models, in which behavioural responses of individuals have jump discontinuities as a function of i-state, are not covered literally by the results that follow.

We define

$$\mathcal{C} := \bigcup_{s \geq 0} C_s,$$

and $l(I)$ as the length of an input I , i.e., $l(I) = s, s \geq 0$ if and only if $I \in C_s$. If $l(I) = 0$ we shall speak of the empty input, which as an individual object will be denoted by \mathbf{I} . We interpret T_{Iy} as the state that has evolved from an initial state y under an input I after $l(I)$ time units. To generalize the usual semigroup property

$$T(s_1)T(s_2) = T(s_1 + s_2) \tag{2.1}$$

to maps parametrized by inputs, we define two operations on \mathcal{C} .

Definition 2.2. For $I \in \mathcal{C}$ and $s \in [0, l(I)]$, we denote by $\rho(s)I$ the *restriction* of I to the interval $[0, s]$, i.e.,

$$(\rho(s)I)(t) = I(t), \quad t \in [0, s].$$

The (left) *shift* $\theta(-s)I$ is, for $s \in [0, l(I)]$, defined by

$$(\theta(-s)I)(t) = I(t + s), \quad t \in [0, l(I) - s].$$

Note, that $\rho(s)(C_t) = C_s$ and $\theta(-s)(C_t) = C_{t-s}$ for all $s \in (0, t]$.

Now we are ready to formulate the analogue of (2.1) for inputs as

Hypothesis 2.3. For every $I \in \mathcal{C}$ there exists a map $T_I : Y \rightarrow Y$, such that

$$T_I = \text{id}_Y, \tag{2.2}$$

$$T_I = T_{\theta(-\sigma)I} T_{\rho(\sigma)I}, \quad 0 \leq \sigma \leq \ell(I). \tag{2.3}$$

For constant inputs we obtain semigroups of maps of Y into Y parametrized by positive real numbers:

Lemma 2.4. *Suppose that \bar{I} is time independent, then with $\bar{T}(s) := T_{\rho(s)\bar{I}}$, one has $\bar{T}(s_1)\bar{T}(s_2) = \bar{T}(s_1 + s_2)$.*

Proof. First note that, for arbitrary inputs one has

$$\rho(s_2)\rho(s_1 + s_2)I = \rho(s_2)I$$

and for constant \bar{I} also

$$\rho(s_1)\bar{I} = \theta(-s_2)\rho(s_1 + s_2)\bar{I}.$$

Therefore,

$$\begin{aligned} \bar{T}(s_1)\bar{T}(s_2) &= T_{\rho(s_1)\bar{I}}T_{\rho(s_2)\bar{I}} = T_{\theta(-s_2)\rho(s_1+s_2)\bar{I}}T_{\rho(s_2)\rho(s_1+s_2)\bar{I}} \\ &= T_{\rho(s_1+s_2)\bar{I}} = \bar{T}(s_1 + s_2). \quad \square \end{aligned}$$

We will discuss Hypothesis 2.3 further in Section 4.1.

2.2. Exponentially bounded linear systems

We shall assume exponential boundedness of the linear system with input. The motivation for this assumption is the following: For any “realistic” population model, individuals have a bounded rate of offspring production, uniformly for all conceivable

inputs, see for instance [21]. Accordingly the population can grow at most exponentially in time or, in other words, there is an exponential a priori bound.

The boundedness will be used to prove the existence of a global solution for the nonlinear system as well as to prove continuous dependence with respect to state and input in the linear theory. Let from now on Y be a Banach space and suppose the T_I are linear operators on Y . Then we can state exponential boundedness as

Hypothesis 2.5. There exist constants $c \geq 1$ and $k \geq 0$, such that for all $y \in Y$ and all $I \in \mathcal{C}$ the estimate $\|T_I y\| \leq c e^{kI} \|y\|$ holds.

We shall verify the hypothesis in Section 4.2.

2.3. Continuous dependence on the initial value

Continuous dependence on the initial population state follows immediately from the linearity of the T_I and the boundedness in Hypothesis 2.5.

Theorem 2.6. Let $s \geq 0$, then $T_I y_n \rightarrow T_I y$ in norm for $n \rightarrow \infty$ if $y_n \rightarrow y$ in Y in norm for $n \rightarrow \infty$, uniformly for $I \in C_s$.

2.4. Adjoint semigroups

We present the concept of duality, which in the more concrete setting of Section 4.3 will allow the combination of a general population state space, which will be a space of measures, and a convenient space to work with, namely the continuous functions.

Suppose that there exists some Banach space X , such that $X^* = Y$, i.e., the population state space Y is the dual space of X . With the pairing

$$\langle \cdot, \cdot \rangle : Y \times X \rightarrow \mathbf{R}$$

we make the identification $y = \langle y, \cdot \rangle$. We assume that the norm on Y is the dual space norm induced by X , i.e.,

$$\|y\| = \sup_{x \in X, \|x\| \leq 1} |\langle y, x \rangle|. \tag{2.4}$$

Now we postulate existence of the preadjoint as

Hypothesis 2.7. Suppose that, for each $I \in \mathcal{C}$, there exists a so-called *preadjoint* operator $\tilde{T}_I : X \rightarrow X$, such that $\langle y, \tilde{T}_I x \rangle = \langle T_I y, x \rangle$, for all $x \in X$ and $y \in Y$.

The verification of this hypothesis will be carried out in Section 4.3. It is easy to prove that, like in the case of one-parameter semigroups, the \tilde{T}_I inherit linearity and the (generalized) semigroup property from their adjoints. Moreover, by Hypothesis 2.5 and

the definition of the dual space norm, one easily deduces that the \tilde{T}_I are bounded with $\|\tilde{T}_I\| = \|T_I\|$. We will sometimes call $\{T_I\}$ the population semigroup to distinguish it from its preadjoint semigroup.

2.5. Weak continuous dependence on the input*

To fill the toolbox for proving continuity properties in the nonlinear theory, we establish continuity of the linear system on the input. For “ordinary” one-parameter semigroups, see [14,6] it is well-known, that the adjoint of a strongly continuous semigroup is in general not strongly continuous but continuous in the weak* topology. Hence, by Lemma 2.4, we cannot expect strong continuity for the T_I either, see Example 6.13. The following continuity property of the preadjoint semigroup will be used to show continuous dependence of the T_I in the weak* topology.

Hypothesis 2.8. There exists some $l > 0$, such that for all $x \in X$ and all $\varepsilon > 0$, there exists some $\delta = \delta_0(\varepsilon, x)$ such, that

$$\|\tilde{T}_I x - \tilde{T}_J x\| \leq \varepsilon \tag{2.5}$$

holds for all $s \in [0, l]$ and all $I, J \in C_s$ with

$$\|I - J\| \leq \delta.$$

Remark 2.9. We cannot assume uniformity in x (on bounded sets), because then from (2.5) one could deduce continuity of the \tilde{T}_I in the operator norm and, since

$$\|T_I - T_J\| = \|\tilde{T}_I - \tilde{T}_J\|,$$

continuity of $I \mapsto T_I$ in the operator norm, which we do not have in the applications that we have in mind (see Example 6.13).

The semigroup property now guarantees that we can extend estimate (2.5) to inputs of arbitrary length. However, since the evolution of the state is input dependent, we lose uniformity in I :

Proposition 2.10. For all $s > 0$, $I_0 \in C_s$, $x \in X$ and $\varepsilon > 0$, there exists some $\delta = \delta_1(\varepsilon, x, s, I_0)$ such that

$$\|\tilde{T}_I x - \tilde{T}_{I_0} x\| \leq \varepsilon$$

holds for all $I \in C_s$ with

$$\|I - I_0\| \leq \delta.$$

Proof. Choose l according to Hypothesis 2.8. Next, define

$$N := \max\{n \in \mathbf{N} : s \geq nl\},$$

then $0 \leq s - Nl \leq l$ and by Hypothesis 2.5 one has

$$\begin{aligned} & \|\tilde{T}_I x - \tilde{T}_{I_0} x\| \\ & \leq \|\tilde{T}_{\theta(-N)I}(\tilde{T}_{\rho(N)I} x - \tilde{T}_{\rho(N)I_0} x)\| \\ & \quad + \|\tilde{T}_{\theta(-N)I} \tilde{T}_{\rho(N)I_0} x - \tilde{T}_{\theta(-N)I_0} \tilde{T}_{\rho(N)I_0} x\| \\ & \leq \|\tilde{T}_{\theta(-N)I} \tilde{T}_{\rho(N)I_0} x - \tilde{T}_{\theta(-N)I_0} \tilde{T}_{\rho(N)I_0} x\| \\ & \quad + c e^{k(s-Nl)} \|\tilde{T}_{\rho(N)I} x - \tilde{T}_{\rho(N)I_0} x\|. \end{aligned}$$

If we continue “cutting” inputs and estimating operator norms in the second term, through iteration we get

$$\begin{aligned} & \|\tilde{T}_I x - \tilde{T}_{I_0} x\| \\ & \leq \|\tilde{T}_{\theta(-N)I} \tilde{T}_{\rho(N)I_0} x - \tilde{T}_{\theta(-N)I_0} \tilde{T}_{\rho(N)I_0} x\| \\ & \quad + \sum_{n=1}^N c^n e^{k(s-(N-n+1)l)} \\ & \quad \times \|\tilde{T}_{\rho(l)\theta(-(N-n)I} \tilde{T}_{\rho((N-n)I_0} x - \tilde{T}_{\rho(l)\theta(-(N-n)I_0} \tilde{T}_{\rho((N-n)I_0} x)\|. \quad (2.6) \end{aligned}$$

Finally all relevant inputs have lengths $\leq l$, such that according to Hypothesis 2.8 we can choose $N + 1$ numbers

$$\delta_{0n} := \delta\left(\frac{\varepsilon}{Q}, \tilde{T}_{\rho(n)I_0} x\right) > 0,$$

where

$$Q := 1 + \sum_{n=1}^N c^n e^{k(s-(N-n+1)l)}$$

and $n \in \{0, \dots, N\}$, such that, if

$$\|I - I_0\| \leq \delta_1 := \min\{\delta_{0n} : n \in \{0, \dots, N\}\},$$

then the right-hand side of (2.6) is bounded by ε and the statement of the proposition follows. \square

Next, we transfer these results to the population operators. Therefore we recall

Definition 2.11. The *weak* topology* is the weakest topology such that all functionals

$$y \mapsto \langle y, x \rangle, \quad x \in X$$

are continuous. A function y of a real argument with values in Y is then *weak* continuous* in λ_0 , if and only if for all $\varepsilon > 0$ and all $x \in X$, there exists some $\delta = \delta(\varepsilon, \lambda_0, x)$, such that

$$|\langle y(\lambda), x \rangle - \langle y(\lambda_0), x \rangle| < \varepsilon$$

for all λ with $|\lambda - \lambda_0| < \delta$.

Now we obtain a local and a global result on weak* continuity of the population semigroup with respect to the input.

Theorem 2.12. (a) *There exists some $l > 0$, such that for all $x \in X$ and all $\varepsilon > 0$ there exists some $\delta = \delta_0(\varepsilon, x)$, such that*

$$|\langle T_I y, x \rangle - \langle T_J y, x \rangle| \leq \|y\| \varepsilon$$

holds for all $y \in Y$ and all $I, J \in C_s$ with $s \in [0, l]$ and $\|I - J\| \leq \delta$.

(b) *For all $s > 0$, $I_0 \in C_s$, $x \in X$ and $\varepsilon > 0$, there exists some $\delta = \delta_1(\varepsilon, x, s, I_0)$, such that*

$$|\langle T_I y, x \rangle - \langle T_{I_0} y, x \rangle| \leq \|y\| \varepsilon$$

holds for all $y \in Y$ and all $I \in C_s$ with $\|I - I_0\| \leq \delta$.

Proof. (a) The statement follows from the estimate

$$|\langle T_I y, x \rangle - \langle T_J y, x \rangle| \leq \|y\| \| \tilde{T}_I x - \tilde{T}_J x \|$$

with $\delta = \delta_0(\varepsilon, x)$ chosen according to Hypothesis 2.8.

(b) The statement follows from the estimate

$$|\langle T_I y, x \rangle - \langle T_{I_0} y, x \rangle| \leq \|y\| \| \tilde{T}_I x - \tilde{T}_{I_0} x \|$$

with $\delta = \delta_1(\varepsilon, x, s, I_0)$ chosen according to Proposition 2.10. \square

2.6. Weak* continuous dependence on time

Through a counterexample below (Example 6.16), similar to the one for continuous dependence with respect to the input, we shall show that in general we do not have continuous dependence on time in the dual norm. However, and again similar to the dependence on the input, we will show continuous dependence in the weak* topology. To that end, we assume that the preadjoint semigroup is continuous on time in the following sense:

Hypothesis 2.13. There exists some $l > 0$, such that for all $x \in X$ and all $\varepsilon > 0$ there exists some $\delta = \delta_2(\varepsilon, x)$, such that

$$\|\tilde{T}_{\rho(s)Ix} - \tilde{T}_{\rho(t)Ix}\| \leq \varepsilon$$

for all $I \in C_l$ and all $s, t \in [0, l]$ with $|s - t| \leq \delta$.

Remark 2.14. Note that the hypothesis as well as the following proposition say in particular, that for fixed and constant I , the family $\{\tilde{T}_{\rho(s)I}\}_{s \geq 0}$ satisfies the usual *strong continuity* property for one parameter semigroups, i.e., that for every $x \in X$ one has

$$\lim_{s \downarrow 0} \|\tilde{T}_{\rho(s)Ix} - x\| = 0,$$

see e.g. [14].

From Hypothesis 2.13, using the semigroup property for \tilde{T}_I , we can deduce continuity for arbitrary time intervals, but lose uniformity in I :

Proposition 2.15. Fix $\sigma > 0$, $I \in C_\sigma$, $x \in X$ and let $\varepsilon > 0$, then there exists some $\delta = \delta_3(\varepsilon, x, \sigma, I)$, such that

$$\|\tilde{T}_{\rho(s)Ix} - \tilde{T}_{\rho(t)Ix}\| \leq \varepsilon \tag{2.7}$$

for all $s, t \in [0, \sigma]$ with $|s - t| \leq \delta$.

