

Linear stability and positivity results for a generalized size-structured *Daphnia* model with inflow*

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Dedicated to Professor Miklós Farkas on the occasion of his 75th birthday.

Abstract

We employ semigroup and spectral methods to analyze the linear stability of positive stationary solutions of a generalized size-structured *Daphnia* model. Using the regularity properties of the governing semigroup, we are able to formulate a general stability condition which permits an intuitively clear interpretation in a special case of model ingredients. Moreover, we derive a comprehensive instability criterion that reduces to an elegant instability condition for the classical *Daphnia* population model in terms of the inherent net reproduction rate of *Daphnia* individuals.

Keywords: Predator-prey interaction; structured population dynamics; semigroup methods; principle of linearized stability

1. Introduction

In the last three decades nonlinear age and size-structured population models have attracted a lot of interest both among theoretical biologists and applied mathematicians. Traditionally, structured population models have been formulated as partial differential equations, starting with the pioneering (first nonlinear) model of Gurtin and MacCamy in [15]. Since then several important physiologically structured population models have been developed and analyzed by different methods. We mention here the well-known monographs [3, 17, 20, 25]

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and some recent papers [10, 13, 14, 19] for relevant related work on the subject. Diekmann et al. have been developing a general mathematical framework for modeling structured populations ([7, 8]). Recently they have rigorously proved that the qualitative behavior of nonlinear physiologically structured population models can be studied by means of linearization ([5, 6]). Such a link between the nonlinear stability and the linearized stability of equilibria, commonly referred to as the “Principle of Linearized Stability”, has been found previously for certain semilinear models, most notably models with age structure ([15, 18, 21, 25]). Tucker and Zimmermann [24] proved the stability part for a quite general class of size-structured models with unbounded size span, but the instability part was left open.

Following the lead of [21, 25] we successfully applied linear semigroup methods to formulate biologically interpretable conditions for the linear stability/instability of equilibria of size-structured population models ([13, 14]). In particular, in [13] we treated the linear stability of a single species size-structured model. Our method allowed us to formulate a very general and elegant instability condition in terms of the net reproduction function (see Theorem 5.4 in [13]).

In the present paper we extend our approach to treat the linearized stability of a generalized size-structured *Daphnia* model: a coupled ODE-PDE model which describes a specific predator-prey interaction. The predator population consists of waterfleas (*Daphnia pulex*), while the prey is alga (*Chlamydomonas reinhardtii*). The evolution of the predator population is governed by the following partial differential equation

$$n_t(x, t) + (\gamma(x, F) n(x, t))_x + \mu(x, F) n(x, t) = 0, \quad x \in (0, m], \quad t > 0, \quad (1.1)$$

with the nonlocal boundary condition

$$n(0, t) = C(F) + \int_0^m \beta(x, F) n(x, t) dx, \quad t > 0. \quad (1.2)$$

This boundary condition models the inflow of minimal size individuals into the population. (For simplicity we assume the minimal size to be zero.) Eqs. (1.1)-(1.2) are accompanied by an initial condition of the form

$$n(x, 0) = n_0(x). \quad (1.3)$$

In Eq. (1.1) $n(x, t)$ denotes the density of the waterflea individuals of size x at time t . We assume a finite maximal size $m > 0$. As usual, γ , μ , β denote the growth, mortality and fertility rates of predator individuals, respectively. All of these vital rates are assumed to be dependent on size x and on the population size F of algae. C represents an inflow of zero size *Daphnia* individuals from an external source. Several biologically relevant situations arise when an external inflow of minimal size individuals is taken into account in the formulation of mathematical models of population dynamics. See e.g. [12] and the references therein for recent developments on structured PDE models with inflow.

The dynamics of the algae population F is determined by the following ordinary differential equation

$$\frac{dF}{dt} = \Psi(F) - \int_0^m I(x, F, N) n(x, t) dx, \quad t > 0, \quad (1.4)$$

accompanied by an initial condition

$$F(0) = F_0. \quad (1.5)$$

Here $\Psi(F)$ models the autonomous algae dynamics, i.e. Ψ determines the dynamics of the algae population in the absence of its consumer. Typically, Ψ assumes the form

$$\Psi(F) = \alpha F \left(1 - \frac{F}{K}\right), \quad \alpha > 0, \quad (1.6)$$

or

$$\Psi(F) = \alpha \left(1 - \frac{F}{K}\right), \quad \alpha > 0. \quad (1.7)$$

The first equation models logistic growth of the algae population with $K > 0$ denoting the carrying capacity of the environment. The second equation corresponds to a constant inflow of fresh non-reproducing food with constant deterioration. The quantity $I(x, F, N)$ denotes the feeding rate of the *Daphnia* individuals of size x , which depends on the total population of algae F and on the total population N of *Daphnia*, given by

$$N(t) = \int_0^m n(x, t) dx. \quad (1.8)$$

Our model (1.1)-(1.5) is a generalization of the “standard” size-structured *Daphnia* model, considered in the literature (see e.g. [20, 22]), where the boundary condition (1.2) is replaced by

$$\gamma(0, F) n(0, t) = \int_0^m \beta(x, F) n(x, t) dx, \quad (1.9)$$

and where the feeding rate I is independent of the *Daphnia* population size N . In contrast we have, for the sake of simplicity, incorporated the growth rate $\gamma(0, F)$ on the left of Eq. (1.9) in the inflow C and in the fertility β on the right of Eq. (1.2). For previous results on the qualitative behavior of solutions of the “standard” *Daphnia* model for special choices of model ingredients γ , μ , β , I , Ψ , we refer to [20, 22]. For developments of other physiologically structured models of similar type we direct the reader to [23] for further reference.

