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Daphnia revisited: Local stability and bifurcation theory for physiologically structured population models explained by way of an example

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Daphnia revisited: local stability and bifurcation theory for physiologically structured population models explained by way of an example

Dedicated to Horst Thieme on the occasion of his 60th birthday

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Abstract We consider the interaction between a general size-structured consumer population and an unstructured resource. We show that stability properties and bifurcation phenomena can be understood in terms of solutions of a system of two delay equations (a renewal equation for the consumer population birth rate coupled to a delay differential equation for the resource concentration). As many results for such systems are available [9], we can draw rigorous conclusions concerning dynamical behaviour from an analysis of a characteristic equation. We derive the characteristic equation for a fairly general class

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of population models, including those based on the Kooijman-Metz *Daphnia* model [19], [34] and a model introduced by Gurney-Nisbet [10], [15], and next obtain various ecological insights by analytical or numerical studies of special cases.

Keywords Physiologically structured population models · Size-structure · Delay equations · Linearised stability · Characteristic equation

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1 Introduction

Population dynamics is first and foremost concerned with changes in numbers of individuals due to death and reproduction. But once one realises that both fertility and the force of mortality may depend heavily on the stage of development of an organism, it becomes clear that population models cannot avoid to incorporate submodels for this development of an organism. In other words, we need to introduce the notion of individual state (i-state) and next model the distribution of i-state-at-birth and the dynamics of the i-state. We refer to de Roos & Persson [32] and the references given there for further ecological motivation.

If individuals would be independent from each other, equations would be linear and the analysis would be relatively easy. Dependence arises, e.g., by competition for food (i.e., the consumption by one individual reduces the availability of food to others) but also via the predation pressure (if an individual falls victim to a predator, that might have as an immediate effect that the predator is satiated and that accordingly the predation pressure on other individuals is reduced; but the long term effect may be that the reproductive success of the predator becomes higher and hence the future predation pressure on other individuals enhanced). By "environmental interaction variables" we denote quantities like food concentration and predation pressure that mediate the dependence. (As a side remark we mention that in the case of cannibalism both the food concentration and the predation pressure are partly determined directly by the focal population.)

The task of a population modeller is to specify how survival, reproduction and development depend on the i-state and environmental interaction variables and, in addition, to specify how the dynamics of the interaction variables is influenced by feedback from the population. Restricting ourselves to "size" of an individual as i-state, a unique size-at-birth and deterministic growth of individuals, and competition for food, we can reformulate this as: a population model consists of a specification of

(i) ξ_b , the size at birth of individuals
(ii) $g(\xi, S)$, the rate of growth of an individual, as a function of size ξ and food concentration S

(iii) $\beta(\xi, S)$, the probability per unit of time of giving birth, as a function of size ξ and food concentration S
(iv) $\mu(\xi, S)$, the probability per unit of time of dying, as a function of size ξ and food concentration S
(v) $\gamma(\xi, S)$, the rate of food consumption of an individual, as a function of size ξ and food concentration S
(vi) the dynamics of the resource S in the absence of consumers

Based on these ingredients, one may now either start with a finite number of individuals and do simulations or consider, at the population level, the deterministic system obtained by letting the interactions depend inversely on a quantity called system size, and taking the limit for system size going to infinity while keeping the initial densities (numbers divided by system size) constant. Here we restrict to the second option and, moreover, neglect any influence that spatial structure might have.

Way back in the late eighties of the last century, de Roos *et al.* [34] analysed a model for *Daphnia* feeding on algae, with exactly this structure. They found, among other things, that variable maturation delay can lead to cohort cycles that differ markedly from the standard prey-predator cycles (see Murdoch *et al.* [29] and de Roos & Persson [33] for a more recent account that also relates to experimental and field data). At the beginning of Section 5 of [34] de Roos *et al.* wrote : "The stability analysis of the internal equilibrium is not a straightforward procedure. At present the existing general theory on structured population models of the type that we study in this paper is not yet sufficiently developed to answer even the first questions about the existence and uniqueness of solutions and the validity of the linearised stability principle. In principle this means that at present there exists no valid and mathematically rigorous technique to analyse the stability of the internal equilibrium."