Proof. Choose l according to Hypothesis 2.13. Next, define $N := \max\{k \in \mathbf{N} : s, t \geq \frac{kl}{2}\}$, and note that

$$\theta(-s)\rho(t+s)I = \rho(t)\theta(-s)I. \tag{2.8}$$

Then, if $|s - t| < \frac{l}{2}$, one has $s, t \in [\frac{Nl}{2}, \frac{Nl}{2} + l]$ and

$$\begin{aligned} & \| \tilde{T}_{\rho(t)Ix} - \tilde{T}_{\rho(s)Ix} \| \\ &= \| \tilde{T}_{\theta(-\frac{Nl}{2})\rho(t)I} \tilde{T}_{\rho(\frac{Nl}{2})Ix} - \tilde{T}_{\theta(-\frac{Nl}{2})\rho(s)I} \tilde{T}_{\rho(\frac{Nl}{2})Ix} \| \\ &= \| \tilde{T}_{\rho(t-\frac{Nl}{2})\theta(-\frac{Nl}{2})I} \tilde{T}_{\rho(\frac{Nl}{2})Ix} - \tilde{T}_{\rho(s-\frac{Nl}{2})\theta(-\frac{Nl}{2})I} \tilde{T}_{\rho(\frac{Nl}{2})Ix} \|. \end{aligned} \tag{2.9}$$

Now, by Hypothesis 2.13 we can choose

$$\delta_3 = \min \left\{ \delta_2(\varepsilon, \tilde{T}_{\rho(\frac{Nl}{2})Ix}, \frac{l}{2}) \right\}. \quad \square$$

Now, for the population semigroup we get a local and a global result.

Theorem 2.16. (a) *There exists some $l > 0$, such that for all $x \in X$ and all $\varepsilon > 0$ there exists some $\delta = \delta_2(\varepsilon, x)$, such that*

$$| \langle T_{\rho(s)I}y, x \rangle - \langle T_{\rho(t)I}y, x \rangle | \leq \|y\| \varepsilon \tag{2.10}$$

holds for all $y \in Y, I \in C_l$ and $s, t \in [0, l]$ with $|s - t| \leq \delta$.

(b) *For all $\sigma > 0, I \in C_\sigma, x \in X$ and $\varepsilon > 0$, there exists some $\delta = \delta_3(\varepsilon, x, \sigma, I)$, such that (2.10) holds for all $y \in Y$ and all $s, t \in [0, \sigma]$ with $|s - t| \leq \delta$.*

Proof. (a) The statement follows from the estimate

$$| \langle T_{\rho(s)I}y, x \rangle - \langle T_{\rho(t)I}y, x \rangle | \leq \|y\| \| \tilde{T}_{\rho(s)Ix} - \tilde{T}_{\rho(t)Ix} \| \tag{2.11}$$

with $\delta = \delta_2(\varepsilon, x)$ according to Hypothesis 2.13.

(b) The statement follows again from (2.11), but now with $\delta = \delta_3(\varepsilon, x, \sigma, I)$ chosen according to Proposition 2.15. \square

3. Nonlinear dynamical systems

First a nonlinear system is constructed from two ingredients, the linear system with input and a map which computes the output that the population produces under a given input. This is basically a repetition from [10]. Then, in Sections 3.3–3.8 we extend the constructions further into the future and in Sections 3.9–3.10 we investigate continuity properties. For the extension parts, we received inspiration from [28].

3.1. Output

Our next step towards the definition of a nonlinear next population state operator is to assume a rule on how a given “population” determines an object in the space of inputs

(recall the construction in Section 1.2), which we call *output*. In the nonlinear theory, we will restrict to a subset Y_+ of the Banach space Y . In the context of population models, Y_+ is the set of *positive* measures (whence the subscript $+$). We assume that Y_+ is invariant under $\{T_I\}$ (and verify this assumption in Section 4.1):

Hypothesis 3.1. One has $T_I(Y_+) \subset Y_+$ for every $I \in \mathcal{C}$.

Hypothesis 3.2. There exists a map $H : Y_+ \rightarrow Z$, which we call *output map* and which is such that, for any $y \in Y_+$ and any $I \in C_s$ with $s > 0$, the so-called *output*

$$t \mapsto H(T_{\rho(t)I}y)$$

belongs to C_s .

Definition 3.3. With the ingredients T_I and H we associate for all $y \in Y_+$ a map $P_y : C_s \rightarrow C_s$, via the formula

$$P_y I = H(T_{\rho(\cdot)I}y). \tag{3.1}$$

We call P_y the *input–output map* and for an input I we call $P_y I$ the corresponding *output*.

Motivated by the often encountered case that the output can be calculated through integration with respect to a weight function (see again Section 1.2), let us assume that $E = \mathbf{R}^n$ and that H is linear and can be represented by an element of the bidual space X^{**} , i.e., let us verify Hypothesis 3.2 via the truth of

Hypothesis 3.4. There exists some $\gamma \in (X^{**})^n$, which we call *output function*, such that

$$H(y) = \langle y, \gamma \rangle \in \mathbf{R}^n \tag{3.2}$$

for $y \in Y_+$ and such that the output

$$t \mapsto \langle T_{\rho(t)I}y, \gamma \rangle$$

belongs to C_s for any $I \in C_s$.

See Remark 5.1 for the more general case of γ dependent on I . It is wellknown that a Banach space can be embedded into its second dual space in a canonical way, see e.g. Theorem II 3.18 in [13] and Section 5.1. For the case $\gamma \in (X)^n \subset (X^{**})^n$ we can identify the pairings (denoting also the pairing between X^* and X^{**} by $\langle \cdot, \cdot \rangle$, as we have done already in (3.2)). Note that (3.2) with $\gamma \in X$ guarantees, because of

the weak* continuity of the linear system that H maps C_s into C_s . So Hypothesis 3.4 follows from the truth of

Hypothesis 3.5. There exists some $\gamma \in (X)^n$, such that $H(y) = \langle y, \gamma \rangle$ for all $y \in Y$.

The implications in this subsection can be summarized as

$$\text{Hypothesis 3.2} \iff \text{Hypothesis 3.4} \iff \text{Hypothesis 3.5.}$$

For the extension purposes below we will stick to Hypothesis 3.2 (and Definition 3.3), which in addition to being more general will facilitate the exposition. In Section 5.1 we will briefly discuss the relevant case, where Hypothesis 3.4 holds but Hypothesis 3.5 does not. Thereafter we give assumptions sufficiently strong for Hypothesis 3.5 to hold.

3.2. Local existence and uniqueness

We start with the key assumption for the nonlinear theory, which is verified in [10] via a contraction argument at various levels of generality:

Assumption 3.6. For every $y \in Y_+$ there is an $\bar{s}(y) \in (0, \infty]$ such that, for all $s < \bar{s}(y)$, the map $P_y|_{C_s}$ has a unique fixed point $I^s \in C_s$

The next two lemmas show that there is no need to provide fixed points with an index s . The first one is for inputs in general (not necessarily fixed points).

Lemma 3.7. *Let $I \in C_s$ and $t \in [0, s]$, then for all $y \in Y_+$*

$$\rho(t)P_y I = P_y \rho(t)I.$$

Proof. Both sides are elements of C_t . For any $r \in [0, t]$ one has

$$(P_y \rho(t)I)(r) = H(T_{\rho(r)\rho(t)I}y) = H(T_{\rho(r)I}y) = (P_y I)(r) = (\rho(t)P_y I)(r). \quad \square$$

Lemma 3.8. *Let $y \in Y_+$ and $0 < s < t < \bar{s}(y)$, then for fixed points $I^s \in C_s$ of $P_y|_{C_s}$ and $I^t \in C_t$ of $P_y|_{C_t}$, we have*

$$\rho(s)I^t = I^s.$$

Proof. By Lemma 3.7, we have

$$P_y \rho(s)I^t = \rho(s)P_y I^t = \rho(s)I^t.$$

Hence, $\rho(s)I^t$ and I^s are fixed points of length s and by the uniqueness assumption they must be equal. \square

In the following we will therefore omit the index s in the notation, implicitly assuming that $l(I) < \bar{s}(y)$ and, when writing $I \in C_s$, that $s < \bar{s}(y)$. With the fixed points we can now define solutions.

Definition 3.9. A local solution starting at $y \in Y_+$, defined on $[0, s]$, is a map

$$\begin{aligned} [0, s] &\longrightarrow Y, \\ t &\longmapsto T_{\rho(t)I}y \end{aligned} \tag{3.3}$$

for some fixed point $I \in C_s$, $s > 0$ of P_y . Moreover, we call

$$\{T_{\rho(t)I}y : t \in [0, s]\}$$

a local orbit starting at y .

Solution here refers to the fixed point problem. The term “starting at y ” is justified, because $T_{\rho(0)I}y = y$ for any I . Local uniqueness follows from Lemma 3.8 and Assumption 3.6:

Corollary 3.10. For any $y \in Y_+$ and all $s \in [0, \bar{s}(y))$, the map (3.3) defined via the fixed point $I \in C_s$ is the unique solution on $[0, s]$ starting at y .

3.3. Uniqueness

For uniqueness and extension purposes, we prove that left shifts of fixed points yield fixed points. A tool for that is given already in [10]:

Lemma 3.11. For $y \in Y_+$, $I \in \mathcal{C}$ and $s \in [0, l(I)]$, one has

$$\theta(-s)P_y(I) = P_{T_{\rho(s)I}y}\theta(-s)I$$

Proof. From the semigroup property we know, that

$$T_{\rho(t+s)I} = T_{\theta(-s)\rho(t+s)I}T_{\rho(s)\rho(t+s)I}.$$

On the other hand, since for any I (2.8) holds and

$$\rho(s)\rho(t + s)I = \rho(s)I,$$

one has

$$\begin{aligned} (\theta(-s)P_y I)(t) &= (P_y I)(t + s) = H(T_{\rho(t+s)I}y) \\ &= H(T_{\rho(t)\theta(-s)I}T_{\rho(s)I}y) = (P_{T_{\rho(s)I}y}\theta(-s)I)(t). \quad \square \end{aligned}$$

Next, we apply this result to shifted fixed points.

Lemma 3.12. *If $P_y I = I$ for $I \in C_t$, then $P_{T_{\rho(s)I}y} \theta(-s)I = \theta(-s)I$ for all $s \in [0, t]$.*

Proof. We have $\theta(-s)I \in C_{t-s}$ and by Lemma 3.11 also

$$P_{T_{\rho(s)I}y} \theta(-s)I = \theta(-s)P_y I = \theta(-s)I. \quad \square$$

Now we can prove that even though the hypotheses only give local uniqueness, fixed points are in fact unique on every compact interval where they are found.

Lemma 3.13. *For $y \in Y_+$ let $I, J \in C_\tau$ be fixed points of P_y , then $I = J$ (on $[0, \tau]$).*

Proof. If $\tau < \bar{s}(y)$, the statement follows since for these values we assumed uniqueness. If $\tau \geq \bar{s}(y)$, define $\bar{t} \geq \bar{s}(y)$ by

$$\bar{t} := \sup\{t \in [0, \tau] : \rho(t)I = \rho(t)J\}.$$

If $\bar{t} = \tau$, the statement follows from the continuity of I and J . Suppose, that $\bar{t} < \tau$, then there exists a unique fixed point \bar{I} of positive length, such that

$$P_{T_{\rho(\bar{t})I}y} \bar{I} = \bar{I}.$$

On the other hand, from Lemma 3.12, we deduce that

$$P_{T_{\rho(\bar{t})I}y} \theta(-\bar{t})I = \theta(-\bar{t})I$$

and the same identity holds when I is replaced by J . Hence, by uniqueness of \bar{I} one has

$$I(\bar{t} + s) = (\theta(-\bar{t})I)(s) = \bar{I}(s) = (\theta(-\bar{t})J)(s) = J(\bar{t} + s)$$

for $s \in [0, \min\{l(\bar{I}), \tau - \bar{t}\}]$, which contradicts the maximality of \bar{t} . \square

As an immediate consequence, we have

Corollary 3.14. *If $T_{\rho(\cdot)I}y$ and $T_{\rho(\cdot)J}y$ are solutions on $[0, s]$ starting at y , then*

$$T_{\rho(\cdot)I}y = T_{\rho(\cdot)J}y$$

on $[0, s]$.

Now that uniqueness of solutions of arbitrary length is settled, we will often simply write *the* fixed point and *the* solution for whatever given interval.

3.4. Concatenation of inputs and local extension

We first turn to extension from a compact interval to a compact interval. We extend inputs via the so-called concatenation.

Definition 3.15. For inputs $I, J \in \mathcal{C}$, define their *concatenation* (glueing together) by

$$(I \odot J)(s) = \begin{cases} J(s) & \text{for } s \in [0, l(J)), \\ I(s - l(J)) & \text{for } s \in [l(J), l(J) + l(I)]. \end{cases}$$

For concatenations, one has $I \odot J \in C_{t+s}$ for $I \in C_t$ and $J \in C_s$, only if $J(s) = I(0)$. If $I \in C_s$ is the fixed point of P_y and J is a fixed point of $P_{T_{\rho(s)}Iy}$, then by Lemma 3.12 and the uniqueness assumption, one has

$$I(s) = (\theta(-s)I)(0) = J(0)$$

and therefore $J \odot I$ is a continuous function of length greater than s . This idea will be used in the proof of the following lemma as well as in later proofs.

Lemma 3.16. For $s < \bar{s}(y)$ let $I \in C_s$ be a fixed point of P_y and for $t < \bar{s}(T_{\rho(s)}Iy)$ let $J \in C_t$ be a fixed point of $P_{T_{\rho(s)}Iy}$, then their concatenation

$$J \odot I$$

is a fixed point of P_y in C_{s+t} .