For the remainder of this work we impose the following conditions on the model ingredients

$$\mu, \beta \in C^1([0, m] \times (0, \infty)), \quad \beta \geq 0, \quad \mu \geq 0, \quad (1.10)$$

$$\gamma \in C^2([0, m] \times (0, \infty)), \quad \gamma > 0, \quad (1.11)$$

$$I \in C^1([0, m] \times (0, \infty) \times (0, \infty)), \quad I \geq 0, \quad (1.12)$$

$$\Psi, C \in C^1(0, \infty), \quad C \geq 0. \quad (1.13)$$

These conditions are sufficiently strong to make our analysis work.

Next we formulate a simple criterion for the existence of a positive stationary solution (n_*, F_*) of Eqs. (1.1)-(1.5). Throughout we will call a stationary solution (n_*, F_*) positive if both $n_* > 0$ and $F_* > 0$.

Proposition 1.1 *For given model ingredients β, μ, γ, I and Ψ , there is a one-to-one correspondence between all positive stationary solutions (n_*, F_*) of problem (1.1)-(1.5) and all pairs (N_*, F_*) of positive numbers that satisfy the conditions*

$$Q^1(F_*, N_*) = 1 = Q^2(F_*, N_*), \quad (1.14)$$

where

$$Q^1(F, N) \stackrel{\text{def}}{=} \frac{C(F)}{N} \int_0^m \Pi(x, F) dx + \int_0^m \beta(x, F) \Pi(x, F) dx, \quad (1.15)$$

$$Q^2(F, N) \stackrel{\text{def}}{=} \frac{\Psi(F) \int_0^m \Pi(x, F) dx}{N \int_0^m I(x, F, N) \Pi(x, F) dx} \quad (1.16)$$

and

$$\Pi(x, F) \stackrel{\text{def}}{=} \exp \left\{ - \int_0^x \frac{\gamma_x(y, F) + \mu(y, F)}{\gamma(y, F)} dy \right\}. \quad (1.17)$$

If (N_*, F_*) is a pair of positive numbers satisfying Eq. (1.14), then the unique positive stationary solution n_* of Eq. (1.1) is given by

$$n_*(x) = \frac{N_*}{\int_0^m \Pi(y, F_*) dy} \Pi(x, F_*). \quad (1.18)$$

Proof. Any time independent solution n_* of (1.1) satisfies

$$n_*(x) = n_*(0) \Pi(x, F_*). \quad (1.19)$$

By integration we obtain

$$n_*(0) = \frac{N_*}{\int_0^m \Pi(y, F_*) dy}, \quad (1.20)$$

where

$$N_* = \int_0^m n_*(x) dx. \quad (1.21)$$

Substituting (1.19) into Eqs. (1.2) and (1.4), we arrive at Eq. (1.14) for (N_*, F_*) . On the other hand, if (N_*, F_*) is a pair of positive numbers solving Eq. (1.14), then n_* , defined by (1.18), is readily seen to be a positive stationary solution of Eq. (1.1), while F_* will vacuously solve Eq. (1.4). □

The criterion given in the preceding proposition is useful to construct specific stationary solutions. From now on we will tacitly associate the total *Daphnia* population N_* to the stationary population density n_* via formula (1.21).

2. The linearized semigroup and positivity

In this section we will derive the linearization of the governing equations at steady state. We will show that solutions of the linearized equations are given by a strongly continuous semigroup and that the semigroup is positive under certain conditions on the model ingredients. The general approach taken here is a significant extension of our previous work in [13, 14].

Given a positive stationary solution (n_*, F_*) , we linearize the system (1.1)-(1.5) by using expansions like

$$\begin{aligned} f(x, F, N) = & f(x, F_*, N_*) + f_F(x, F_*, N_*) (F - F_*) + \\ & f_N(x, F_*, N_*) (N - N_*) + \text{higher order terms.} \end{aligned} \quad (2.1)$$

We write G and w for the “infinitesimal” perturbations of F_* and n_* , respectively. This ansatz yields the linearized system

$$\begin{aligned} w_t(x, t) + \gamma(x, F_*) w_x(x, t) + (\gamma_x(x, F_*) + \mu(x, F_*)) w(x, t) + \\ (\gamma_{xF}(x, F_*) n_*(x) + \mu_F(x, F_*) n_*(x) + \gamma_F(x, F_*) n'_*(x)) G(t) = 0, \end{aligned} \quad (2.2)$$

$$w(0, t) = \left(C_F(F_*) + \int_0^m \beta_F(x, F_*) n_*(x) dx \right) G(t) + \int_0^m \beta(x, F_*) w(x, t) dx, \quad (2.3)$$

$$\begin{aligned} \frac{dG}{dt} = & \left(\Psi_F(F_*) - \int_0^m I_F(x, F_*, N_*) n_*(x) dx \right) G(t) - \\ & \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \right) w(x, t) dx \end{aligned} \quad (2.4)$$

together with the initial conditions

$$G(0) = F_0 - F_* \stackrel{\text{def}}{=} G_0, \quad w(x, 0) = n_0 - n_*(0) \stackrel{\text{def}}{=} w_0. \quad (2.5)$$