The first aim of the present paper is to show that now, at last, such a "mathematically rigorous technique" exists. A second aim is to present a gentle derivation of the relevant characteristic equation for a wider class of models, thus showing that the new framework has more to offer than just mathematical underpinning. We then use this characteristic equation to study some aspects of variable maturation delay in more detail.

The mathematical theory that justifies the principle of linearised stability for a quite general class of delay equations was presented by Diekmann, Getto & Gyllenberg [9]. Here we assert that for a large class of physiologically structured population models, the long term dynamics are fully described by solutions of delay equations. The trick is to reconsider the notion of population state.

As explained in detail by Metz & Diekmann [28], the natural way to represent a population is by way of a distribution (a measure that may or may not correspond to a density) over the i-state space. The corresponding mathematical theory is involved [6, 7, 1] and despite hard work over a long period of time, we did not manage to prove the principle of linearised stability for the corresponding nonlinear semigroups of operators. The breakthrough came

when we realised that the current population size and composition is fully determined by the population birth rate in the past, *provided* we also prescribe the environmental interaction variables in the past (as indeed we then can use the submodels for survival and development to cover the period in between being born and the current time). For *Daphnia*-type models, this means that we prescribe the history of the *Daphnia* birth rate as well as the history of the algae concentration. The future values of these variables are next determined by solving the system consisting of an equation for the population birth rate b and a differential equation for the food concentration S. As the b-equation also involves the history of S, this is a system of delay equations, more precisely, a coupled system of a renewal equation and a delay-differential equation.

By restricting ourselves to initial distributions that can be constructed from a history of b and S, we put up with a certain loss of generality. Should we care? We claim we should not! The point is that we do not miss any candidate attractors (or, more generally, invariant sets) and that instability has to manifest itself within the restricted class of initial conditions. This is easiest observed if there is an upper bound, say $A_{\max}$, on the length of the life of any consumer individual, as then the population state is necessarily of the "restricted" type for $t > A_{\max}$. In the general case one has to exploit that for any reasonable model the *direct* influence of those initially present goes to zero for $t \to \infty$.

We shall formulate our results for a one-dimensional i-state, interpreted as size. However, they hold equally well for a higher dimensional i-state, as long as there is a unique state-at-birth. If finitely many states-at-birth are feasible, one has to add a certain dose of linear algebra. If there is a continuum of possibilities for state-at-birth, one has to work a bit harder (Diekmann & Gyllenberg [2]) and it is no longer possible to separate the determination of eigenvalues via a characteristic equation from the determination of the corresponding eigenvectors.

It is well-known that some age-structured models incorporating a juvenile period of fixed length can be described by delay differential equations, see e.g. Kuang & So [20] and the references in there. Here we consider a *general* size-structured model with *variable* maturation delay and yet we find that the dynamical behaviour is completely described by the solutions of a system of delay equations (more precisely : a coupled system consisting of one renewal equation and one delay-differential equation). Since the length of the juvenile period depends on the food supply, one could call this a system of state-dependent delay equations.

The structure of the paper is as follows. In Section 2 we derive the system of delay equations directly from biological assumptions and we show that, under additional but still natural assumptions, a unique steady state exists. In Section 3 we describe the structure of the linearised system and the corresponding characteristic equation, while in Section 4 we express the ingredients of the linearised system in terms of quantities that can be computed from the ingredients ξ_b, g, β, μ, γ and the rules for production and decay of substrate (first for the smooth case and next for models that involve an abrupt juvenile-adult

transition upon reaching a critical size ξ_A). In Section 5 we introduce some didactical examples of how to analyse the characteristic equation. In Section 6 we present the results of numerical studies and interpret these. In Section 7 we show that for the *Daphnia* model of de Roos *et al.* [34], we recover exactly the characteristic equation studied in that paper. The final Section 8 is devoted to a summary in recipe form.

2 *Daphnia* models

In this section we describe a class of consumer-resource models that is built from assumptions concerning the behaviour of individuals. More specifically, we describe how individuals grow in size, survive, reproduce and consume food, dependent on their own size and the concentration of food. (We do so in somewhat abstract mathematical generality, meaning that we introduce functions that need to be specified in more and more detail when one moves towards concrete applications.) In a second step we then derive bookkeeping equations that pertain to the population level. For historical reasons and for the ease of formulation we call the consumers *Daphnia* and the food algae.