Proof. First note that, by the above remark, we have that $J \odot I \in C_{s+t}$.

Next, we show the fixed point property:

For $r \in [0, s]$ one has

$$P_y(J \odot I)(r) = H(T_{\rho(r)J \odot I}y) = H(T_{\rho(r)I}y) = (P_y I)(r) = I(r) = J \odot I(r).$$

For $r \in (s, s + t]$

$$\begin{aligned} P_y(J \odot I)(r) &= H(T_{\rho(r)(J \odot I)}y) = H(T_{\rho(r-s)J \odot \rho(s)I}y) = H(T_{\rho(r-s)J}T_{\rho(s)I}y) \\ &= (P_{T_{\rho(s)}I}J)(r - s) = J(r - s) = J \odot I(r). \quad \square \end{aligned}$$

As a direct consequence, all solutions can be extended to the right:

Proposition 3.17. *Let $T_{\rho(\cdot)I}y$ be the solution on $[0, t_1]$, then there exists some $t_2 > 0$ and some $\bar{I} \in C_{t_1+t_2}$, such that*

- (i) $T_{\rho(\cdot)\bar{I}}y$ is the solution on $[0, t_1 + t_2]$,
- (ii) $T_{\rho(\cdot)\bar{I}}y|_{[0,t_1]} = T_{\rho(\cdot)I}y$.

Proof. Let J be the fixed point of $P_{T_{\rho(t_1)I}y}$ on $[0, t_2]$, where $t_2 \in (0, \bar{s}(T_{\rho(t_1)I}y))$. By Lemma 3.16 the concatenation $\bar{I} := J \odot I$ is the fixed point on $[0, t_1 + t_2]$ of P_y . Therefore the map

$$T_{\rho(\cdot)\bar{I}}y = T_{\rho(\cdot)(J \odot I)}y$$

is the solution on $[0, t_1 + t_2]$ and (ii) also holds. \square

3.5. Maximal solutions

In order to have certain dynamic properties, which we will relate to the notion of a semiflow, and to investigate global existence, we consider solutions on a maximal interval of existence:

Definition 3.18. For any $y \in Y_+$ define

$$t_y := \sup\{t > 0 : \text{there exists an } I \in C_t \text{ with } P_y I = I\} \in \mathbf{R}_+ \cup \{\infty\}$$

then the map $t \rightarrow T_{\rho(t)I}y$ is defined on $[0, t_y)$ (via the fixed point $I \in C_t$ of P_y on $[0, t]$) and we call it *the maximal solution starting at y* .

The ideal case now, is the existence of a global solution, i.e., $t_y = \infty$.

3.6. Semiflows

We show that the maximal solutions induce a so-called *semiflow*. First one more tool:

Lemma 3.19. *For $y \in Y_+$, if $0 < s < t_y < \infty$ and I is the fixed point of P_y on $[0, s]$, then $t_y = s + t_{T_{\rho(s)I}y}$. Moreover, $t_y = \infty$ if and only if $t_{T_{\rho(s)I}y} = \infty$.*

Proof. Assume $t_y < s + t_{T_{\rho(s)I}y}$. Choose some $r \in (t_y, t_{T_{\rho(s)I}y} + s)$ then since $r - s < t_{T_{\rho(s)I}y}$ we find a fixed point $J \in C_{r-s}$. By Lemma 3.16, the concatenation $J \odot I$ is the fixed point of P_y in C_r , which is a contradiction to the maximality of t_y .

Now assume there exists an $r \in (s + t_{T_{\rho(s)I}y}, t_y)$. For this r consider a fixed point $I \in C_r$, then $\theta(-s)I$ is the fixed point of $P_{T_{\rho(s)I}y}$ in C_{r-s} , which contradicts the maximality of $t_{T_{\rho(s)I}y}$.

The second statement follows analogously.

The following definition is inspired by Definition VII 2.1. from [9] (there for complete metric spaces) but can also be found in [1] (for general metric spaces). In both there is additionally required (for extension purposes) that the operators depend continuously on the initial value in a stronger sense than we manage to prove in Section 3.10.

Definition 3.20. A *semiflow* on Y is a map $S : D \rightarrow Y_+$ on a subset

$$D \subset [0, \infty) \times Y_+$$

with the following properties:

- (i) For every $y \in Y_+$ there exists a possibly infinite interval $I_y = [0, \infty)$ or $I_y = [0, t_y)$, such that

$$\{(t, y) \in [0, \infty) \times Y_+ : t \in I_y\} = D, \tag{3.4}$$

- (ii) $S(0, y) = y$ on Y_+ ,
- (iii) $y \in Y_+, s \in I_y$ and $t \in I_{S(s,y)}$ imply $t + s \in I_y$ and

$$S(t, S(s, y)) = S(t + s, y).$$

Now we let t_y from this definition coincide with the earlier introduced t_y denoting the length of the maximal solution starting at y and for this t_y make

Definition 3.21. With $I_y := [0, t_y)$, let D denote the left-hand side of (3.4) and define

$$\begin{aligned} S : D &\longrightarrow Y_+, \\ (t, y) &\longmapsto T_{\rho(t)I}y, \end{aligned}$$

where $T_{\rho(\cdot)I}y$ is the maximal solution starting at y .

In this terminology, we get

Theorem 3.22. S is a semiflow.

Proof. (i) and (ii) are trivial.

The first statement of (iii) follows from Lemma 3.19. Let $I \in C_{t+s}$ be the fixed point of P_y and $\theta(-s)I \in C_t$ be the fixed point of $P_{S(s,y)}$. Then we get

$$\begin{aligned} S(t, S(s, y)) &= T_{\rho(t)\theta(-s)I}T_{\rho(s)I}y = T_{\rho(t)\theta(-s)I \circ \rho(s)I}y \\ &= T_{\rho(t+s)I}y = S(t + s, y). \quad \square \end{aligned}$$

3.7. Exponential boundedness

Exponential boundedness of the nonlinear system follows immediately from exponential boundedness of the linear system. Combining Definition 3.21 and Hypothesis 2.5, one deduces

Theorem 3.23. *There exist constants $c \geq 1$ and $k \geq 0$, such that for all $y \in Y_+$ the inequality*

$$\|S(t, y)\| \leq ce^{kt} \|y\|$$

holds.

In particular, S is bounded on bounded intervals, which excludes blow up in finite time.

3.8. Global solutions

For many dynamical systems, a combination of compactness and continuity arguments allows one to conclude from Theorems 3.22 and 3.23 that $t_y = \infty$ for all y , i.e., that solutions exist for all time. As in the present setting we manage to show continuity on the initial value for small time intervals, but not for maximal time intervals (see Section 3.10), we deduce global existence from a different approach. The following hypothesis, and its elaboration in Section 5.2, resemble the proof of local contractivity of P_y in [10]. To prove global existence, however, we need a sharper version: we require a lower bound for the existence time, uniformly for y in bounded sets. Moreover it will prove convenient as well as appropriate to assume that the Lipschitz factor depends linearly on y .

Hypothesis 3.24. There exists some $\delta > 0$ and some monotonically increasing function $K : [0, \delta] \rightarrow \mathbf{R}_+$ with $\lim_{s \downarrow 0} K(s) = 0$, such that

$$\|P_y I - P_y J\| \leq K(s) \|y\| \|I - J\|$$

for all $y \in Y_+$, all $s \in [0, \delta]$ and all $I, J \in C_s$.

Now we can prove that, if we consider evolution from some initial state on a finite time interval, there exists some uniform positive length for which there are fixed points for all states, that can evolve from this state during this time interval.

Lemma 3.25. *Let $y \in Y_+$ and suppose that $\bar{t} \leq t_y < \infty$. There exists some $r = r(y) > 0$, such that for all $t \in [0, \bar{t}]$ the map $P_{S(t,y)}$ has a unique fixed point in C_s for all $s \leq r$.*

Proof. Choose $K(s)$ and δ according to Hypothesis 3.24 and, in accordance with Theorem 3.23, $B := ce^{k\bar{t}} < \infty$, then one has

$$\|P_{S(t,y)}I - P_{S(t,y)}J\| \leq K(s)B\|y\|\|I - J\|$$

for all $s \in [0, \delta]$, $I, J \in C_s$ and all $t \in [0, \bar{t})$. Next choose $r \in (0, \delta)$ so small that $K(s)B\|y\| < 1$ for all $s \in [0, r]$, then $P_{S(t,y)}$ has a unique fixed point in C_s for all $t \in [0, \bar{t})$. \square

Now, global existence and uniqueness can be proved via concatenation of fixed points.

Proposition 3.26. *For all $y \in Y_+$ one has $t_y = \infty$, i.e., for all $\sigma > 0$, there exists an $I \in C_\sigma$, such that $P_y I = I$.*

Proof. We will deduce a contradiction for the case $t_y < \infty$, t_y as in Definition 3.18. Choose $\bar{t} := t_y < \infty$ and r according to Lemma 3.25. Choose $\tau \in (\max\{0, t_y - \frac{r}{2}\}, t_y)$ and consider the fixed points $I \in C_\tau$ of P_y and $J \in C_s$ of $P_{S(\tau,y)}$ for some s with $\tau + s > t_y$. Then, by Lemma 3.16, $J \odot I$ is the fixed point of P_y of length $\tau + s > t_y$, which contradicts the maximality of t_y . \square

Theorem 3.27. *The map $S(t, y)$ is defined for all $y \in Y_+$ and all $t \in [0, \infty)$.*

3.9. Weak* continuous dependence on time

Like exponential boundedness, weak* continuous dependence on time of the nonlinear system follows immediately from the corresponding property of the linear system.

Theorem 3.28. (a) *There exists some $l > 0$, such that for all $x \in X$ and all $\varepsilon > 0$ there exists some $\delta = \delta(\varepsilon, x)$, such that*

$$|\langle S(s, y), x \rangle - \langle S(t, y), x \rangle| \leq \|y\|\varepsilon \tag{3.5}$$

holds for all $y \in Y_+$ and all $s, t \in [0, l]$ with $|s - t| \leq \delta$.

(b) *For all $\sigma > 0$, $x \in X$, $y \in Y_+$ and $\varepsilon > 0$, there exists some $\delta = \delta(\varepsilon, x, \sigma, y)$, such that (3.5) holds for all $s, t \in [0, \sigma]$ with $|s - t| \leq \delta$.*

Proof. (a) Choose l according to Theorem 2.16 (a), fix $x \in X$ and $\varepsilon > 0$ and choose $\delta = \delta_2(\varepsilon, x)$ according to Theorem 2.16 (a). Now for any $y \in Y$ denote by I the fixed point of P_y of length l . Then we get

$$|\langle S(s, y), x \rangle - \langle S(t, y), x \rangle| = |\langle T_{\rho(s)}Iy, x \rangle - \langle T_{\rho(t)}Iy, x \rangle| \leq \|y\|\varepsilon$$

for all $y \in Y$ and all $s, t \in [0, l]$ with $|s - t| \leq \delta$.

(b) Fix σ, x, y and consider the fixed point $I \in C_\sigma$ of P_y . Now choose $\delta_3(\varepsilon, x, \sigma, I)$ according to Theorem 2.16 (b). Since I depends on y and y and σ uniquely determine I , we write $\delta(\varepsilon, x, \sigma, y) := \delta_3(\varepsilon, x, \sigma, I)$ and get

$$|\langle S(s, y), x \rangle - \langle S(t, y), x \rangle| = |\langle T_{\rho(s)}Iy, x \rangle - \langle T_{\rho(t)}Iy, x \rangle| \leq \|y\|\varepsilon$$

for all $s, t \in [0, I]$ with $|s - t| \leq \delta$. \square

3.10. Weak continuous dependence on the initial value*

The continuous dependence of the nonlinear system on the initial value can be deduced from the linear theory and the continuous dependence of the fixed point with respect to the initial value. In order to prove the latter, we reformulate Theorem 0.3.2. in [17] for our situation.

Theorem 3.29. *Let $y_0 \in Y_+$ and suppose that there exists some $s > 0$ such that for every $I \in C_s$ the map $y \mapsto P_y I$ is continuous in y_0 and that the map $P_y : C_s \rightarrow C_s$ is locally uniformly contracting in y_0 , i.e., there exists some $q = q(y_0) \in [0, 1)$ and some $\delta = \delta(y_0, q) > 0$, such that*

$$\|P_y I - P_y J\| \leq q \|I - J\|$$

for all $I, J \in C_s$ if $\|y - y_0\| \leq \delta$. Then the unique fixed point $I_y \in C_s$ of P_y is continuous in y_0 .

Now note that, if we choose $s \in [0, \delta]$ appropriately, with δ according to Hypothesis 3.24, the contractivity property required in the theorem follows from this hypothesis. The continuity of $y \mapsto P_y I$ is stated in the following hypothesis, which will be verified in Section 5.3 once the fixed point map has been specified in more detail.

Hypothesis 3.30. For all $s > 0$ and all $I \in C_s$, the map $y \mapsto P_y I$ is continuous from Y_+ provided with the norm topology to C_s .

Now we can prove

Theorem 3.31. *Choose δ according to Hypothesis 3.24 and let $t \in [0, \delta]$, then for all $\varepsilon > 0, x \in X$ and all $y_0 \in Y_+$, there exists some $\delta' = \delta'(\varepsilon, t, x, y_0) > 0$, such that*

$$|\langle S(t, y), x \rangle - \langle S(t, y_0), x \rangle| < \varepsilon$$

for all y with $\|y - y_0\| < \delta'$.