Let \mathcal{X} be the product space $L^1(0, m) \times \mathbb{C}$, where $L^1(0, m)$, endowed with the usual L^1 -norm $\|\cdot\|$, consists of complex-valued, Lebesgue integrable functions on $(0, m)$. We define the bounded linear functional Λ on \mathcal{X} by

$$\Lambda \begin{pmatrix} w \\ G \end{pmatrix} = \left(C_F(F_*) + \int_0^m \beta_F(x, F_*) n_*(x) dx \right) G + \int_0^m \beta(x, F_*) w(x) dx \quad (2.6)$$

and introduce the operators

$$\mathcal{A} \begin{pmatrix} w \\ G \end{pmatrix} = \begin{pmatrix} -\gamma(\cdot, F_*) w_x \\ \left(\kappa + \Psi_F(F_*) - \int_0^m I_F(x, F_*, N_*) n_*(x) dx \right) G \end{pmatrix} \quad (2.7)$$

$$\text{with Dom}(\mathcal{A}) = \left\{ \begin{pmatrix} w \\ G \end{pmatrix} \in W^{1,1}(0, m) \times \mathbb{C} \mid w(0) = \Lambda \begin{pmatrix} w \\ G \end{pmatrix} \right\},$$

$$\mathcal{B} \begin{pmatrix} w \\ G \end{pmatrix} = - \begin{pmatrix} (\gamma_x(\cdot, F_*) + \mu(\cdot, F_*)) w \\ \kappa G \end{pmatrix} \quad (2.8)$$

$$\text{with Dom}(\mathcal{B}) = \mathcal{X},$$

$$\mathcal{C} \begin{pmatrix} w \\ G \end{pmatrix} = - \begin{pmatrix} (\gamma_x F(x, F_*) n_*(x) + \mu_F(x, F_*) n_*(x) + \gamma_F(x, F_*) n'_*(x)) G \\ \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \right) w(x) dx \end{pmatrix} \quad (2.9)$$

$$\text{with Dom}(\mathcal{C}) = \mathcal{X},$$

where κ is chosen such that

$$M_* = \kappa + \Psi_F(F_*) - \int_0^m I_F(x, F_*, N_*) n_*(x) dx \neq 0. \quad (2.10)$$

The space $W^{1,1}(0, m)$ used above is the well-known Sobolev space of Lebesgue integrable functions on $(0, m)$ with Lebesgue integrable weak derivative.

Now we can cast the linearized system (2.2)–(2.4) in the form of an abstract ordinary differential equation on \mathcal{X} :

$$\frac{d}{dt} \begin{pmatrix} w \\ G \end{pmatrix} = (\mathcal{A} + \mathcal{B} + \mathcal{C}) \begin{pmatrix} w \\ G \end{pmatrix}, \quad (2.11)$$

together with the initial condition

$$\begin{pmatrix} w(0) \\ G(0) \end{pmatrix} = \begin{pmatrix} w_0 \\ G_0 \end{pmatrix}. \quad (2.12)$$

We will also need the following functions

$$\Gamma(x, F) = \int_0^x \frac{dy}{\gamma(y, F)}, \quad \Theta(x, F) = \frac{\gamma_x(x, F) + \mu(x, F)}{\gamma(x, F)}. \quad (2.13)$$

The inverse of the function $x \mapsto \Gamma(x, F)$ for fixed F will be denoted by $\Gamma_{\{F\}}^{-1}$.

Theorem 2.1 *The operator $\mathcal{A} + \mathcal{B} + \mathcal{C}$ generates a strongly continuous semigroup $T = \{T(t)\}_{t \geq 0}$ of bounded linear operators on \mathcal{X} .*

Proof. First we study the operator \mathcal{A}_0 , defined by

$$\mathcal{A}_0 \begin{pmatrix} w \\ G \end{pmatrix} = \begin{pmatrix} -\gamma(\cdot, F_*) w_x \\ M_* G \end{pmatrix} \quad (2.14)$$

with $\text{Dom}(\mathcal{A}_0) = \left\{ \begin{pmatrix} w \\ G \end{pmatrix} \in W^{1,1}(0, m) \times \mathbb{C} \mid w(0) = 0 \right\}$,

It is readily seen that \mathcal{A}_0 is invertible and generates a strongly continuous semigroup $\{\mathcal{T}_0(t)\}_{t \geq 0}$ on \mathcal{X} , given explicitly by

$$\left(\mathcal{T}_0(t) \begin{pmatrix} w \\ G \end{pmatrix} \right) (x) = \begin{cases} \begin{pmatrix} w \left(\Gamma_{\{F_*\}}^{-1}(\Gamma(x, F_*) - t) \right) \\ \exp(M_* t) G \end{pmatrix} & \text{if } \Gamma(x, F_*) \geq t, \\ \begin{pmatrix} 0 \\ \exp(M_* t) G \end{pmatrix} & \text{otherwise,} \end{cases} \quad (2.15)$$

Next let \mathcal{X}_{-1} be the completion of \mathcal{X} in the norm $\|\cdot\|_{-1} \stackrel{\text{def}}{=} \|\mathcal{A}_0^{-1} \cdot\|$. Then we define the lifted semigroup $\{\mathcal{T}_{-1}(t)\}_{t \geq 0}$ on \mathcal{X}_{-1} by

$$\mathcal{T}_{-1}(t) = \mathcal{A}_0 \mathcal{T}_0(t) \mathcal{A}_0^{-1}. \quad (2.16)$$