We assume that all *Daphnia* are born with the same size ξ_b and that their growth is deterministic according to the differential equation

$$\frac{d\xi}{da}(a) = g(\xi(a), S(t(a))), \tag{2.1}$$

where ξ denotes the size, a the age, S the food concentration and $t(a)$ the time at which the individual that we consider has age a. (We postpone the formulation of smoothness and other assumptions concerning the function $g(\xi, S)$, but have in mind that these should at the very least guarantee that (2.1) with initial condition $\xi_0 = \xi_b$ has a unique solution for any given continuous and positive function $S(t)$.) We assume that the survival probability $\mathcal{F}$ of an individual decreases with age according to

$$\frac{d\mathcal{F}}{da}(a) = -\mu(\xi(a), S(t(a)))\mathcal{F}(a) \tag{2.2}$$

and that a newborn is produced with probability per unit of time

$$\beta(\xi(a), S(t(a))). \tag{2.3}$$

The energy needed for maintenance, growth and reproduction is derived from the ingestion of algae which proceeds at a rate

$$\gamma(\xi(a), S(t(a))) \tag{2.4}$$

but for the time being we leave the relationship between, on the one hand g respectively β and, on the other, γ, unspecified. Finally we assume that in the absence of *Daphnia* the algal concentration evolves in time according to the differential equation

$$\frac{dS}{dt} = f(S). \tag{2.5}$$

Essentially the model is now specified, the rest is bookkeeping. To do the bookkeeping in an efficient way, we need to introduce some notation.

As in the theory of delay differential equations, we use the symbol S_t to denote the *history* of the food concentration relative to t, that is, to denote the function

$$\sigma \mapsto S(t+\sigma), \quad \sigma \leq 0 \tag{2.6}$$

(In case of a maximal age $A_{\max}$ we can restrict to $\sigma \geq -A_{\max}$, but otherwise we need to allow σ to take any value less than or equal to zero.) It is convenient to let ψ denote an arbitrary nonnegative continuous function defined on $\mathbb{R}_-$.

Now consider an individual that has age a at the current time t and suppose $S_t = \psi$. Denote the size of this individual at age τ, with $0 \leq \tau \leq a$, by $\xi(\tau) = \xi(\tau; a, \psi)$ (variables listed after the semicolon are suppressed in the notation whenever that helps to keep formulas readable). It can be computed from

$$\frac{d\xi}{d\tau}(\tau) = g(\xi(\tau), \psi(-a+\tau)), \quad \xi(0) = \xi_b. \tag{2.7}$$

The size at the current time is then given by

$$\Xi(a; \psi) := \xi(a; a, \psi). \tag{2.8}$$

The fraction of individuals born at time $t-a$ that are still alive at time t, is given by the survival probability $\mathcal{F}(a; \psi)$. Let $\mathcal{G}(\tau) = \mathcal{G}(\tau; a, \psi)$ be the survival probability up till time $t - a + \tau$. Then $\mathcal{G}$ can be computed from

$$\frac{d\mathcal{G}}{d\tau}(\tau) = -\mu(\xi(\tau; a, \psi), \psi(-a+\tau))\mathcal{G}(\tau),\ \mathcal{G}(0) = 1 \tag{2.9}$$

and next, by definition,

$$\mathcal{F}(a; \psi) = \mathcal{G}(a; a, \psi). \tag{2.10}$$

Let $b(t)$ denote the *Daphnia* population birth rate at time t. Then the assumptions above imply that

$$\begin{aligned} b(t) &= \int_0^\infty b(t-a)\beta(\Xi(a; S_t), S(t))\mathcal{F}(a; S_t)da, \\ \frac{dS}{dt}(t) &= f(S(t)) - \int_0^\infty b(t-a)\gamma(\Xi(a; S_t), S(t))\mathcal{F}(a; S_t)da. \end{aligned} \tag{2.11}$$

As written, this refers to *Daphnia* and algae that have been interacting as described by the model since the dawn of time. When looking for steady states, periodic solutions *et cetera*, this is indeed the right perspective. But alternatively we can require the system of equations (2.11) to hold only for $t > 0$ (or, if you wish, $t \geq 0$) and to provide initial data in the form of the history of both b and S at time zero, the first as a nonnegative locally integrable function and the second as a nonnegative continuous function. In the mathematical theory concerning (2.11), for which we refer to [9, in particular Section 4] and [3, Section 5], both points of view play a role.