Proof. By Hypothesis 2.5 choose c and k , such that

$$\begin{aligned} & |\langle S(t, y), x \rangle - \langle S(t, y_0), x \rangle| \\ & \leq |\langle T_{\rho(t)I_y} y, x \rangle - \langle T_{\rho(t)I_y} y_0, x \rangle| + |\langle T_{\rho(t)I_y} y_0, x \rangle - \langle T_{\rho(t)I_{y_0}} y_0, x \rangle| \\ & \leq ce^{kt} \|x\| \|y - y_0\| + |\langle T_{\rho(t)I_y} y_0, x \rangle - \langle T_{\rho(t)I_{y_0}} y_0, x \rangle|. \end{aligned}$$

By Theorem 2.12 (b), choose $\delta_1 = \delta_1(\frac{\varepsilon}{2}, x, t, I_{y_0})$, such that the second term is bounded by $\frac{\varepsilon}{2}$, if $\|\rho(t)I_y - \rho(t)I_{y_0}\| \leq \delta_1$. Then, by Theorem 3.29, there exists some $\delta'' = \delta''(\delta_1, t, y_0)$, such that $\|\rho(t)I_y - \rho(t)I_{y_0}\| \leq \delta_1$ if $\|y - y_0\| \leq \delta''$. So finally with

$$\delta' := \min \left\{ \frac{\varepsilon e^{-kt}}{2c\|x\|}, \delta'' \right\}$$

the statement of the theorem follows. \square

When considering the property for arbitrarily large times, extension via the semigroup property seems difficult, since on the one hand norm convergence is required, while on the other hand one gets only weak* convergence and hence iteration is not possible. We remark, however, that for any time for which the Lipschitz property Hypothesis 3.24 holds, one can also deduce contractivity uniformly for y in a neighbourhood of zero and hence also gets weak* continuous dependence for this time and this neighbourhood of zero.

4. Linear structured population models

First, we define a linear dynamical system with input for structured populations in the way it is done in [10]. For the proofs of Section 4.1, we refer to this article as well as to [12]. In Sections 4.2–4.5 we elaborate the hypotheses made in Section 2 for this system.

4.1. The linear model on a state space of measures

In structured populations, one distinguishes between individual state (i-state) and population state (p-state). The i-state we denote by x . Examples for i-states are size, age or energy reserves of an individual or combinations of these (resulting in an i-state space of dimension greater than one).

Hypothesis 4.1. The i-state space is a measurable space Ω with a countably generated σ -algebra Σ .

When considering PDEs a natural choice for the population state space is L^1 . On the other hand, in a situation where all individuals have the same state, the

population cannot be represented by a L^1 function but is represented by a Dirac measure (concentrated in this state) and a space of measures (in which the L^1 -functions can be embedded; they then correspond to the absolutely continuous measures) seems the natural population state space. Denoting by $M(\Omega)$ the Banach space of signed real measures and by $M_+(\Omega)$ the cone of positive measures in $M(\Omega)$, we make

Assumption 4.2. The population state at time t can be described by a measure $m_t \in M_+(\Omega)$, i.e.,

$$Y_+ := M_+(\Omega) \subset M(\Omega) =: Y.$$

For measure theoretic background see the books [26,18]. The goal is now to construct a linear semigroup $\{T_I\}$ on $M(\Omega)$, such that for all $m \in M_+(\Omega)$, $I \in \mathcal{C}$ and $\omega \in \Sigma$

$$T_I m(\omega)$$

represents the part of the population with i-state in ω that has evolved from an initial state m under an input I (after $l(I)$ time units).

Remark 4.3. Note that the T_I used in the introduction, which act on $L^1(\Omega)$, correspond to the restriction of the current T_I to the subspace of absolutely continuous measures, when assuming that this subspace is invariant.

We want to base the construction of T_I on two modelling ingredients with the following interpretations:

- $u_I(x, \omega)$ is the probability that an individual with i-state x , survives under an input I during the time interval $[0, l(I)]$ and then has state in ω .
- $\Lambda_I(x, \omega)$ is the expected number of children with state-at-birth in ω , produced by an individual starting out with state x under an input I (within $l(I)$ units of time).

Mathematically, we assume that u_I and Λ_I are the so-called input parametrized kernels:

Definition 4.4. A (positive) kernel is a map $k : \Omega \times \Sigma \rightarrow \mathbf{R}_{(+)}$, such that for fixed $\omega \in \Sigma$, the function $x \mapsto k(x, \omega)$ is bounded and measurable, while for fixed $x \in \Omega$, the map $\omega \mapsto k(x, \omega)$ defines a finite signed measure on Ω . An input parametrized (positive) kernel is a map $k_I : \Omega \times \Sigma \rightarrow \mathbf{R}_{(+)}$, such that for fixed $I \in \mathcal{C}$, the map $k_I(\cdot, \cdot)$ is a kernel and additionally $[0, t] \times \omega \mapsto k_{\rho(t)I}(x, \omega)$ defines a positive measure on $[0, l(I)] \times \Sigma$.

Hypothesis 4.5. u_I and Λ_I are parametrized families of positive kernels.

Motivated by the interpretation, we call u_I the *survival kernel* and A_I the *reproduction kernel*. We define the product of two kernels, say k_1 and k_2 as

$$(k_1 \times k_2)(x, \omega) := \int_{\Omega} k_1(y, \omega)k_2(x, dy).$$

Lemma 4.6. *The \times -product of two kernels defines a kernel.*

To represent $T_I m$, we construct a further kernel u_I^c (c stands for clan) such that

$$(T_I m)(\omega) = \int_{\Omega} u_I^c(y, \omega)m(dy) =: (u_I^c \times m)(\omega), \tag{4.1}$$

where for shorter notation, we have also introduced the \times -product of a kernel and a measure. We mention

Lemma 4.7. *The \times -product of a kernel and a measure defines a measure.*

Then, u_I^c should be interpreted as follows: given an individual with i-state x , $u_I^c(x, \omega)$ represents the part of the clan (including the individual itself) of the individual that has survived under an input I and after $l(I)$ time units has i-state in ω . By *clan*, we mean all offspring, direct children, grandchildren, etc.

Now the problem reduces to defining u_I^c in terms of u_I and A_I . To do so, we introduce below a kernel A_I^c , which has the same interpretation as A_I , when replacing “children” by “all offspring”. We define the convolution of u_I and A_I^c (and analogously the convolution of two kernels in general) as the integral

$$(u * A^c)_I := \int_{[0, l(I)]} u_{\theta(-\sigma)I} \times A_{\rho(d\sigma)I}^c, \tag{4.2}$$

or written out in more detail,

$$(u * A^c)_I(x, \omega) = \int_{[0, l(I)]} \int_{\Omega} u_{\theta(-\sigma)I}(y, \omega)A_{\rho(d\sigma)I}^c(x, dy). \tag{4.3}$$

The interpretation is, in less words than before, “survived offspring”. Now, following the interpretation, we can express u_I^c in terms of u_I and A_I^c via

$$u_I^c = u_I + (u * A^c)_I. \tag{4.4}$$

Then, (4.1) can be written as

$$T_I m = u_I \times m + (u * A^c)_I \times m \tag{4.5}$$

and it remains to construct A_I^c in terms of A_I . We will do so by using the interpretation that the number of total offspring is the sum of the number of children, grandchildren, etc. An individuals k th generation offspring can be inductively defined via

$$A_I^{1*} := A_I, \tag{4.6}$$

$$A_I^{k*} := (A^{(k-1)*} * A)_I, \quad k \geq 2. \tag{4.7}$$

One then defines

$$A_I^c := \sum_{k=1}^{\infty} A_I^{k*}, \tag{4.8}$$

the convergence of which (leading to boundedness of T_I) will be investigated in Section 4.2. So finally, via (4.8) and (4.5), we managed to define T_I in terms of u_I and A_I . Note that at this point, the truth of Hypothesis 3.1 can be guaranteed via the positivity of u_I and A_I . In order to verify the semigroup property Hypothesis 2.3, we first make

Hypothesis 4.8. For $I \in \mathcal{C}$ and $\sigma \in [0, l(I)]$, the two consistency relations

$$\begin{aligned} A_I &= A_{\rho(\sigma)I} + A_{\theta(-\sigma)I} \times u_{\rho(\sigma)I}, \\ u_I &= u_{\theta(-\sigma)I} \times u_{\rho(\sigma)I} \end{aligned}$$

hold.

The second of these is called the Chapman Kolmogorov identity. Under the assumptions made, one can prove that this identity also holds for u_I^c :

Lemma 4.9. For $I \in \mathcal{C}$, $\sigma \in [0, l(I)]$, one has

$$u_I^c = u_{\theta(-\sigma)I}^c \times u_{\rho(\sigma)I}^c.$$

Corollary 4.10. For $m \in M_+(\Omega)$, $I \in \mathcal{C}$ and $\sigma \in [0, l(I)]$, one has

$$T_I m = T_{\theta(-\sigma)I} T_{\rho(\sigma)I} m.$$

Proof.

$$T_I m = u_I^c \times m = u_{\theta(-\sigma)I}^c \times u_{\rho(\sigma)I}^c \times m = T_{\theta(-\sigma)I} T_{\rho(\sigma)I} m. \quad \square$$

We close this section, by formulating some natural properties of u_I and A_I for later use.

Hypothesis 4.11. (i) For $x \in \Omega$, $\omega \in \Sigma$ and $I \in \mathcal{C}$, the function $\sigma \rightarrow A_{\rho(\sigma)I}(x, \omega)$ is nondecreasing on $[0, l(I)]$ and $\lim_{\sigma \downarrow 0} A_{\rho(\sigma)I}(x, \omega) = 0$.

(ii) For $x \in \Omega$ and $I \in \mathcal{C}$, the function $\sigma \rightarrow u_{\rho(\sigma)I}(x, \Omega)$ is nonincreasing on $[0, l(I)]$ and $\lim_{\sigma \downarrow 0} u_{\rho(\sigma)I}(x, \omega) = \delta_x(\omega)$ for $\omega \in \Sigma$. In particular $u_I(x, \Omega) \leq 1$.

The following lemma formulates the consistency relation that, roughly speaking, the clan of an individual consists of the individual itself plus the clan of its direct children.

Lemma 4.12. For $I \in \mathcal{C}$, one has

$$u_I^c = u_I + (u^c * A)_I. \tag{4.9}$$

4.2. Exponentially bounded linear operators

Exponential boundedness of a general linear system with input was stated as Hypothesis 2.5. We now discuss this hypothesis for operators of the type (4.5).

On $M(\Omega)$, for the dual space norm (see also Section 4.4), in the case of positive measures, it holds that $\|m\| = m(\Omega)$, whereas for (signed) real measures with the Jordan decomposition into two positive measures

$$m = m_+ - m_-,$$

we have $\|m\| = m_+(\Omega) + m_-(\Omega)$. Since the T_I are positive operators, the decomposition for $T_I m$ is given by

$$T_I m = T_I m_+ - T_I m_-$$

and estimates for $T_I m_+$ and $T_I m_-$ yield estimates for $T_I m$. Hence, in the following we restrict our attention to the positive cone $M_+(\Omega)$. Using representation (4.5) and that, by Hypothesis 4.11 (ii), the probability of survival never exceeds one, we will estimate the linear next state operator. It is convenient to first introduce the set of possible states at birth.

Definition 4.13. A set $\Omega_b \in \Sigma$ is called a *set representing the birth states*, if for all $x \in \Omega$ and all $I \in \mathcal{C}$ the measure $A_I(x, \cdot)$ is concentrated on Ω_b , i.e., if $A_I(x, \omega) = 0$, whenever $\omega \cap \Omega_b = \emptyset$.

Proposition 4.14. For all $I \in \mathcal{C}$ and $m \in M_+(\Omega)$, we have

$$\|T_I m\| \leq \|m\| + \|m\| \sup_{x \in \Omega} A_I^c(x, \Omega_b). \tag{4.10}$$

Therefore, if

$$\sup_{x \in \Omega} A_I^c(x, \Omega_b) < \infty, \tag{4.11}$$

then T_I is a bounded linear operator on $M(\Omega)$ and

$$\|T_I\| \leq 1 + \sup_{x \in \Omega} A_I^c(x, \Omega_b).$$

Proof. Using that, by Hypothesis 4.11 (ii), always $u_{\rho(t)I}(x, \Omega) \leq 1$, a straightforward estimation of (4.5) leads to the statement. \square

Condition (4.11) says that, for given environmental conditions I in the course of time and finite time, an individual has a finite expected number of descendants, no matter in what state it is. We will guarantee this first, by the biologically reasonable assumption that the birth kernel is bounded and reproduction starts only with some delay after birth, which is uniform for all states at birth. The boundedness assumption is used already in the local theory in [10] and will not be further investigated.

Assumption 4.15. There exists some $K > 0$, such that $A_I(x, \Omega_b) \leq K$ for all $x \in \Omega$ and all $I \in \mathcal{C}$.

Hypothesis 4.16. There exists a constant $\delta > 0$, such that $A_{\rho(s)I}(x, \Omega_b) = 0$, for all $s \in [0, \delta]$, $x \in \Omega_b$ and $I \in \mathcal{C}$

Now we can show that $A_I^c(x, \Omega_b)$ is dominated by a function that is bounded in K , δ and $l(I)$ on compact (positive) intervals.