The generator \mathcal{A}_{-1} of the semigroup $\{\mathcal{T}_{-1}(t)\}_{t \geq 0}$ is an extension of \mathcal{A}_0 . Its domain $\text{Dom}(\mathcal{A}_{-1})$ is \mathcal{X} , while its range is contained in \mathcal{X}_{-1} . Now we introduce the operator $\mathcal{P} \in L(\mathcal{X}, \mathcal{X}_{-1})$, given by

$$\mathcal{P} \begin{pmatrix} w \\ G \end{pmatrix} \stackrel{\text{def}}{=} \begin{pmatrix} -\Lambda(w, G)^T & 0 \\ 0 & 0 \end{pmatrix} \mathcal{A}_{-1} \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad (2.17)$$

where $1 = 1(\cdot)$ is the constant function 1 in $L^1(0, m)$. Then the operator \mathcal{A} is just the part of the operator $\mathcal{A}_{-1} + \mathcal{P}$ in \mathcal{X} (see [9]), i.e.

$$\mathcal{A} = (\mathcal{A}_{-1} + \mathcal{P})|_{\mathcal{X}}, \quad (2.18)$$

where

$$\text{Dom}((\mathcal{A}_{-1} + \mathcal{P})|_{\mathcal{X}}) = \{x \in \mathcal{X} \mid (\mathcal{A}_{-1} + \mathcal{P})x \in \mathcal{X}\}. \quad (2.19)$$

Our objective now is to apply the Desch-Schappacher Perturbation Theorem¹, thus proving that \mathcal{A} generates a semigroup on \mathcal{X} . To this end, we have to show

¹We refer here to the following version of the Desch-Schappacher Perturbation Theorem (see Corollary III.3.4 in [9]) which we state verbatim for the reader's convenience:

Theorem *Let \mathcal{A}_0 be the generator of a strongly continuous semigroup $\{\mathcal{T}_0(t)\}$ on the Banach space \mathcal{X} and let $\mathcal{P} \in L(\mathcal{X}, \mathcal{X}_{-1})$. Moreover, assume that there exists $t_0 > 0$ and $p \in [1, \infty)$ such that*

$$\int_0^{t_0} \mathcal{T}_{-1}(t_0 - r) \mathcal{P} f(r) dr \in \mathcal{X}$$

for all functions $f \in L^p([0, t_0]; \mathcal{X})$. Then $(\mathcal{A}_{-1} + \mathcal{P})|_{\mathcal{X}}$ generates a strongly continuous semigroup on \mathcal{X} .

that, for given $(f, h)^T \in L^1([0, m]; \mathcal{X})$, the integral

$$\begin{aligned} & \int_0^m \mathcal{T}_{-1}(m-t) \mathcal{P} \begin{pmatrix} f(t) \\ h(t) \end{pmatrix} dt = \\ & \mathcal{A}_{-1} \int_0^m \begin{pmatrix} -\Lambda(f(t), h(t))^T & 0 \\ 0 & 0 \end{pmatrix} \mathcal{T}_{-1}(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \end{pmatrix} dt \end{aligned} \quad (2.20)$$

belongs to \mathcal{X} . This condition is equivalent to

$$\int_0^m \begin{pmatrix} -\Lambda(f(t), h(t))^T & 0 \\ 0 & 0 \end{pmatrix} \mathcal{T}_0(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \end{pmatrix} dt \in \text{Dom}(\mathcal{A}_0). \quad (2.21)$$

Since

$$\int_0^m \begin{pmatrix} -\Lambda(f(t), h(t))^T & 0 \\ 0 & 0 \end{pmatrix} \mathcal{T}_0(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \end{pmatrix} dt = \quad (2.22)$$

$$\int_{m-\Gamma(\cdot, F_*)}^m \begin{pmatrix} -\Lambda(f(t), h(t))^T \\ 0 \end{pmatrix} dt, \quad (2.23)$$

condition (2.21) holds true. Hence \mathcal{A} is a semigroup generator. Finally we note that $\mathcal{B} + \mathcal{C}$ is a bounded perturbation of \mathcal{A} on \mathcal{X} . Therefore the claim of the theorem follows. \square

Typical linear stability studies of stationary solutions proceed as follows: First one shows that the spectrum of the underlying differential operator (= semigroup generator) is contained in the left half-plane of the complex plane and bounded away from the imaginary axis. Then one tries to conclude that this result implies asymptotic stability. However, this second step is applicable only if the so-called spectrally determined growth condition holds true (see [9]). Specifically, in our situation one has to show that the spectral bound $s(\mathcal{A} + \mathcal{B} + \mathcal{C})$ of the semigroup generator $\mathcal{A} + \mathcal{B} + \mathcal{C}$, defined by

$$s(\mathcal{A} + \mathcal{B} + \mathcal{C}) = \sup\{\text{Re } \lambda \mid \lambda \in \sigma(\mathcal{A} + \mathcal{B} + \mathcal{C})\}, \quad (2.24)$$

and the growth bound $\omega(T)$ of the semigroup $T = \{\mathcal{T}(t)\}$, defined by

$$\omega(T) = \lim_{t \rightarrow \infty} \frac{\ln \|\mathcal{T}(t)\|}{t}, \quad (2.25)$$

are equal. Moreover, it would be desirable to guarantee that linear stability is governed by a leading real eigenvalue. Our next results will prove that both the spectral condition and the spectrally determined growth condition are satisfied under certain assumptions on the model ingredients. The elementary size-structured case and the size-structured case of juvenile-adult interaction was analyzed in a similar fashion (see [13, 14]).