Note that the right hand side of (2.11) is linear in b, reflecting that the environmental interaction variables are chosen such that all dependence is by

way of feedback via these variables (i.e., if one considers S as prescribed, then the *Daphnia* are independent from one another).

We now consider constant solutions of (2.11), i.e., steady population states. If food is kept at the constant concentration $\overline{S}$, then the basic reproduction number R_0 of the *Daphnia* is well defined and in fact given by

$$R_0(\overline{S}) = \int_0^\infty \beta(\Xi(a;\overline{S}),\overline{S})\mathcal{F}(a;\overline{S})da \tag{2.12}$$

(note that here we use the same symbol to denote the value and the constant function taking on that value). The equation

$$R_0(\overline{S}) = 1 \tag{2.13}$$

determines the constant concentrations that lead to a steady *Daphnia* population. As a rule, (2.13) has a unique solution, simply since $R_0(0) < 1$, $R_0(\infty) > 1$ and R_0 is a monotone function of $\overline{S}$ (of course other scenarios are possible if, for instance, the food is toxic at high concentrations).

Once $\overline{S}$ is determined, we have explicitly

$$\overline{b} = f(\overline{S}) / \int_0^\infty \gamma(\Xi(a;\overline{S}),\overline{S})\mathcal{F}(a;\overline{S})da \tag{2.14}$$

for the *Daphnia* population birth rate that keeps the algae at the steady level $\overline{S}$. (The steady states of more general physiologically structured population models can be determined by following essentially the same steps, see [8].)

For later use we introduce the notation

$$\overline{\xi}(a) := \Xi(a;\overline{S}) \tag{2.15}$$

$$\overline{\mathcal{F}}(a) := \mathcal{F}(a;\overline{S}) \tag{2.16}$$

to denote, respectively, the steady state age-size relation and the steady state survival probability. But is the steady population state stable? How does the answer depend on the parameters? What dynamic phenomena accompany the loss of stability? The standard way to answer such questions is to first linearise the equations around the steady state, next substitute exponential trial solutions into the linearised equations to deduce a characteristic equation and finally to investigate how the roots of the characteristic equation are positioned in the complex plane relative to the imaginary axis (and how positions change if we vary parameters; see for instance the stability boundaries in a two dimensional parameter space depicted in Figure 2 of [34]). The key point of the paper [9] is that the information about the roots of the characteristic equation allows one to indeed draw conclusions concerning solutions of (2.11), in other words, the standard way works for (2.11)! Hence we feel encouraged to present the general form of the linearised system and the characteristic equation in the next section and to work out in Section 4 the details of how to obtain the constants and the kernels that figure in the linearised system from g, μ, β, γ and f.

3 The linearised equation

Linearising the system (2.11) one obtains a system of the form

$$\begin{aligned} y(t) = &\quad c_1 z(t) + \int_0^\infty (k_{11}(a)y(t-a) + k_{12}(a)z(t-a))da, \\ \frac{dz}{dt}(t) = &\quad c_2 z(t) + \int_0^\infty (k_{21}(a)y(t-a) + k_{22}(a)z(t-a))da \end{aligned} \tag{3.1}$$

with y a small perturbation of $\bar{b}$ and z a small perturbation of $\overline{S}$. It has a solution of the form

$$\begin{pmatrix} y(t) \\ z(t) \end{pmatrix} = e^{\lambda t} \begin{pmatrix} y_0 \\ z_0 \end{pmatrix} \tag{3.2}$$

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

$$\left(1 - \widehat{k}_{11}(\lambda)\right)\left(\lambda - c_2 - \widehat{k}_{22}(\lambda)\right) = \widehat{k}_{21}(\lambda)\left(c_1 + \widehat{k}_{12}(\lambda)\right), \tag{3.3}$$

where the hat denotes Laplace transform, that is,

$$\widehat{k}_{ij}(\lambda) := \int_0^\infty e^{-\lambda a} k_{ij}(a)da. \tag{3.4}$$

The underlying assumptions are presented soon, but let us first observe that by combining Section 4 and Corollary 2.19 of [9], one obtains the principle of linearised stability for (2.11), albeit under the assumption of a maximal age $A_{\max}$. And by combining Section 4 and Theorem 2.21 of [9] one obtains a Hopf bifurcation theorem for (2.11).