Lemma 4.17. Choose K and δ according to Hypothesis 4.16 and Assumption 4.15, then for $x \in \Omega$ and $I \in \mathcal{C}$ one has

$$A_I^c(x, \Omega_b) \leq \begin{cases} \frac{l(I)}{\delta} & \text{for } K = 1, \\ \frac{K}{K-1} \left(e^{\frac{l(I)}{\delta} \ln K} - 1 \right) & \text{for } K \neq 1. \end{cases}$$

Proof. We combine Hypothesis 4.16 and Assumption 4.15 into $A_I(x, \Omega_b) \leq \chi_{[\delta, \infty)}(l(I))K$, where χ denotes the characteristic function, i.e.,

$$\chi_\omega(x) := \begin{cases} 1 & \text{for } x \in \omega, \\ 0 & \text{otherwise.} \end{cases}$$

Then

$$\begin{aligned}
 &A_I^{2*}(x, \Omega_b) \\
 &= \int_{[0, l(I))} \int_{\Omega_b} A_{\theta(-\sigma)I}(\zeta, \Omega_b) A_{\rho(d\sigma)I}(x, d\zeta) \\
 &\leq K \chi_{[\delta, \infty)}(l(I)) \int_{[0, l(I)-\delta)} \int_{\Omega_b} A_{\rho(d\sigma)I}(x, d\zeta) \\
 &= K \chi_{[\delta, \infty)}(l(I)) \int_{[0, l(I)-\delta)} A_{\rho(d\sigma)I}(x, \Omega_b) = K \chi_{[\delta, \infty)}(l(I)) A_{\rho(l(I)-\delta)I}(x, \Omega_b) \\
 &\leq K^2 \chi_{[\delta, \infty)}(l(I)) \chi_{[\delta, \infty)}(l(I) - \delta) = K^2 \chi_{[2\delta, \infty)}(l(I))
 \end{aligned}$$

and inductively

$$A_I^{n*}(x, \Omega_b) \leq K^n \chi_{[n\delta, \infty)}(l(I)).$$

Denoting by $[a]$ the greatest integer smaller or equal to a , one can sum to arrive at

$$\begin{aligned}
 A_I^c(x, \Omega_b) &\leq \sum_{n=1}^{\infty} \chi_{[n\delta, \infty)}(l(I)) K^n = \sum_{n=1}^{[\frac{l(I)}{\delta}]} K^n = \frac{K - K^{[\frac{l(I)}{\delta}+1]}}{1 - K} \\
 &\leq \frac{K}{K - 1} (e^{\frac{l(I)}{\delta} \ln K} - 1),
 \end{aligned}$$

for $K \neq 1$ and $A_I^c(x, \Omega_b) \leq \frac{l(I)}{\delta}$ for $K = 1$. \square

We combine Proposition 4.14 and Lemma 4.17 in Theorem 4.20. An alternative to prove convergence of the clan kernel series is to require a bound on the birth kernel which is linear in time while dropping the reproduction delay assumption. This is a weaker condition than Hypothesis 4.16 and Assumption 4.15 together, which leads to a different and possibly weaker estimate of A_I^c .

Hypothesis 4.18. There exists some $k \geq 0$ such that, for all $I \in \mathcal{C}$ and all $x \in \Omega$,

$$A_I(x, \Omega_b) \leq kl(I). \tag{4.12}$$

We then estimate the clan kernel as follows.

Lemma 4.19. Under Hypothesis 4.18 there exists a constant $k \geq 0$ such that, for all $I \in \mathcal{C}$ and all $x \in \Omega$,

$$A_I^c(x, \Omega_b) \leq e^{kl(I)} - 1.$$

Proof. If we suppress the dependence on (x, Ω_b) in the notation, it follows from (4.12) that

$$A_I^{2*} = \int_{[0,l(I))} A_{\theta(-\sigma)I} \times A_{\rho(d\sigma)I} \leq k^2 \int_{[0,l(I))} (l(I) - \sigma) d\sigma = \frac{1}{2}k^2l^2(I),$$

from which we arrive by induction at an estimate in terms of the Taylor expansion of the exponential function

$$A_I^{n*} \leq \frac{1}{n!}k^n l^n(I).$$

The rest follows by summation. \square

We conclude that, in the present setting, for fixed $l(I)$, the operator T_I is bounded uniformly with respect to I , which establishes Hypothesis 2.5:

Theorem 4.20. (a) *Under Hypothesis 4.16 and Assumption 4.15, one has*

$$\|T_I m\| \leq \begin{cases} \|m\| \left(\frac{l(I)}{\delta} + 1 \right), & \text{for } K = 1, \\ \|m\| \frac{1}{K-1} \left(K e^{\frac{l(I)}{\delta} \ln K} - 1 \right), & \text{for } K \neq 1. \end{cases}$$

(b) *Under Hypothesis 4.18, one has*

$$\|T_I m\| \leq \|m\| e^{kl(I)}.$$

(c) *Under the conditions of either (a) or (b), there exist constants $c \geq 1$ and $k \geq 0$, such that*

$$\|T_I m\| \leq c e^{kl(I)} \|m\|. \tag{4.13}$$

In the remainder of Section 4, we will use Hypothesis 4.18 or directly (4.13). Conditions guaranteeing that Hypothesis 4.16 or Hypothesis 4.18 holds will be given in Section 6.2.

4.3. Existence of the preadjoint

In Section 2.4, we introduced the concept of duality in the abstract setting. In order to guarantee that Hypothesis 2.7 holds, we first define a space X , such that $X^* = M(\Omega)$ and on which there can be defined operators to which the operators (4.1) are adjoint. We start by making

Assumption 4.21. The i-state space Ω is a locally compact Hausdorff space.

This guarantees Hypothesis 4.1 and enables us to define

$$\begin{aligned} X &:= C_0(\Omega) \\ &= \{f \in C(\Omega) : \forall \varepsilon > 0 \exists K_\varepsilon \subset \Omega \text{ compact,} \\ &\quad \text{with } |f(s)| < \varepsilon \quad \forall s \in \Omega \setminus K_\varepsilon\} \end{aligned} \tag{4.14}$$

equipped with the supremum norm. Here $C(\Omega)$ denotes the vector space of all continuous functions on Ω . We call X the *continuous functions vanishing at infinity*, see e.g. [26]. Note that for compact Ω we have $X = C(\Omega)$. The dual space of X then indeed can be represented by the population state space, i.e.,

$$X^* = C_0(\Omega)^* = M(\Omega) = Y,$$

when the pairing is defined by

$$\langle m, \phi \rangle := \phi \times m = \int_{\Omega} \phi(x)m(dx). \tag{4.15}$$

Here and in Section 4.4 we establish results that will also be used in the nonlinear theory where one might have merely bounded and measurable functions, see Section 5.1. Denoting the Banach space of bounded and measurable functions equipped with the sup-norm by $BM(\Omega)$, we therefore remark that the canonical embedding (see the remarks and reference below Hypothesis 3.4) of $C_0(\Omega)$ in its bidual space $C_0(\Omega)^{**} = M(\Omega)^*$

$$\begin{aligned} C_0(\Omega) &\longrightarrow M(\Omega)^* \\ \phi &\longmapsto \langle \cdot, \phi \rangle \end{aligned}$$

can be extended to $BM(\Omega)$ in a natural way: one easily proves that

$$\begin{aligned} BM(\Omega) &\longrightarrow M(\Omega)^* \\ \phi &\longmapsto \langle \cdot, \phi \rangle \end{aligned}$$

also defines an imbedding. In particular, the right-hand side of (4.15) is well defined if $\phi \in BM(\Omega)$ and for such ϕ the estimate

$$\left| \int_{\Omega} \phi(x) dx \right| \leq \sup_{x \in \Omega} |\phi(x)| \|m\|$$

holds.

Now recall that, for every I and x , $u_I^c(x, \cdot) \in M(\Omega)$. Hence the pairing

$$\langle u_I^c(x, \cdot), \phi \rangle = (\phi \times u_I^c)(x) = \int_{\Omega} \phi(y)u_I^c(x, dy) \tag{4.16}$$

is well defined.

In order to define preadjoint operators $\tilde{T}_I\phi$ by (4.16), one has to guarantee that the map

$$x \mapsto (\phi \times u_I^c)(x)$$

belongs to $C_0(\Omega)$. To do so in terms of u_I and A_I , we first recall

Definition 4.22. For a measure m , the *total variation measure* $|m|$ is given by

$$|m|(\omega) := \sup \sum_{i=1}^{\infty} |m(\omega_i)|,$$

the supremum being taken over all partitions $\{\omega_i\}$ of ω . For a kernel k we use the notation $|k|(x, \omega) = |k(x, \cdot)|(\omega)$, that is, we define $|k|$ as a kernel. The *total variation* of a real-valued function f defined on an interval $[0, s]$ is given as

$$V(f) := \sup \sum_{j=1}^n |f(x_j) - f(x_{j-1})|,$$

the supremum being taken over all choices $\{x_i\}$, such that

$$0 \leq x_0 < \dots < x_n \leq s.$$

Note that, by monotonicity and positivity of A_I , see Hypothesis 4.11 (i), for $I \in \mathcal{C}$ and $x \in \Omega$, one has

$$V(|A_{\rho(\cdot)I}|(x, \Omega_b)) = V(A_{\rho(\cdot)I}(x, \Omega_b)) = A_I(x, \Omega_b). \tag{4.17}$$

Hypothesis 4.23. (a) For every $\phi \in C_0(\Omega)$ and every $I \in \mathcal{C}$, the map

$$x \mapsto (\phi \times u_I)(x)$$

is continuous on Ω .

(b) For every $I \in \mathcal{C}$, $x_0 \in \Omega$, $\varepsilon > 0$ there exists some $\delta = \delta(I, x_0, \varepsilon)$ such that

$$V(|A_{\rho(\cdot)I}(x, \cdot) - A_{\rho(\cdot)I}(x_0, \cdot)|(\Omega_b)) < \varepsilon$$

on $[0, l(I)]$ for all $x \in \Omega$ with $|x - x_0| < \delta$.

(In other words, we should have that, when defining

$$f(s) := |A_{\rho(s)I}(x, \cdot) - A_{\rho(s)I}(x_0, \cdot)|(\Omega_b),$$

then $V(f) < \varepsilon$ on $[0, l(I)]$).

(c) Let $I \in \mathcal{C}$ and $\phi \in C_0(\Omega)$, then the functions

$$x \mapsto A_I(x, \Omega_b), \tag{4.18}$$

$$x \mapsto (\phi \times u_I)(x) \tag{4.19}$$

vanish at infinity in the sense of (4.14).

Remark 4.24. When interpreting (4.18) in terms of size or age structure, for large classes of models the assumption is natural (see Section 6.3). Nevertheless, we remark that the estimate (4.25) in the proof of Theorem 4.25 below shows that (c) is not sharp and hence one might alternatively choose a weaker assumption, with a possibly less clear interpretation.

To prove that Hypothesis 4.23 is sufficient for well-defining $\tilde{T}_I\phi$ by (4.16), we will estimate products and convolutions. Again it will prove convenient to introduce some notation. For $\phi \in BM(\Omega)$ by

$$o_I := \phi \times u_I \tag{4.20}$$

we define a function on Ω , which we call an individuals *output* (with respect to ϕ , see Section 5.1). Analogously, by

$$o_I^c := \phi \times u_I^c, \tag{4.21}$$

we define an individuals *clan output*. The exposition will lead us to use both notations, more precisely, for estimating we shall use the “ ϕ -notation” and for abbreviating the “ o -notation”.

From (4.9) we get a generalized Volterra convolution equation (where generalized refers to the convolution product where the variable is a function of time rather than time itself) which will be central in following estimates:

$$o_I^c = o_I + (o^c * A)_I. \tag{4.22}$$

For functions $x \rightarrow \varphi_{I,J}(x)$ parametrized by two inputs of not necessarily the same length, define

$$\overline{\varphi}_{I,J} := \sup_{\xi \in \Omega_b, \sigma \in [0, \min\{l(I), l(J)\}]} |\varphi_{\theta(-\sigma)I, \theta(-\sigma)J}(\xi)|$$

and make an analogous definition for functions parametrized by one input.

Theorem 4.25. *One has $o_I^c \in C_0(\Omega)$ and therefore the map $\tilde{T}_I : C_0(\Omega) \rightarrow C_0(\Omega)$,*

$$\tilde{T}_I \phi := \phi \times u_I^c \tag{4.23}$$

is well defined.

Proof. We first show the continuity of $x \mapsto o_I^c(x)$. Using (4.22), by subtraction we arrive at

$$\begin{aligned} |o_I^c(x) - o_I^c(x_0)| &\leq |o_I(x) - o_I(x_0)| + |(o^c * A)_I(x) - (o^c * A)_I(x_0)| \\ &= |o_I(x) - o_I(x_0)| + |(o_I^c * (A_I(x, \cdot) - A_I(x_0, \cdot)))|. \end{aligned} \tag{4.24}$$

In order to estimate the second difference on the right-hand side of (4.24), we first show that \overline{o}_I^c is finite: Using (4.4) and (4.3) and Hypothesis 4.11 (ii), one can estimate

$$\begin{aligned} |o_I^c(x)| &= |(\phi \times u_I^c)(x)| \leq |(\phi \times u_I)(x)| + |(\phi \times (u * A^c)_I)(x)| \\ &\leq \|\phi\| (1 + A_I^c(x, \Omega)). \end{aligned}$$

Then, one deduces from Lemma 4.17 or Lemma 4.19, that $\overline{o}_I^c < \infty$ and we can continue estimating in (4.24):

$$|(o_I^c * (A_{\rho(\cdot)I}(x, \cdot) - A_{\rho(\cdot)I}(x_0, \cdot)))| \leq \overline{o}_I^c V(|A_{\rho(\cdot)I}(x, \cdot) - A_{\rho(\cdot)I}(x_0, \cdot)|(\Omega_b)).$$

Hence, we arrive at

$$|o_I^c(x) - o_I^c(x_0)| \leq |o_I(x) - o_I(x_0)| + \overline{o}_I^c V(|A_{\rho(\cdot)I}(x, \cdot) - A_{\rho(\cdot)I}(x_0, \cdot)|(\Omega_b))$$

and the continuity follows from Hypothesis 4.23 (a) and (b).