Lemma 2.2 *The spectrum of the semigroup generator $\mathcal{A} + \mathcal{B} + \mathcal{C}$ consists of isolated eigenvalues of finite multiplicity.*

Proof. Since \mathcal{A} has a bounded resolvent mapping \mathcal{X} into $W^{1,1}(0, m) \times \mathbb{C}$ and since $W^{1,1}(0, m) \times \mathbb{C}$ is compactly embedded in \mathcal{X} , the claim follows from Riesz-Schauder Theory. \square

Next we turn to the positivity properties of the semigroup. To this end, we note that the real part of the Banach space \mathcal{X} is a vector lattice if $(w, G)^T$ is defined as positive whenever $w \geq 0$ in $L^1(0, m)$ and $G \geq 0$ in \mathbb{R} . Moreover, we define the absolute value of $(w, G)^T \in \mathcal{X}$ to be $(|w|, |G|)^T$. Hence it is readily seen that \mathcal{X} is a Banach lattice and the notions of positive operator, positive semigroup and positive linear functional are well-defined.

Theorem 2.3 *Suppose that*

$$\Theta_F(\cdot, F_*) \leq 0, \quad (2.26)$$

$$C_F(F_*) + \int_0^m \beta_F(x, F_*) n_*(x) dx \geq 0, \quad (2.27)$$

$$I(\cdot, F_*, N_*) + \int_0^m I_N(x, F_*, N_*) n_*(x) dx \leq 0. \quad (2.28)$$

Then the semigroup $T = \{\mathcal{T}(t)\}_{t \geq 0}$, generated by the operator $\mathcal{A} + \mathcal{B} + \mathcal{C}$, is positive.

Note that, for a positive stationary solution (n_*, F_*) , condition (2.26) is equivalent with

$$\gamma_{xF}(\cdot, F_*) n_* + \mu_F(\cdot, F_*) n_* + \gamma_F(\cdot, F_*) n_*' \leq 0. \quad (2.29)$$

Proof of Theorem 2.3. We consider the solution of the initial value problem

$$\frac{d}{dt} \begin{pmatrix} w \\ G \end{pmatrix} = (\mathcal{A} + \mathcal{B}) \begin{pmatrix} w \\ G \end{pmatrix}, \quad \begin{pmatrix} w(0) \\ G(0) \end{pmatrix} = \begin{pmatrix} w_0 \\ G_0 \end{pmatrix} \in \text{Dom}(\mathcal{A}). \quad (2.30)$$

Then the function u , defined by

$$u(x, t) = w(x, t) \exp \left\{ \int_0^x \Theta(y, F_*) dy \right\}, \quad (2.31)$$

is the solution of the problem

$$u_t(x, t) + \gamma(x, F_*) u_x(x, t) = 0, \quad (2.32)$$

$$u(0, t) = \Lambda \begin{pmatrix} u(\cdot, t) \\ \Delta_* \\ G \end{pmatrix}, \quad (2.33)$$

$$u(x, 0) = w_0(x), \quad (2.34)$$

where Δ_* is defined by

$$\Delta_*(x) = \exp \left\{ \int_0^x \Theta(y, F_*) dy \right\}. \quad (2.35)$$

Consequently, problem (2.30) can be cast in the form

$$\frac{d}{dt} \begin{pmatrix} u \\ G \end{pmatrix} = \mathcal{A}_M \begin{pmatrix} u \\ G \end{pmatrix}, \quad \begin{pmatrix} u(0) \\ G(0) \end{pmatrix} = \begin{pmatrix} w_0 \\ G_0 \end{pmatrix} \in \text{Dom}(\mathcal{A}_M), \quad (2.36)$$

where \mathcal{A}_M is the modified semigroup generator, defined by

$$\mathcal{A}_M \begin{pmatrix} u \\ G \end{pmatrix} = \begin{pmatrix} -\gamma(\cdot, F_*) u_x \\ \left(\Psi_F(F_*) - \int_0^m I_F(x, F_*, N_*) n_*(x) dx \right) G \end{pmatrix} \quad (2.37)$$

with $\text{Dom}(\mathcal{A}_M) = \left\{ \begin{pmatrix} u \\ G \end{pmatrix} \in W^{1,1}(0, m) \times \mathbb{C} \mid u(0) = \Lambda_* \begin{pmatrix} u \\ G \end{pmatrix} \right\}$,

where

$$\Lambda_* \begin{pmatrix} u \\ G \end{pmatrix} = \Lambda \begin{pmatrix} u \\ \Delta_* \\ G \end{pmatrix}. \quad (2.38)$$

There is a constant $C_0 > 0$ such that, for $(f, h)^T \in \mathcal{X}$, the resolvent equation

$$\lambda \begin{pmatrix} u \\ G \end{pmatrix} - \mathcal{A}_M \begin{pmatrix} u \\ G \end{pmatrix} = \begin{pmatrix} f \\ h \end{pmatrix} \quad (2.39)$$

has the implicit solution

$$u(x) = e^{-\lambda \Gamma(x, F_*)} \Lambda_* \begin{pmatrix} u \\ G \end{pmatrix} + \int_0^x e^{\lambda(\Gamma(y, F_*) - \Gamma(x, F_*))} \frac{f(y)}{\gamma(y, F_*)} dy, \quad (2.40)$$

$$G = \frac{h}{\lambda - \left(\Psi_F(F_*) - \int_0^m I_F(x, F_*, N_*) n_*(x) dx \right)}. \quad (2.41)$$

for $\lambda \geq C_0$. Hence for such λ we obtain

$$\Lambda_* \begin{pmatrix} u \\ G \end{pmatrix} = \left(1 - \Lambda_* \begin{pmatrix} e^{-\lambda \Gamma(\cdot, F_*)} \\ G \end{pmatrix} \right)^{-1} \Lambda_* \left(\int_0^\cdot e^{\lambda(\Gamma(y, F_*) - \Gamma(\cdot, F_*))} \frac{f(y)}{\gamma(y, F_*)} dy \right). \quad (2.42)$$