For the infinite delay case one has to invoke additional arguments, see Diekmann & Gyllenberg [2,3], and to perform a more detailed spectral analysis, as there may be essential spectrum next to the eigenvalues that are obtained as roots of the characteristic equation; so the principle of linearised stability and the Hopf bifurcation theorem hold in that case too. In [3] these results were derived by combining the methods of [4,9] which results concerning (3.1) from [12], thus avoiding the task of characterising the essential spectrum.

We shall explain the derivation of the linearised system below, but its general form can be predicted by combining a general mathematical result, that a linear translation invariant integral operator is necessarily of convolution type, (see, for a far reaching generalization, [36, Theorem 6.33]), with an observation concerning (2.11), viz., that $S(t)$ appears at its right hand side (but not $b(t)$). In general, the convolution kernel is a measure. In the present case, that measure is absolutely continuous (the k part, deriving from the S_t and b_t at the right hand side of (2.11)), except for an atom in zero (the c part) in the second component that derives from the $S(t)$ in the right hand side of (2.11).

Our task is now to derive expressions for six quantities, the two components of c and the four components of k, in terms of the model ingredients. Four out of six are very easy. Since the system (2.11) is linear in b, the elements k_{11} and k_{21} are given by

$$k_{11}(a) = \beta(\overline{\xi}(a), \overline{S})\overline{\mathcal{F}}(a), \tag{3.5}$$

$$k_{21}(a) = -\gamma(\overline{\xi}(a), \overline{S})\overline{\mathcal{F}}(a). \tag{3.6}$$

Since $S(t)$ is a scalar quantity, taking derivatives is straightforward and leads to the expressions

$$c_1 = \overline{b} \int_0^\infty \frac{\partial \beta}{\partial S}(\overline{\xi}(a), \overline{S})\overline{\mathcal{F}}(a)da, \tag{3.7}$$

$$c_2 = f'(\overline{S}) - \overline{b} \int_0^\infty \frac{\partial \gamma}{\partial S}(\overline{\xi}(a), \overline{S})\overline{\mathcal{F}}(a)da. \tag{3.8}$$

The derivation of expressions for k_{12} and k_{22} is far more difficult, as we have to deal with quantities that are implicitly defined, viz., as solutions of (2.1) and (2.2). We delegate this derivation till the next section. The result is presented as formulas (4.14), (4.15) for the smooth case and as formulas (4.31), (4.32) for the case of an abrupt juvenile-adult transition. The underlying assumptions concerning the model ingredients are

(i) $f : \mathbb{R}_+ \to \mathbb{R}$ is continuously differentiable.
(ii) g, μ, β and γ as maps from $\mathbb{R}^2$ to $\mathbb{R}_+$ are continuously differentiable on $[\xi_b, \xi_A] \times \mathbb{R}_+$ and on $[\xi_A, \infty) \times \mathbb{R}_+$, but need not be continuous, let alone differentiable, at $\xi = \xi_A$.

The biological idea motivating the assumption labelled (ii) is that the individual organisms turn from juveniles into adults upon reaching size ξ_A and that the behaviour of juveniles and adults may differ substantially. Note that by assuming $g \geq 0$ we have excluded shrinking. (The Kooijman-Metz model [19,34] has additional rules to preclude shrinking, but for S not too far below the steady state these do not kick in.) But note carefully that in the case of a jump discontinuity at ξ_A we shall require strict positivity of g in ξ_A, see (4.16) and the text that preceeds it for explanation and motivation.

In the remainder of this section we prepare the way for the derivation and, while doing so, also present more details about the mathematical framework for studying (2.11). We restrict the precise formulation to the finite delay case and denote $A_{\max}$ by h. But we close with some remarks about the case of infinite delay.

For the history of the population birth rate b we require only integrability, but for the resource concentration we require continuity (from $t = 0$ onwards the birth rate will actually be continuous and the resource concentration differentiable). To express this and other aspects more precisely and more concisely we shall use some mathematical formalism that may not be familiar to all our readers. Such readers may skip the rest of this section.