The vanishing at infinity property follows from (4.22), (4.17) and Hypothesis 4.23(c) and the estimate

$$|\tilde{T}_I \phi(x)| \leq (\phi \times u_I)(x) + \overline{o}_I^c A_I(x, \Omega_b). \quad \square \tag{4.25}$$

4.4. Weak* continuous dependence on the input

We verify the continuity assumption Hypothesis 2.8 by estimating outputs and differences of outputs via convolution equations. From (4.22), (4.17) and Hypothesis 4.18 one gets

$$|o_I^c(x)| \leq |o_I(x)| + \bar{o}_I^c A_I(x, \Omega_b) \leq \|\phi\| + \bar{o}_I^c kl(I) \tag{4.26}$$

(with here and in the rest of this section k as introduced in Hypothesis 4.18). Next, we deduce an analogous inequality for the difference of clan outputs. For inputs of equal length, we deduce from (4.22) by subtraction that

$$o_I^c - o_J^c = o_I - o_J + o_I^c * (A_I - A_J) + (o_I^c - o_J^c) * A_J, \tag{4.27}$$

where we slightly adapted the convolution notation in an obvious manner. Hence, for $x \in \Omega$ we can estimate

$$\begin{aligned} |o_I^c(x) - o_J^c(x)| &\leq |o_I(x) - o_J(x)| + \bar{o}_I^c V(|A_{\rho(\cdot)I} - A_{\rho(\cdot)J}|(x, \Omega_b)) \\ &\quad + \overline{o_I^c - o_J^c} A_J(x, \Omega_b) \\ &\leq g_{I,J}(x) + \overline{o_I^c - o_J^c} kl(J), \end{aligned} \tag{4.28}$$

where

$$g_{I,J}(x) := |o_I(x) - o_J(x)| + \bar{o}_I^c V(|A_{\rho(\cdot)I} - A_{\rho(\cdot)J}|(x, \Omega_b)). \tag{4.29}$$

The next goal is to work out an estimate for clan outputs from (4.26) and for their differences from (4.28) (note the common structure) by establishing a result somewhat similar to Gronwalls Lemma for functions parametrized by inputs. For the case of dependence on merely one input, the following lemma has already been proved in [10].

Lemma 4.26. *Suppose for $I, J \in \mathcal{C}$ and $x \in \Omega$ it holds that*

$$\varphi_{I,J}(x) \leq h_{I,J}(x) + \bar{\varphi}_{I,J} K_{I,J}(x) \tag{4.30}$$

and $\bar{K}_{I,J} < 1$, then we obtain the estimate

$$\varphi_{I,J}(x) \leq h_{I,J}(x) + (1 - \bar{K}_{I,J})^{-1} \bar{h}_{I,J} K_{I,J}(x).$$

Proof. Let $\sigma < \min\{l(I), l(J)\}$ then, since $\bar{\varphi}_{\theta(-\sigma)I, \theta(-\sigma)J} \leq \bar{\varphi}_{I,J}$, we get from (4.30)

$$\varphi_{\theta(-\sigma)I, \theta(-\sigma)J}(x) \leq h_{\theta(-\sigma)I, \theta(-\sigma)J}(x) + \bar{\varphi}_{I,J} K_{\theta(-\sigma)I, \theta(-\sigma)J}(x)$$

and hence, by taking suprema,

$$\bar{\varphi}_{I,J} \leq \bar{h}_{I,J} + \bar{\varphi}_{I,J} \bar{K}_{I,J}.$$

Therefore, as $\bar{K}_{I,J} < 1$, we have

$$\bar{\varphi}_{I,J} \leq (1 - \bar{K}_{I,J})^{-1} \bar{h}_{I,J},$$

which can be plugged into the right-hand side of (4.30) to yield the result. \square

Applying this lemma to (4.28) we obtain

Lemma 4.27. *Let g be defined by (4.29), then the estimate*

$$|(\phi \times u_I^c)(x) - (\phi \times u_J^c)(x)| \leq g_{I,J}(x) + (1 - ks)^{-1} \overline{g_{I,J}} ks$$

holds for all $x \in \Omega$, $I, J \in C_s$, provided $s < \frac{1}{k}$.

For the special case of functions depending merely on one input, Lemma 4.26 can be applied to (4.26):

Lemma 4.28. *For $s < \frac{1}{k}$, $I \in C_s$, $\phi \in BM(\Omega)$ and $x \in \Omega$, one has*

$$|(\phi \times u_I^c)(x)| \leq \|\phi\| (1 - ks)^{-1}. \tag{4.31}$$

While so far the results only require $\phi \in BM(\Omega)$, in Theorem 6.11 we will restrict ourselves to $C_0(\Omega)$. Then we can formulate continuity assumptions on u_I and A_I as

Hypothesis 4.29. (a) There exists some $l > 0$ and some nondecreasing function $C(s)$ on $[0, l]$, tending to zero as s tends to zero, such that

$$V(|A_{\rho(\cdot)I} - A_{\rho(\cdot)J}|(x, \Omega_b)) \leq C(s) \|I - J\| \tag{4.32}$$

for all $s \in [0, l]$, $x \in \Omega$, $I, J \in C_s$.

(b) There exists some $l > 0$, such that for all $\phi \in C_0(\Omega)$ and all $\varepsilon > 0$, there exists some $\delta = \delta(\varepsilon, \phi)$, such that

$$|(\phi \times u_I)(x) - (\phi \times u_J)(x)| \leq \varepsilon \tag{4.33}$$

for all $x \in \Omega$, $s \in [0, l]$ and all $I, J \in C_s$ with $\|I - J\| \leq \delta$.

Finally, we can prove the main result of this subsection, which guarantees that Hypothesis 2.8 is fulfilled.

Theorem 4.30. *There exists some $l > 0$, such that for all $\phi \in C_0(\Omega)$ and all $\varepsilon > 0$, there exists some $\delta = \delta(\varepsilon, \phi)$, such that*

$$|(\phi \times u_I^c)(x) - (\phi \times u_J^c)(x)| \leq \varepsilon$$

for all $x \in \Omega$, $s \in [0, l]$ and all $I, J \in C_s$ with

$$\|I - J\| \leq \delta.$$

Proof. By Lemma 4.27, one has

$$|(\phi \times u_I^c)(x) - (\phi \times u_J^c)(x)| \leq g_{I,J}(x) + (1 - ks)^{-1} ks \overline{g_{I,J}}. \tag{4.34}$$

On the other hand, from (4.29) and Lemma 4.28 one has

$$\begin{aligned} g_{I,J}(x) &= |(\phi \times u_I)(x) - (\phi \times u_J)(x)| \\ &\quad + \overline{o}_I^c V(|A_{\rho(\cdot)I} - A_{\rho(\cdot)J}|(x, \Omega_b)) \\ &\leq |(\phi \times u_I)(x) - (\phi \times u_J)(x)| \\ &\quad + \|\phi\| (1 - ks)^{-1} V(|A_{\rho(\cdot)I} - A_{\rho(\cdot)J}|(x, \Omega_b)). \end{aligned}$$

The rest follows by plugging this estimate into (4.34) and using Hypothesis 4.29. \square

4.5. Weak* continuous dependence on time

Working along the same lines as in Section 4.4, we verify Hypothesis 2.13 in terms of the behaviour of the map $t \mapsto u_{\rho(t)I}$, which itself will be investigated in Section 6.5. Note, that for $I \in \mathcal{C}$ and $s, t \in [0, l(I)]$, from (4.22) we get

$$o_{\rho(t)I}^c - o_{\rho(s)I}^c = o_{\rho(t)I} - o_{\rho(s)I} + (o^c * A)_{\rho(t)I} - (o^c * A)_{\rho(s)I}. \tag{4.35}$$

If $t > s$, we rewrite the second difference on the right-hand side as

$$\begin{aligned} &(o^c * A)_{\rho(t)I} - (o^c * A)_{\rho(s)I} \\ &= \int_{[0,s]} (o_{\theta(-\sigma)\rho(t)I}^c - o_{\theta(-\sigma)\rho(s)I}^c) \times A_{\rho(d\sigma)\rho(s)I} \\ &\quad + \int_{[s,t]} o_{\theta(-\sigma)\rho(t)I}^c \times A_{\rho(d\sigma)\rho(t)I}. \end{aligned} \tag{4.36}$$

For $x \in \Omega$, the first integral can be estimated as

$$\begin{aligned} & \left| \int_{[0,s)} ((o_{\theta(-\sigma)\rho(t)I}^c - o_{\theta(-\sigma)\rho(s)I}^c) \times A_{\rho(d\sigma)\rho(s)I})(x) \right| \\ & \leq \sup_{\xi \in \Omega_b, \sigma \in [0,s)} |o_{\theta(-\sigma)\rho(t)I}^c(\xi) - o_{\theta(-\sigma)\rho(s)I}^c(\xi)| k s \\ & = \overline{o_{\rho(t)I}^c - o_{\rho(s)I}^c} k s. \end{aligned}$$

Similarly, we estimate the second integral of (4.36) as

$$\begin{aligned} & \left| \int_{[s,t)} (o_{\theta(-\sigma)\rho(t)I}^c \times A_{\rho(d\sigma)\rho(t)I})(x) \right| \\ & \leq \sup_{\xi \in \Omega_b, \sigma \in [s,t)} |o_{\theta(-\sigma)\rho(t)I}^c(\xi)| k(t - s) \\ & \leq \overline{o_{\rho(t)I}^c} k(t - s). \end{aligned}$$

Hence, for $x \in \Omega$ and $0 \leq s < t \leq l(I)$, we can derive from (4.35) that

$$\begin{aligned} & |o_{\rho(t)I}^c(x) - o_{\rho(s)I}^c(x)| \\ & \leq |o_{\rho(t)I}(x) - o_{\rho(s)I}(x)| + \overline{o_{\rho(t)I}^c} k(t - s) + \overline{o_{\rho(t)I}^c - o_{\rho(s)I}^c} k s. \\ & = g_{\rho(t)I, \rho(s)I}(x) + \overline{o_{\rho(t)I}^c - o_{\rho(s)I}^c} k s, \end{aligned} \tag{4.37}$$

where

$$g_{\rho(t)I, \rho(s)I}(x) := |o_{\rho(t)I}(x) - o_{\rho(s)I}(x)| + \overline{o_{\rho(t)I}^c} k(t - s). \tag{4.38}$$

Now, we can apply Lemma 4.26 to (4.37).

Lemma 4.31. *For $x \in \Omega$ and sufficiently small $l(I)$, one has*

$$|o_{\rho(t)I}^c(x) - o_{\rho(s)I}^c(x)| \leq g_{\rho(t)I, \rho(s)I}(x) + (1 - kl(I))^{-1} \overline{g_{\rho(t)I, \rho(s)I}} kl(I), \tag{4.39}$$

where g is defined by (4.38).

Before estimating (4.39) using (4.38), it remains to state a continuity assumption for u :

Hypothesis 4.32. There exists some $l > 0$, such that for all $\phi \in C_0(\Omega)$ and all $\varepsilon > 0$ there exists some $\delta = \delta(\varepsilon, \phi)$, such that

$$|(\phi \times u_{\rho(s)I})(x) - (\phi \times u_{\rho(t)I})(x)| \leq \varepsilon \tag{4.40}$$

for all $x \in \Omega$, $I \in C_l$ and all $s, t \in [0, l]$ with $|s - t| \leq \delta$.

Now Hypothesis 2.13 can be verified:

Theorem 4.33. There exists some $l > 0$, such that for all $\phi \in C_0(\Omega)$ and all $\varepsilon > 0$ there exists some $\delta = \delta(\varepsilon, \phi)$, such that

$$|(\phi \times u_{\rho(s)I}^c)(x) - (\phi \times u_{\rho(t)I}^c)(x)| \leq \varepsilon \tag{4.41}$$

for all $x \in \Omega$, $I \in C_l$ and all $s, t \in [0, l]$ with $|s - t| \leq \delta$.

Proof. By Lemma 4.31, one has for $x \in \Omega$ and sufficiently small $l(I)$ that

$$\begin{aligned} & |(\phi \times u_{\rho(t)I}^c)(x) - (\phi \times u_{\rho(s)I}^c)(x)| \\ & \leq g_{\rho(t)I, \rho(s)I}(x) + (1 - kl(I))^{-1}kl(I)\bar{g}_{\rho(t)I, \rho(s)I}, \end{aligned} \tag{4.42}$$

where by Lemma 4.28 and (4.38) one has

$$\begin{aligned} 0 \leq g_{\rho(t)I, \rho(s)I}(x) & \leq |(\phi \times u_{\rho(t)I})(x) - (\phi \times u_{\rho(s)I})(x)| \\ & \quad + \|\phi\|(1 - kl(I))^{-1}k(t - s). \end{aligned} \tag{4.43}$$

The first term on the right-hand side of (4.43) tends to zero as $|s - t| \rightarrow 0$ for $l(I)$ sufficiently small, uniformly in I and $x \in \Omega$ by Hypothesis 4.32 and hence so does $g_{\rho(t)I, \rho(s)I}(x)$. Using this, the statement follows from (4.42). \square

5. Nonlinear structured population models

We elaborate the hypotheses made in Section 3.

5.1. Linear continuous output

Remember that for the case $\gamma \in (C_0(\Omega))^n$, the continuity of the map

$$t \mapsto \gamma \times u_{\rho(t)I}^c \times m$$

is guaranteed, see Section 3.1. Since also for the subsequent verification of global existence and continuity properties of the nonlinear system, the continuity of γ is of

great use, we will concentrate on this case. For the class of models where γ can be represented by an element of the bidual space, we can suppose $\gamma \in (BM(\Omega))^n \subset (C_0(\Omega)^{**})^n$ (where more precisely “ \subset ” refers to embedding, see the remarks below Assumption 4.21). We refer to [10] for a technically more involved method to treat the case of a γ with jumps.

Remark 5.1. In biologically relevant models γ depends on I . In [10] it is suggested however that most (if not all) models have a hierarchical structure of the form

$$I_1 = \gamma_1 \times m, \quad I_2 = \gamma_2(I_1) \times m, \dots \tag{5.1}$$

In that paper it is also argued that this structure can be used to construct solutions via a similar contraction argument as in the case where γ is independent of I . We are confident that also the arguments used in the following to derive global existence can be generalized to models having the hierarchical structure, but leave the elaboration for future work.

Assumption 5.2. There exists some $\gamma \in (C_0(\Omega))^n$, such that

$$H(u_{\rho(\cdot)I}^c \times m) = \gamma \times u_{\rho(\cdot)I}^c \times m, \tag{5.2}$$

for all $m \in M_+(\Omega)$, $I \in C_s$, $s > 0$.

Corollary 5.3. Hypothesis 3.5 holds and when, as in Definition 3.3, we define $P_m I = H(u_{\rho(\cdot)I}^c \times m)$, then for all $s > 0$ it holds that $P_m(C_s) \subset C_s$.