By condition (2.27), Λ (or equivalently Λ_*) is a positive linear functional. Hence both u and G , given by Eqs. (2.40), (2.41), are nonnegative if λ is sufficiently large and f and h are nonnegative. Thus we conclude that the resolvent operator of \mathcal{A}_M (or equivalently of $\mathcal{A} + \mathcal{B}$) is positive. Finally, since the operator \mathcal{C} is positive by conditions (2.26) and (2.28), the claim follows. \square

A minor variant of Derndinger's Theorem and the theory of positive semigroups gives us the following result (see [4, 9]).

Corollary 2.4 *Assume that conditions (2.26)–(2.28) are satisfied. Then the following holds true:*

- The growth bound $\omega(T)$ of the semigroup is equal to the spectral bound $s(\mathcal{A} + \mathcal{B} + \mathcal{C})$ of its generator.
- If $\mathcal{A} + \mathcal{B} + \mathcal{C}$ has nonempty spectrum, the spectral bound $s(\mathcal{A} + \mathcal{B} + \mathcal{C})$ is an eigenvalue of the generator $\mathcal{A} + \mathcal{B} + \mathcal{C}$.

Other related regularity properties (eventual compactness, eventual differentiability) have been discussed in [13, 16] for one-dimensional transport equations in population dynamics and fluid mechanics.

3. Stability

In this section we use the positivity conditions deduced in the previous section to formulate conditions for the linear stability of positive equilibria of Eqs. (1.1)-(1.5). We use the approach established in [13, 14] for the case of other (single-species) size-structured population models. As done in [10, 11, 13, 14] we will be able to relate our stability condition to a biologically interpretable and intuitively clear condition at least in a special case of model ingredients. To formulate our stability result, we introduce the following function

$$R(F) = \int_0^m \beta(x, F) \Pi(x, F) dx = \int_0^m \beta(x, F) \frac{\gamma(0, F)}{\gamma(x, F)} \exp \left\{ - \int_0^x \frac{\mu(y, F)}{\gamma(y, F)} dy \right\} dx. \quad (3.1)$$

The function R can be interpreted as the *inherent net reproduction rate* of *Daphnia* individuals in analogy with the age-structured case: Since the original fertility function is divided by $\gamma(0, F)$ in the boundary condition (1.2), the quantity $R(F)$ is the expected number of newborns of an individual during its lifetime.

Theorem 3.1 *Given a positive stationary solution (n_*, F_*) , suppose that the positivity conditions (2.26)–(2.28) are satisfied. Then the stationary solution is linearly asymptotically stable if*

$$(1 - R(F_*)) \left(\int_0^m I_F(x, F_*, N_*) n_*(x) dx - \Psi_F(F_*) \right) > \int_0^m \Pi(x, F_*) \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \right) \times \left(n_*(0) (1 - R(F_*)) \int_0^x \Theta_F(y, F_*) dy - C_F(F_*) - n_*(0) R_F(F_*) \right) dx. \quad (3.2)$$

We break the proof of this theorem up in several parts.

Lemma 3.2 *The spectrum of the semigroup generator $\mathcal{A} + \mathcal{B} + \mathcal{C}$ consists of all $\lambda \in \mathbb{C}$ such that*

$$K(\lambda) = 0, \quad (3.3)$$

where the function K is defined on \mathbb{C} by

$$\begin{aligned}
K(\lambda) \stackrel{\text{def}}{=} & \left(1 - \int_0^m \beta(x, F_*) \Phi(\lambda, x, F_*) dx\right) \times \\
& \left(\lambda - \Psi_F(F_*) + \int_0^m I_F(x, F_*, N_*) n_*(x) dx - \right. \\
& n_*(0) \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy\right) \Phi(\lambda, x, F_*) \times \\
& \left. \int_0^x \exp(\lambda \Gamma(y, F_*)) \Theta_F(y, F_*) dy dx\right) + \\
& \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy\right) \Phi(\lambda, x, F_*) dx \times \\
& \left(C_F(F_*) + \int_0^m \beta_F(x, F_*) n_*(x) dx - \right. \\
& \left. n_*(0) \int_0^m \beta(x, F_*) \Phi(\lambda, x, F_*) \int_0^x \exp(\lambda \Gamma(y, F_*)) \Theta_F(y, F_*) dy dx\right)
\end{aligned} \tag{3.4}$$

and

$$\Phi(\lambda, x, F) \stackrel{\text{def}}{=} \exp \left\{ -\lambda \Gamma(x, F) - \int_0^x \Theta(y, F) dy \right\}. \tag{3.5}$$

Proof. Since the semigroup generator has compact resolvent, its spectrum consists of all values $\lambda \in \mathbb{C}$ for which the following linear problem admits a non-trivial solution $(W, g) \neq (0, 0)$

$$\begin{aligned}
& (\lambda + \gamma_x(x, F_*) + \mu(x, F_*)) W(x) + \gamma(x, F_*) W'(x) + \\
& (\gamma_{xF}(x, F_*) n_*(x) + \mu_F(x, F_*) n_*(x) + \gamma_F(x, F_*) n'_*(x)) g = 0,
\end{aligned} \tag{3.6}$$

$$W(0) = \left(C_F(F_*) + \int_0^m \beta_F(x, F_*) n_*(x) dx\right) g + \int_0^m \beta(x, F_*) W(x) dx, \tag{3.7}$$

$$\begin{aligned}
& \left(\lambda - \Psi_F(F_*) + \int_0^m I_F(x, F_*, N_*) n_*(x) dx\right) g + \\
& \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy\right) W(x) dx = 0.
\end{aligned} \tag{3.8}$$