Let

$$\begin{aligned} X &:= L^1\left([-h, 0]; \mathbb{R}\right), \\ Y &:= C\left(([-h, 0]; \mathbb{R}\right). \end{aligned} \tag{3.9}$$

We require that (2.11) holds for $t \geq 0$ and supplement the system by the initial condition

$$\begin{aligned} b(t) &= \varphi(t), \quad -h \leq t \leq 0, \\ S(t) &= \psi(t), \quad -h \leq t \leq 0, \end{aligned} \tag{3.10}$$

where $(\varphi, \psi) \in X \times Y$. We want to rewrite (2.11) in the form

$$\begin{aligned} b(t) &= F_1(b_t, S_t), \\ \frac{dS}{dt}(t) &= F_2(b_t, S_t) \end{aligned} \tag{3.11}$$

since that brings us into exactly the setting studied in Section 4 of [9]. (Alternatively one may work with non-densely defined Hille-Yosida operators and integrated semigroups, see Thieme [38], Magal & Ruan [24,25].) So we need to define, for $i = 1, 2$,

$$F_i : X \times Y \to \mathbb{R}$$

and check that these maps are continuously differentiable. The linearity in b_t motivates us to introduce the dual space X^*, which we represent by

$$X^* = L^\infty([0, h]; \mathbb{R}) \tag{3.12}$$

with the pairing between X and X^* defined by

$$\langle \varphi, \varphi^* \rangle := \int_0^h \varphi(-\tau)\varphi^*(\tau)d\tau. \tag{3.13}$$

If we now make sure, by making appropriate assumptions about the model ingredients, that the maps Q and R defined by

$$\begin{aligned} Q(\psi)(a) &= \beta(\Xi(a; \psi), \psi(0))\mathcal{F}(a; \psi), \\ R(\psi)(a) &= \gamma(\Xi(a; \psi), \psi(0))\mathcal{F}(a; \psi) \end{aligned} \tag{3.14}$$

map Y into X^* and are as such continuously differentiable, then we only have to define

$$\begin{aligned} F_1(\varphi, \psi) &= \langle \varphi, Q(\psi) \rangle, \\ F_2(\varphi, \psi) &= f(\psi(0)) - \langle \varphi, R(\psi) \rangle \end{aligned} \tag{3.15}$$

and require that f is C^1, to achieve our aim. This motivates us to require that the maps from Y into X^* that send ψ to, respectively $\Xi(.; \psi)$ and $F(.; \psi)$, so

$$\begin{aligned} \psi &\mapsto \Xi(\cdot; \psi), \\ \psi &\mapsto \mathcal{F}(\cdot; \psi) \end{aligned} \tag{3.16}$$

are continuously differentiable. Since evaluation in zero $\psi \mapsto \psi(0)$ is a continuous linear map from Y into $\mathbb{R}$, it only remains to check the smoothness of the maps defined in (3.16) and this we shall do in the next section (strictly speaking Q and R, and hence F_i, are only defined for functions ψ that take nonnegative values; there are various ways to see that we should not worry about that, the easiest is perhaps to restrict the assumption about the continuous differentiability of the maps F_i to a neighbourhood of $(\overline{b}, \overline{S}) \in X \times Y$).

In the infinite delay case, i.e., when individuals can, in principle, pass any conceivable age, any choice of space entails restrictions concerning the growth behaviour at (minus) infinity. It is these restrictions that obstruct the construction of the resolvent (of the generator of the linearised semigroup) for

λ in some left half plane. As a consequence there is an essential spectrum filling a left half plane. As long as this left half plane lies strictly to the left of the imaginary axis and, in addition, we have suitable estimates for the essential spectrum of the semigroup operators themselves, this need not bother us. This is achieved by considering the initial value problem on exponentially weighted spaces. To find a suitable weight function we first identify a $\varrho > 0$ such that the survival probability is bounded by $Ce^{-\varrho a}$ for even ideal environmental conditions. Next we choose

$$X = L^1_\varrho(\mathbb{R}_-) = \{\varphi \in L^1_{\mathrm{loc}}(\mathbb{R}_-) : a \mapsto \varphi(a)e^{\varrho a} \text{ belongs to } L^1(\mathbb{R}_-)\} \tag{3.17}$$

and

$$Y = C_{0,\varrho} = \left\{\psi \in C(\mathbb{R}_-) : \lim_{a\to-\infty} e^{\varrho a}\psi(a) = 0\right\}. \tag{3.18}$$