In analogy to (4.20) and (4.21), we rewrite (5.2) as

$$P_m I = o_{\rho(\cdot)I}^c \times m, \tag{5.3}$$

while defining o_I and o_I^c by

$$o_I^{(c)} := \gamma \times u_I^{(c)}. \tag{5.4}$$

5.2. Global solutions

For a linear output the Lipschitz condition on the input output map Hypothesis 3.24 is fulfilled, if a corresponding condition for the clan output holds:

Lemma 5.4. Assume there exists some $\delta > 0$ and some nondecreasing function $K : [0, \delta] \rightarrow \mathbf{R}_+$ with $\lim_{s \downarrow 0} K(s) = 0$, such that

$$|o_I^c(x) - o_J^c(x)| \leq K(s) \|I - J\| \tag{5.5}$$

for all $s \in [0, \delta]$, all $I, J \in C_s$ and all $x \in \Omega$, then Hypothesis 3.24 holds, i.e.,

$$\|P_m I - P_m J\| \leq K(s)\|I - J\|$$

for all $m \in M_+(\Omega)$, $s \in [0, \delta]$ and $I, J \in C_s$.

Proof. Let $s \in [0, \delta]$ and $t \in [0, s]$, then the statement follows from the estimate

$$\begin{aligned} |P_m I(t) - P_m J(t)| &= \left| \int_{\Omega} (o_{\rho(t)I}^c(x) - o_{\rho(t)J}^c(x))m(dx) \right| \\ &\leq K(t)\|\rho(t)I - \rho(t)J\|\|m\| \leq K(s)\|m\|\|I - J\|. \quad \square \end{aligned}$$

Hence, we estimate the differences of clan outputs, more precisely we guarantee the Lipschitz property (5.5) via a corresponding property for individual outputs:

Hypothesis 5.5. There exists some $\delta > 0$ and some nondecreasing function $C_2 : [0, \delta] \rightarrow \mathbf{R}_+$, tending to zero as s tends to zero, such that

$$|o_I(x) - o_J(x)| \leq C_2(s)\|I - J\| \tag{5.6}$$

for all $s \in [0, \delta]$, $x \in \Omega$, $I, J \in C_s$.

Proposition 5.6. There exists some $\delta > 0$ and a nondecreasing function $K : [0, \delta] \rightarrow \mathbf{R}_+$, tending to zero as s tends to zero, such that

$$|o_I^c(x) - o_J^c(x)| \leq K(s)\|I - J\|$$

for all $s \in [0, \delta]$, all $I, J \in C_s$ and all $x \in \Omega$.

Proof. Like in the proof of Theorem 4.30, with ϕ specified to be γ , one deduces

$$|o_I^c(x) - o_J^c(x)| \leq g_{I,J}(x) + (1 - ks)^{-1}ks\overline{g_{I,J}}, \tag{5.7}$$

where

$$\begin{aligned} g_{I,J}(x) &\leq |o_I(x) - o_J(x)| \\ &\quad + \|\gamma\|(1 - ks)^{-1}V(|A_{\rho(\cdot)I} - A_{\rho(\cdot)J}|(x, \Omega_b)). \end{aligned}$$

Then by Hypotheses 4.29 (a) and 5.5, one arrives at a Lipschitz estimate for $g_{I,J}(x)$, which can be plugged into (5.7) to yield the statement. \square

5.3. *Weak* continuous dependence on the initial value*

Using that by Corollary 5.3, (5.2) and (4.1) we have

$$P_m I = \gamma \times T_{\rho(\cdot)I} m,$$

we can now verify Hypothesis 3.30 via the boundedness of γ .

Lemma 5.7. *For all $s > 0$ and all $I \in C_s$, the map*

$$m \mapsto \gamma \times T_{\rho(\cdot)I} m$$

is continuous from $M(\Omega)$, provided with the norm topology, to C_s .

Proof. Let $s > 0$, $I \in C_s$ and $\theta \in [0, s]$ and suppose, that $m_n \rightarrow m$ in $M_+(\Omega)$, then from the boundedness of γ (Assumption 5.2) and T_I (Hypothesis 2.5), we get

$$\|\gamma \times T_{\rho(\theta)I} m_n - \gamma \times T_{\rho(\theta)I} m\| \leq c e^{ks} \|\gamma\| \|m_n - m\| \tag{5.8}$$

(recall that $\rho(\theta)$ is a bounded linear operator of norm one). Hence, also the supremum of the left-hand side over all $\theta \in [0, s]$ tends to zero for n tending to infinity and the statement of the lemma follows. \square

6. Deterministic individual development for linear systems with input

For the verification of the hypotheses made in Sections 4 and 5 we concentrate on the case of deterministic individual development, which we call *growth*. Moreover, we shall assume that there is only one possible state at birth.

6.1. *Vital functions*

Assumption 6.1. (a) There exists some $x_b \in \Omega$ such that $\Omega_b := \{x_b\}$ (see Definition 4.13). We call x_b the *state at birth*

(b) There exist functions X_I, \mathcal{F}_I and L_I with the following interpretations:

$X_I(x)$ denotes the *i-state (size)* of an individual that has evolved under an input I during $l(I)$ time units after the individual had state x .

$\mathcal{F}_I(x)$ denotes the *survival probability* of such an individual.

$L_I(x)$ denotes the *reproduction function*, i.e., the expected number of offspring produced by such an individual in the time interval of length $l(I)$ experiencing input I .

Remark 6.2. In case that individual development can be described by birth, growth and death rates β, g and μ , like in the class of models described by the PDE given in

the introduction, one can easily define vital functions in terms of these rates: one uses that the function $t \mapsto X_{\rho(t)I}(x_0)$ is the unique solution of the initial value problem

$$\begin{aligned} \frac{d}{dt}x(t) &= g(x(t), I(t)), \\ x(0) &= x_0 \end{aligned}$$

and that

$$\mathcal{F}_I(x_0) = e^{-\int_0^{l(I)} \mu(X_{\rho(s)I}(x_0), I(s)) ds}$$

and

$$L_I(x_0) = \int_0^{l(I)} \beta(X_{\rho(s)I}(x_0), I(s)) \mathcal{F}_{\rho(s)I}(x_0) ds.$$

For an example for the modelling of individual behaviour via rates, we refer to the cannibalism model described in [7,10,15,16]. This model is very instructive as it is on the one hand simple in the way that only one (structured) population is involved, but on the other hand features structure (size-dependence) and nonlinearities (cannibalistic interactions).

Now the earlier defined kernels take the form

$$u_I(x, \omega) = \delta_{X_I(x)}(\omega) \mathcal{F}_I(x), \tag{6.1}$$

$$A_I(x, \omega) = L_I(x) \delta_{x_b}(\omega) \tag{6.2}$$

for $x \in \Omega$ and $\omega \in \Sigma$ and we formulate Hypotheses 4.5, 4.8 and 4.11 in terms of the vital functions.

Assumption 6.3. (i) $(x, \omega) \mapsto \delta_{X_I(x)}(\omega) \mathcal{F}_I(x)$ and $(x, \omega) \mapsto L_I(x) \delta_{x_b}(\omega)$ are parametrized families of positive kernels.

(ii) For $I \in \mathcal{C}$, $\sigma \in [0, l(I)]$ and $x \in \Omega$ the two consistency relations

$$\begin{aligned} L_I(x) &= L_{\rho(\sigma)I}(x) + L_{\theta(-\sigma)I}(X_{\rho(\sigma)I}(x)) \mathcal{F}_{\rho(\sigma)I}, \\ \mathcal{F}_I(x) &= \mathcal{F}_{\rho(\sigma)I}(x) \mathcal{F}_{\theta(-\sigma)I}(X_{\rho(\sigma)I}(x)) \end{aligned}$$

hold.

(iii) For $x \in \Omega$ and $I \in \mathcal{C}$ the function $\sigma \mapsto L_{\rho(\sigma)I}(x)$ is nondecreasing on $[0, l(I)]$ and $\lim_{\sigma \downarrow 0} L_{\rho(\sigma)I}(x) = 0$.

(iv) For $x \in \Omega$ and $I \in \mathcal{C}$ the function $\sigma \mapsto \mathcal{F}_{\rho(\sigma)I}(x)$ is nonincreasing on $[0, l(I)]$ and $\lim_{\sigma \downarrow 0} \mathcal{F}_{\rho(\sigma)I}(x) = 1$, in particular $\mathcal{F}_I(x) \leq 1$.

Note that, when X_I, \mathcal{F}_I and L_I are defined via rates, like suggested in Remark 6.2, Assumption 6.3 can be guaranteed in a straightforward and natural manner.

6.2. *Exponential boundedness*

Concerning exponential boundedness, all that is left to do at this level is to verify either the reproduction delay or the linear boundedness of the reproduction kernel, which leads to the following alternatives.

Assumption 6.4. There exists some $\delta > 0$, such that for all $s \in [0, \delta]$ and all $I \in C_s$, one has

$$L_I(x_b) = 0.$$

Assumption 6.5. There exists some $k > 0$, such that for all $x \in \Omega$ and all $I \in \mathcal{C}$ one has

$$L_I(x) \leq kl(I).$$

6.3. *Existence of the preadjoint*

We guarantee Hypothesis 4.23 using that, by (6.1) and (6.2), we get

$$(\phi \times u_I)(x) = \int_{\Omega} \phi(y)\mathcal{F}_I(x)\delta_{X_I(x)}(dy) = \phi(X_I(x))\mathcal{F}_I(x), \tag{6.3}$$

$$A_I(x, \Omega_b) = L_I(x). \tag{6.4}$$

Assumption 6.6. (a) For every $I \in \mathcal{C}$, the maps $x \mapsto X_I(x)$ and $x \mapsto \mathcal{F}_I(x)$ are continuous on Ω .

(b) For every $I \in \mathcal{C}, x_0 \in \Omega, \varepsilon > 0$ there exists some $\delta = \delta(I, x_0, \varepsilon)$ such that

$$V(L_{\rho(\cdot)I}(x) - L_{\rho(\cdot)I}(x_0)) < \varepsilon,$$

for all $x \in \Omega$ with $|x - x_0| < \delta$.

(c) For every compact set $K' \subset \Omega$ there exists some compact set $K \subset \Omega$, such that $X_I(x) \in \Omega \setminus K'$ if $x \in \Omega \setminus K$.

(d) The function $x \mapsto L_I(x)$ vanishes at infinity.

Note that for the large class of models with compact Ω , (c) and (d) are always guaranteed. For noncompact Ω , when $X_I(x) \in \mathbf{R}$ represents age or size, one can verify (c) via a monotonicity assumption on $x \mapsto X_I(x)$.

Remark 6.7. For noncompact Ω , (d) is too strong for many models (an exception is “humans” and “age dependence”) (see also Remark 4.24): Individuals, in general, do not stop reproducing upon reaching a certain age (or size), its the mortality, in fact, that stops the reproduction. We hope in future work to incorporate this idea into the modelling by restricting the set of possible population states to exponentially weighted measures and as a consequence to be able to allow a pairing of such measures with functions that do not necessarily vanish at infinity.

Lemma 6.8. For every $\phi \in C_0(\Omega)$ and every $I \in \mathcal{C}$, the function

$$x \mapsto (\phi \times u_I)(x)$$

is an element of $C_0(\Omega)$.

Proof. The continuity follows via (6.3), Assumption 6.6(a) and the continuity of ϕ . The vanishing at infinity follows from Assumption 6.6(c) and the vanishing at infinity of ϕ . \square

Finally note that the continuity property in Assumption 6.6(b) clearly implies the truth of Hypothesis 4.23(b) and the vanishing at infinity in Assumption 6.6(d) implies the vanishing at infinity of $x \rightarrow A_I(x, \Omega_b)$. Hence Hypothesis 4.23 is verified.

6.4. Weak* continuous dependence on input

We elaborate Hypothesis 4.29. There we assumed weak* continuity of the survival kernel u_I , for some $l > 0$ uniformly for $x \in \Omega$ and $I, J \in C_l$, which will be guaranteed via

Assumption 6.9. There exists some $\delta > 0$ and positive functions C_X and C_F , bounded on $[0, \delta]$, such that

$$|X_I(x) - X_J(x)| \leq C_X(s) \int_0^s |I(\sigma) - J(\sigma)| d\sigma, \tag{6.5}$$

$$|\mathcal{F}_I(x) - \mathcal{F}_J(x)| \leq C_F(s) \int_0^s |I(\sigma) - J(\sigma)| d\sigma \tag{6.6}$$

for all $s \in [0, \delta]$, all $I, J \in C_s$ and all $x \in \Omega$.

Remark 6.10. Estimates (6.5)–(6.7) are precisely the estimates that are already used in the local theory in [10]. There, their realization is guaranteed for the case that X_I , \mathcal{F}_I and L_I are prescribed by corresponding rates (see Remark 6.2), by imposing Lipschitz assumptions on the rates. We therefore take these for granted.

Theorem 6.11. Hypothesis 4.29 (b) holds, i.e., there exists some $l > 0$, such that for all $\phi \in C_0(\Omega)$ and all $\varepsilon > 0$ there exists some $\delta = \delta(\varepsilon, \phi)$, such that

$$|(\phi \times u_I)(x) - (\phi \times u_J)(x)| \leq \varepsilon$$

for all $x \in \Omega$ and all $I, J \in C_s$, $s \in [0, l]$ with $\|I - J\| \leq \delta$.

Proof. We estimate

$$\begin{aligned} & |(\phi \times u_I)(x) - (\phi \times u_J)(x)| \\ &= |\phi(X_I(x))\mathcal{F}_I(x) - \phi(X_J(x))\mathcal{F}_J(x)| \\ &\leq |\phi(X_I(x)) - \phi(X_J(x))| + \|\phi\| |\mathcal{F}_I(x) - \mathcal{F}_J(x)|. \end{aligned}$$

The statement now follows from Assumption 6.9 and the uniform continuity of ϕ . \square

Next, we give the assumption corresponding to the variation estimate Hypothesis 4.29(a).