The solution of Eq. (3.6) is readily found to be

$$W(x) = \Phi(\lambda, x, F_*) \left(W(0) - n_*(0) g \int_0^x \exp(\lambda \Gamma(y, F_*)) \Theta_F(y, F_*) dy\right). \tag{3.9}$$

Now we substitute the solution W into Eqs. (3.7), (3.8) to obtain the equations

$$\begin{aligned} & \left(1 - \int_0^m \beta(x, F_*) \Phi(\lambda, x, F_*) dx \right) W(0) - \\ & \left(C_F(F_*) + \int_0^m \beta_F(x, F_*) n_*(x) dx - \right. \\ & \left. n_*(0) \int_0^m \beta(x, F_*) \Phi(\lambda, x, F_*) \int_0^x \exp(\lambda \Gamma(y, F_*)) \Theta_F(y, F_*) dy dx \right) g = 0 \end{aligned} \quad (3.10)$$

and

$$\begin{aligned} & \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \right) \Phi(\lambda, x, F_*) dx W(0) + \\ & \left(\lambda - \Psi_F(F_*) + \int_0^m I_F(x, F_*, N_*) n_*(x) dx - \right. \\ & \left. n_*(0) \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \right) \Phi(\lambda, x, F_*) \times \right. \\ & \left. \int_0^x \exp(\lambda \Gamma(y, F_*)) \Theta_F(y, F_*) dy dx \right) g = 0. \end{aligned} \quad (3.11)$$

These two equations form a linear system in the unknowns $W(0)$ and g . Hence for a nonzero solution $(W(0), g)$ (and consequently for a nonzero solution (W, g)), it is necessary and sufficient that the corresponding determinant vanish. This determinant is, however, just the function K , defined in (3.4).

□

Lemma 3.3 *Suppose that the positivity conditions (2.26)–(2.28) and condition (3.2) are satisfied. Then the function K , defined by (3.4), is (strictly) positive for $\lambda \geq 0$.*

Proof. Let

$$f_1(\lambda) = 1 - \int_0^m \beta(x, F_*) \Phi(\lambda, x, F_*) dx, \quad (3.12)$$

$$\begin{aligned} f_2(\lambda) &= \lambda - \Psi_F(F_*) + \int_0^m I_F(x, F_*, N_*) n_*(x) dx - \\ & n_*(0) \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \right) \times \\ & \Phi(\lambda, x, F_*) \int_0^x \exp(\lambda \Gamma(y, F_*)) \Theta_F(y, F_*) dy dx, \end{aligned} \quad (3.13)$$

$$\begin{aligned} f_3(\lambda) &= \int_0^m \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \right) \Phi(\lambda, x, F_*) dx \times \\ & \left(C_F(F_*) + \int_0^m \beta_F(x, F_*) n_*(x) dx - \right. \\ & \left. n_*(0) \int_0^m \beta(x, F_*) \Phi(\lambda, x, F_*) \int_0^x \exp(\lambda \Gamma(y, F_*)) \Theta_F(y, F_*) dy dx \right) \end{aligned} \quad (3.14)$$

Then one readily finds

$$f_1(\lambda) \geq 0 \text{ and } f_1'(\lambda) \geq 0 \text{ for } \lambda \geq 0, \quad f_1(\lambda) > 0 \text{ for } \lambda > 0, \quad (3.15)$$

$$f_2'(\lambda) \geq 0 \text{ for } \lambda \geq 0, \quad (3.16)$$

$$f_3(\lambda) \leq 0 \text{ and } f_3'(\lambda) \geq 0 \text{ for } \lambda \geq 0. \quad (3.17)$$

To obtain these results, we take into account that $R(F_*) \leq 1$ and make use of the positivity conditions and the monotonicity of the function Γ . Consequently, the function

$$\lambda \mapsto \frac{K(\lambda)}{f_1(\lambda)} = f_2(\lambda) + \frac{f_3(\lambda)}{f_1(\lambda)} \quad (3.18)$$

is non-decreasing on $(0, \infty)$. Since we also have $K(0) > 0$ by condition (3.2) and $f_1(\lambda) > 0$ for all $\lambda > 0$, we deduce $K(\lambda) > 0$ for all $\lambda \geq 0$. \square

Proof of Theorem 3.1. The positivity of the semigroup implies that the spectrum of the semigroup generator is either empty or contains a dominant real eigenvalue (Corollary 2.4). By Lemmata 3.2, 3.3, the dominant eigenvalue, if any, must be negative. In either case, the spectral bound of the semigroup generator and hence the growth bound of the semigroup are contained in $[-\infty, 0)$. This proves the claim. \square

Example 3.4 Consider the special choice of the feeding rate I , given by

$$I(x, F, N) = \frac{\tilde{I}(F)}{N}, \quad F, N > 0, \quad \tilde{I} \geq 0 \quad (3.19)$$

and assume $C(F_*) > 0$. In this case we readily obtain

$$I(\cdot, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \equiv 0 \quad (3.20)$$

and

$$Q^2(F, N) = Q^2(F) = \frac{\Psi(F)}{\tilde{I}(F)}. \quad (3.21)$$

Thus our criterion (3.2) for the linear stability of the stationary solution (n_*, F_*) reduces to

$$\Psi_F(F_*) - \tilde{I}_F(F_*) < 0, \quad (3.22)$$

which is readily seen to be equivalent to

$$Q_F^2(F_*) = \left(\frac{\Psi}{\tilde{I}} \right)_F (F_*) < 0, \quad (3.23)$$

if $\tilde{I}(F_*) \neq 0$. Condition (3.23) is intuitively clear since Q^2 can be interpreted as the net growth rate of the algae population. In case of (3.19), the algae dynamics is driven solely by Ψ and \tilde{I} and is thus independent of the *Daphnia* population.