As representation of the dual space of X we take

$$X^* = L^\infty_\varrho(\mathbb{R}_+) = \{\varphi^* \in L^\infty_{loc}(\mathbb{R}_+) : a \mapsto \varphi^*(a)e^{\varrho a} \text{ belongs to } L^\infty(\mathbb{R}_+)\} \tag{3.19}$$

with the pairing being given by

$$\langle \varphi, \varphi^* \rangle = \int_0^\infty \varphi(-a)\varphi^*(a)da = \int_0^\infty \varphi(-a)e^{\varrho(-a)}e^{\varrho a}\varphi^*(a)da. \tag{3.20}$$

The definitions of Q, R and F_i given in (3.14) and (3.15) remain unchanged.

One reason to introduce the exponential weight function is to make sure that constant functions belong to the space X. A second reason is that once spectral properties come into play, we need the weight in order to achieve that the essential spectrum is bounded away from the imaginary axis, or, which amounts to the same thing, that we can define Laplace transforms in a half plane that extends to the strict left of the imaginary axis. In [3] this is worked out in detail but here, from now on, we restrict our attention to the case of finite delay.

4 Linearising individual growth and survival

Recall that $\xi(\tau; a, \psi)$ is defined by

$$\frac{d\xi}{d\tau}(\tau) = g(\xi(\tau), \psi(-a+\tau)), \quad \xi(0) = \xi_b. \tag{4.1}$$

We start by considering a smooth g, and postpone the incorporation of a jump at ξ_A. Let

$$\Omega = \{(\tau, a) : 0 \le a \le h, 0 \le \tau \le a\},$$

then ξ is defined on $\Omega \times Y$ and maps to $\mathbb{R}$. Assume that ξ is differentiable with respect to ψ and denote the derivative in the point (τ, a, ψ) by $D_3\xi(\tau; a, \psi)$. This is, for fixed τ, a, ψ, a linear map from Y to $\mathbb{R}$. We now consider $\psi = \overline{S}$,

the constant function and re-use the symbol ψ to denote the element of Y on which the linear map acts. The image we denote by η. So

$$\eta(\tau; a, \overline{S}, \psi) := D_3\xi(\tau; a, \overline{S})\psi. \tag{4.2}$$

We claim that, on fixing a and ψ, η can be found as a function of τ by solving the ODE

$$\frac{d\eta}{d\tau}(\tau) = \frac{\partial g}{\partial \xi}(\overline{\xi}(\tau), \overline{S})\eta(\tau) + \frac{\partial g}{\partial S}(\overline{\xi}(\tau), \overline{S})\psi(-a+\tau), \quad \eta(0) = 0. \tag{4.3}$$

The actual proof that ξ is differentiable with respect to ψ proceeds by introducing, for any $a \in [0, h]$ and $\psi \in Y$, the solution of (4.3) and next, by combining (4.1) and (4.3), checking that (4.2), read from right to left, is indeed the derivative [13].

The solution of (4.3) can be written in the form

$$\eta(\tau) = \int_0^\tau K(\tau, \alpha)\psi(-a+\alpha)d\alpha \tag{4.4}$$

with

$$K(\tau, \alpha) := e^{\int_\alpha^\tau \frac{\partial g}{\partial \xi}(\overline{\xi}(\theta), \overline{S})d\theta} \frac{\partial g}{\partial S}(\overline{\xi}(\alpha), \overline{S}). \tag{4.5}$$

(Note that for higher dimensional i-state one has to replace the explicit exponential function with the implicit fundamental matrix solution, which then acts on the vector $\frac{\partial g}{\partial \overline{S}}(\overline{\xi}(\alpha), \overline{S})$.) By simply taking $\tau = a$ we obtain

$$D_2\Xi(a; \overline{S})\psi = \eta(a) = \int_0^a K(a, \alpha)\psi(-a+\alpha)d\alpha \tag{4.6}$$

which is a rather explicit expression for the derivative of the first of the two maps considered in (3.16). We next set out to compute the derivative of the second map.