Assumption 6.12. There is some $\delta > 0$ and some nondecreasing function C_L on $[0, \delta]$, such that for all $s \in [0, \delta]$, all $I, J \in C_s$ and all $x \in \Omega$ one has

$$V(L_{\rho(\cdot)I}(x) - L_{\rho(\cdot)J}(x)) \leq C_L(s) \int_0^s |I(\sigma) - J(\sigma)| d\sigma. \tag{6.7}$$

We conclude with a counterexample showing that in general continuous dependence on the input is not given in the dual space norm on $M(\Omega)$. (This means of course that we cannot expect differentiability in that sense either).

Example 6.13. Let $\Omega \subset R_+$ and consider a population disregarding births and deaths (which could apply, when considering a population for a short time) under a given constant input $I \in \mathcal{C}$. Define

$$X_I(x) = x + l(I)I$$

(e.g., via an individual growth rate $g(x, I) = I$). As survival probability we take $\mathcal{F}_I(x) = 1$ and so

$$u_I(x, \cdot) = \mathcal{F}_I(x)\delta_{x+l(I)I} = \delta_{x+l(I)I}.$$

The next state operator takes the form

$$\begin{aligned} T_I m &= u_I^c \times m = u_I \times m \\ &= \delta_{+l(I)I} \times m = \int_{\Omega} \delta_{x+l(I)I} m(dx). \end{aligned}$$

Now let the initial population be concentrated in one individual state $m := \delta_{x_0}$, then

$$T_I \delta_{x_0} = \delta_{X_I(x_0)} = \delta_{x_0+l(I)I}.$$

Fix a length $l(I) =: s$ and define $I_n, I \in C_s$ with $I_n := \frac{1}{n}$ and $I := 0$, then clearly $I_n \rightarrow I$.

Now consider the dual space norm or strong topology given by

$$\|m\| = \sup_{\|\phi\|=1} \left| \int_{\Omega} \phi(x)m(dx) \right|$$

and choose for every $n \in \mathbb{N}$ some continuous function ϕ_n with $\phi_n(x_0) = 1$ and $\phi_n(x_0 + \frac{s}{n}) = -1$. Then

$$\begin{aligned} \|T_{I_n} \delta_{x_0} - T_I \delta_{x_0}\| &= \|\delta_{x_0} - \delta_{x_0+\frac{s}{n}}\| = \sup_{\|\phi\|=1} \left| \int_{\Omega} \phi(x)(\delta_{x_0} - \delta_{x_0+\frac{s}{n}})(dx) \right| \\ &\geq \left| \int_{\Omega} \phi_n(x)(\delta_{x_0} - \delta_{x_0+\frac{s}{n}})(dx) \right| = \left| \phi_n(x_0) - \phi_n\left(x_0 + \frac{s}{n}\right) \right| \\ &= |1 - (-1)| = 2 \end{aligned}$$

for all $n \in \mathbb{N}$, which proves that the next state operator does not depend continuously on the input in this topology.

6.5. Weak* continuous dependence on time

We elaborate Hypothesis 4.32.

Assumption 6.14. There exists some $l > 0$, such that for all $\varepsilon > 0$ there exists some $\delta = \delta(\varepsilon)$ such that

$$\begin{aligned} |X_{\rho(s)I}(x) - X_{\rho(t)I}(x)| &\leq \varepsilon, \\ |\mathcal{F}_{\rho(s)I}(x) - \mathcal{F}_{\rho(t)I}(x)| &\leq \varepsilon \end{aligned}$$

for all $x \in \Omega$, $I \in C_l$ and all $s, t \in [0, l]$ with $|s - t| < \delta$.

Theorem 6.15. Hypothesis 4.32 holds, i.e., there exists some $l > 0$, such that for all $\phi \in C_0(\Omega)$ and all $\varepsilon > 0$ there exists some $\delta = \delta(\varepsilon, \phi)$, such that

$$|(\phi \times u_{\rho(s)I})(x) - (\phi \times u_{\rho(t)I})(x)| \leq \varepsilon$$

for all $x \in \Omega$, $I \in C_l$ and all $s, t \in [0, l]$ with $|s - t| \leq \delta$.

Finally we show that, like in the case of continuity with respect to the input, we cannot expect strong continuity.

Example 6.16. Consider the linear semigroup with input from Example 6.13, but define

$$X_I(x) = x + I(I) \tag{6.8}$$

(e.g., via a growth rate $g(x) = 1$), then

$$T_I m = \delta_{x+I(I)} \times m$$

and

$$T_I \delta_{x_0} = \delta_{x_0+I(I)}$$

for populations concentrated in one individual state. Then

$$T_{\rho(\frac{1}{n})I} \delta_{x_0} = \delta_{x_0+\frac{1}{n}},$$

$$T_{\rho(0)I} \delta_{x_0} = \delta_{x_0},$$

but a computation like in Example 6.13 shows that

$$\|T_{\rho(\frac{1}{n})I} \delta_{x_0} - T_{\rho(0)I} \delta_{x_0}\| = 2.$$

7. Nonlinear deterministic individual development and fixed state at birth

The only hypothesis in Section 5 is Hypothesis 5.5, which will be verified now.

7.1. Global solutions

The Lipschitz property for the output map o_I can be guaranteed via a corresponding property of γ .

Assumption 7.1. The output function γ is globally Lipschitz.

Lemma 7.2. *There exists some $\delta > 0$ and some nondecreasing function $C_2 : [0, \delta] \rightarrow \mathbf{R}_+$ tending to zero for s tending to zero, such that for all $s \in [0, \delta]$, $I, J \in C_s$ and all $x \in \Omega$ one has*

$$|o_I(x) - o_J(x)| \leq C_2(s) \|I - J\|. \tag{7.1}$$

Proof. One uses the same estimate as in the proof of Theorem 6.11, while replacing ϕ by γ and using Assumptions 5.2 and 7.1. \square

8. Summarizing the results for populations with deterministic individual growth

We illustrate the results of this paper by applying them to a class of models describing the dynamics of a size structured one species population with deterministically growing individuals. The development of an individual can then be modelled with size and input dependent growth, survival and reproduction functions $X_I(x)$, $\mathcal{F}_I(x)$ and $L_I(x)$ (for precise interpretations see Section 6.1), a size dependent output function $\gamma(x)$ (Section 5.1), and a fixed size at birth x_b . Define

$$L_I^c(x) := \sum_{k=1}^{\infty} L_I^{k*}(x),$$

with inductively

$$\begin{aligned} L_I^{1*} &:= L_I, \\ L_I^{k*} &:= L_I^{(k-1)*} * L_I, \quad k \geq 2 \end{aligned}$$

and

$$(L * L)_I(x) = \int_{[0, l(I))} L_{\theta(-s)I}(x_b) L_{\rho(ds)I}(x)$$

(the last identity follows by plugging (6.2) into (4.6) and (4.7). The population state is described by a measure m over the possible individual sizes. We have proven

Theorem 8.1. *Suppose X_I, \mathcal{F}_I, L_I and γ satisfy Assumptions 6.3, 6.5, 6.9, 6.12 and 7.1 then, for the nonlinear dynamical system $S(s, m) = T_{\rho(s)I_m} m$ defined via the linear system with input*

$$\begin{aligned} (T_I m)(\omega) &:= \int_{\Omega} \mathcal{F}_I(x) \delta_{X_I(x)}(\omega) m(dx) \\ &+ \int_{\Omega} \int_{[0, l(I))} \mathcal{F}_{\theta(-\sigma)I}(x_b) \delta_{X_{\theta(-\sigma)I}(x_b)}(\omega) L_{\rho(d\sigma)I}^c(x) m(dx) \end{aligned}$$

and the fixed point I_m of the contraction

$$I \mapsto P_m I = \int_{\Omega} \gamma(x) (T_{\rho(\cdot)I} m)(dx),$$

one has global existence via Theorem 3.27. Moreover, S defines a semiflow in the sense of Definition 3.20 (Theorem 3.22) and is bounded in the sense of Theorem 3.23.

If additionally Assumptions 6.6 and 6.14 hold, then S is weak* continuously dependent on time and state in the sense of Theorems 3.28 and 3.31.

9. Conclusions and outlook

Comparing the linear and nonlinear sections at each level, we see that for the nonlinear theory much can be established at an abstract level, via the linear theory and by concatenating inputs. We hope it also became clear how in many ways introducing interaction variables allows one to analyse nonlinear problems mainly in terms of linear problems.

For multispecies models one can define the i -state space Ω as the disjoint union of the single species i -state spaces Ω_j , $j = 1, \dots, k$ and model the interactions between species via inputs.

Finally we mention that structural stability, in the sense of continuous dependence with respect to the modelling ingredients, is still to be established. This is rather important in view of numerical approximation.

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References

- [1] H. Amann, *Gewöhnliche Differentialgleichungen*, Walter de Gruyter, Berlin, New York, 1995.
- [2] O. Angulo, J.C. Lopez-Marcos, Numerical schemes for size-structured population equations, *Math. Biosci.* 157 (1999) 169–188.
- [3] O. Angulo, J.C. Lopez-Marcos, Numerical integration of autonomous and nonautonomous non-linear size-structured population models, *Math. Biosci.* 177,178 (2002) 39–71.
- [4] O. Angulo, J.C. Lopez-Marcos, Numerical integration of fully non-linear size-structured population models, *Appl. Numer. Math.* 50 (3–4) (2004) 291–327.
- [5] O. Arino, K.P. Hadeler, M.L. Hbid, Existence of periodic solutions for delay differential equations with state dependent delay, *J. Differential Equations* 144 (2) (1998) 301–362.
- [6] P.L. Butzer, H. Berens, *Semi-Groups of Operators and Approximation*, Springer, Berlin, Heidelberg, New York, 1967.
- [7] D. Claessen, A.M. de Roos, Bistability in a size-structured population model of cannibalistic fish—a continuation study, *Theoret. Pop. Biol.* 64 (1) (2003) 49–65.
- [8] A.M. de Roos, O. Diekmann, J.A.J. Metz, Studying the dynamics of structured population models: a versatile technique and its application to *Daphnia*, *Amer. Nat.* 139 (1992) 123–147.
- [9] O. Diekmann, S. van Gils, S.M. Verduyn Lunel, H.-O. Walthert, *Delay equations, Functional-, Complex-, and Nonlinear Analysis*, Springer, New York, 1995.
- [10] O. Diekmann, M. Gyllenberg, H. Huang, M. Kirkilionis, J.A.J. Metz, H.R. Thieme, On the formulation and analysis of general deterministic structured population models: II. Nonlinear theory, *J. Math. Biol.* 43 (2001) 157–189.

- [11] O. Diekmann, M. Gyllenberg, J.A.J. Metz, Steady-state analysis of structured population models, *Theoret. Pop. Biol.* 65 (2003) 309–338.
- [12] O. Diekmann, M. Gyllenberg, J.A.J. Metz, H.R. Thieme, On the formulation and analysis of general deterministic structured population models: I. Linear theory, *J. Math. Biol.* 36 (1998) 349–388.
- [13] N. Dunford, J.T. Schwartz, *Linear Operators Part I: General Theory*, Interscience Publishers, Inc., New York, 1964.
- [14] K.-J. Engel, R. Nagel, *One-Parameter Semigroups for Linear Evolution Equations*, Springer, Berlin, 2000.
- [15] Ph. Getto, O. Diekmann, A.M. de Roos, On the (dis) advantages of cannibalism, *J. Math. Biol.*, submitted.
- [16] Ph. Getto, O. Diekmann, A.M. de Roos, Steady state analysis for a size structured cannibalism model with two dynamic resources, in: Ph. Getto, Ph.D. Thesis, in preparation.
- [17] J.K. Hale, *Ordinary Differential Equations*, Wiley-Interscience, New York, 1969.
- [18] E. Hewitt, K. Stromberg, *Real and Abstract Analysis*, Springer, Berlin, Heidelberg, New York, 1965.
- [19] E. Hille, R.S. Phillips, *Functional Analysis and Semi-Groups*, AMS Colloquium Publications, vol. xxxi, Waverly Press, Inc., Baltimore, 1967.
- [20] M. Kirkilionis, O. Diekmann, B. Lissner, M. Nool, B. Sommeijer, A.M. de Roos, Numerical continuation of equilibria of physiologically structured population models, I. Theory, *Math. Models Methods Appl. Sci.* 11 (2001) 1101–1127.
- [21] S.A.L.M. Kooijman, *Dynamic Energy and Mass Budgets in Biological Systems*, Cambridge University Press, Cambridge, 2000.
- [22] J. Mallet Paret, R.D. Nussbaum, Boundary layer phenomena for differential-delay equations with state-dependent time lags: III, *J. Differential Equations* 189 (2003) 640–692.
- [23] M. Marcus, V. Mizel, Limiting equations for problems involving long range memory, *Mem. AMS* 43 (1983) 278.
- [24] J.A.J. Metz, O. Diekmann, *The Dynamics of Physiologically Structured Populations*, Lecture Notes in Biomathematics, vol. 68, Springer, Berlin, 1986.
- [25] J. Prüss, Stability analysis for equilibria in age-specific population dynamics, *Nonlinear Anal.* 7 (1983) 1291–1313.
- [26] W. Rudin, *Real and Complex Analysis*, McGraw-Hill Series in Higher Mathematics, McGraw-Hill, New York, 1974.
- [27] R.J. Sacker, G.R. Sell, Dichotomies for linear evolutionary equations in Banach spaces, *J. Differential Equations* 113 (1994) 17–67.
- [28] H. Thieme, PDEs and ∞ -dim, *Dynamical Systems*, Lecture notes (unpublished).
- [29] H.-O. Walther, The solution manifold and C^1 -smoothness for differential equations with state-dependent delay, *J. Differential Equations* 195 (2003) 46–65.
- [30] G.F. Webb, *Nonlinear Age-Dependent Population Dynamics*, Marcel Dekker, New York, 1985.