Remark 3.5 If $I_N \equiv 0$, the positivity criterion for the linear semigroup is violated (except in the trivial case $I \equiv 0$). Consequently stability need not be governed by a leading real eigenvalue. This observation is in accordance with previous results on the classical *Daphnia* model in [22] where it was shown that stationary solutions lose stability via a Hopf bifurcation.

4. Instability

In this section we give an instability criterion for positive stationary solutions of Eqs. (1.1)-(1.5). We illustrate the result for the classical *Daphnia* population model considered in [20, 22].

Theorem 4.1 *The stationary solution (n_*, F_*) of Eqs. (1.1)-(1.5) is linearly unstable if*

$$\begin{aligned} (1 - R(F_*)) \left(\int_0^m I_F(x, F_*, N_*) n_*(x) dx - \Psi_F(F_*) \right) < \\ \int_0^m \Pi(x, F_*) \left(I(x, F_*, N_*) + \int_0^m I_N(y, F_*, N_*) n_*(y) dy \right) \times \\ \left(n_*(0) (1 - R(F_*)) \int_0^x \Theta_F(y, F_*) dy - C_F(F_*) - n_*(0) R_F(F_*) \right) dx. \end{aligned} \quad (4.1)$$

Proof. The function K , defined in Eq. (3.4), satisfies

$$\lim_{\lambda \rightarrow \infty} K(\lambda) = +\infty, \quad (4.2)$$

where the limit is taken in \mathbb{R} . To see this, note that all the terms involving Φ decay to zero. By assumption, we have, however, $K(0) < 0$. Hence K has a positive zero, i.e. the semigroup generator has a positive eigenvalue. \square

Example 4.2 We consider the standard *Daphnia* model, where

$$C \equiv 0, \quad I_N \equiv 0, \quad I > 0. \quad (4.3)$$

In this case the instability criterion (4.1) assumes the form

$$R_F(F_*) < 0. \quad (4.4)$$

It is intuitively clear that $R_F(F_*) < 0$ implies instability: If an increase of the algae population decreases its consumer population (*Daphnia*), then the consumption of algae decreases and hence the algae population grows.

In the simple single-species size-structured case discussed in [13] the equivalent instability condition for the corresponding inherent net reproduction rate $R(P)$ was shown to be $R_P(P_*) > 0$ where P_* denotes a positive equilibrium total population size of the size-structured species. In contrast the condition $R_P(P_*) < 0$ was a necessary condition for stability.

Remark 4.3 We point out that the positive inflow C has a stabilizing effect as observed previously (see [12, 14]). If

$$I(x, F_*, N_*) + \int_0^m I_N(x, F_*, N_*) n_*(x) dx \leq 0, \quad (4.5)$$

then the instability criterion (4.1) holds true in case $C \equiv 0$ if $R_F(F_*) > 0$. If, however, $C > 0$, the stability condition (3.2) of Theorem 3.1 (and the positivity conditions) may be satisfied for some stationary solutions, even if $R_F(F_*) > 0$.

5. Conclusion

In the present paper we have analyzed a nonlinear size-structured predator-prey model which generalizes the standard *Daphnia* model studied previously in the literature (see [20, 22, 23]). Specifically, we introduced a food dependent inflow term C in the boundary condition of the governing equations and a general feeding rate I describing the consumption rate of prey individuals. We refer the reader to [1, 2, 12, 19] where size-structured models with similar inflow terms were discussed. Our motivation for introducing a food dependent inflow was to demonstrate its stabilizing effect as observed previously for simpler size-structured models of similar type (see [12, 14]).

Using semigroup and spectral methods we studied the linearized dynamical behavior of initially small perturbations of steady state via roots of the associated characteristic equation. Our positivity result for the semigroup under certain conditions for the vital rates allowed us to stay within the framework of real calculus when addressing stability of stationary solutions. We point out that comprehensive linear stability results, even in the special case of the standard *Daphnia* population model, have so far not appeared in the literature. In addition, as observed previously in [10, 11, 12, 13, 14], we succeeded in formulating stability/instability conditions in terms of a net reproduction rate associated to the model. To this end, we introduced the relative net reproduction rate of predator individuals $R(F)$. For the standard *Daphnia* model this approach gave us a remarkably simple stability criterion. We anticipate that our analysis can be extended to more general situations, including multispecies competition models and problems with infinite size span.

Using sun-star calculus for Volterra functional equations, Diekmann et al. [5, 6] have recently proved both the stability and instability part of the principle of linearized stability for general classes of quasilinear size-structured models. These important results emphasize and corroborate our objective to formulate straightforward and biologically interpretable conditions for the stability/instability of equilibria of physiologically structured population models. It

is left for future work to establish the principle of linearized stability for the model treated in this work.

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