Define

$$\zeta(\tau; a, \overline{S}, \psi) := D_3\mathcal{G}(\tau; a, \overline{S})\psi, \tag{4.7}$$

then ζ satisfies

$$\frac{d\zeta}{d\tau}(\tau) = -\mu(\overline{\xi}(\tau), \overline{S})\zeta(\tau) - \rho(\tau), \quad \zeta(0) = 0 \tag{4.8}$$

with

$$\rho(\tau) := \frac{\partial \mu}{\partial \xi}(\overline{\xi}(\tau), \overline{S})\eta(\tau)\overline{\mathcal{F}}(\tau) + \frac{\partial \mu}{\partial S}(\overline{\xi}(\tau), \overline{S})\psi(-a+\tau)\overline{\mathcal{F}}(\tau). \tag{4.9}$$

Hence

$$\zeta(\tau) = -\int_0^\tau e^{-\int_\alpha^\tau \mu(\overline{\xi}(\theta), \overline{S})d\theta}\rho(\alpha)d\alpha = -\int_0^\tau \frac{\overline{\mathcal{F}}(\tau)}{\overline{\mathcal{F}}(\alpha)}\rho(\alpha)d\alpha \tag{4.10}$$

which, by inserting the expression (4.9) for ρ, (4.4) for η and changing the order of integration, leads to

$$\zeta(\tau) = \int_0^\tau L(\tau,\theta)\psi(-a+\theta)d\theta \tag{4.11}$$

with

$$L(\tau,\theta) := -\overline{\mathcal{F}}(\tau)\left\{\int_\theta^\tau \frac{\partial\mu}{\partial\xi}(\overline{\xi}(\alpha),\overline{S})K(\alpha,\theta)d\alpha + \frac{\partial\mu}{\partial S}(\overline{\xi}(\theta),\overline{S})\right\}. \tag{4.12}$$

In particular

$$D_2\mathcal{F}(a;\overline{S})\psi = \zeta(a) = \int_0^a L(a,\theta)\psi(-a+\theta)d\theta. \tag{4.13}$$

The final formulas

$$k_{12}(a) = \overline{b}\int_0^\infty \left\{\beta(\overline{\xi}(a+\theta),\overline{S})L(a+\theta,\theta) + \frac{\partial\beta}{\partial\xi}(\overline{\xi}(a+\theta),\overline{S})K(a+\theta,\theta)\overline{\mathcal{F}}(a+\theta)\right\}d\theta \tag{4.14}$$

$$k_{22}(a) = -\overline{b}\int_0^\infty \left\{\gamma(\overline{\xi}(a+\theta),\overline{S})L(a+\theta,\theta) + \frac{\partial\gamma}{\partial\xi}(\overline{\xi}(a+\theta),\overline{S})K(a+\theta,\theta)\overline{\mathcal{F}}(a+\theta)\right\}d\theta \tag{4.15}$$

are obtained by combining (3.14) and (3.15), the chain rule, (4.6), (4.13) and a change in the order of integration. Note that the expression for k_{22} is obtained from the expression for k_{12} by changing the sign and replacing β by γ.

In many consumer-resource models a distinction is made between juvenile consumers and adult consumers, with individual behaviour changing abruptly at the transition from juvenile to adult. In particular, reproduction is reserved to adults. We now show that a jump discontinuity at $\xi = \xi_A$ yields additional terms to the expressions for k_{12} and k_{22}.

As demonstrated in detail by Thieme in his pioneering paper [37], models are no longer well-posed if, possibly, individuals linger at the transition (or, in mathematical jargon, if characteristics are not necessarily transversal to discontinuities; also see [6]). Here we exclude such a situation by requiring that, at the very least,

$$g(\xi_A-,\overline{S}) > 0 \qquad g(\xi_A+,\overline{S}) > 0 \tag{4.16}$$

where the "$-$" denotes the limit from below and the "$+$" the limit from above. By continuity these inequalities extend to a neighbourhood (in $\mathbb{R}$) of $\overline{S}$ and that suffices for the present considerations. But in a full model analysis one should certainly be more conservative and check that transversality holds for a wider range of conditions.

With $\xi(\tau;a,\psi)$ defined by (4.1) we now first consider

$$\xi(\tau;a,\psi) = \xi_A \tag{4.17}$$

as an equation for τ, for given a, ψ with a large enough and ψ in some neighbourhood of the constant function $\overline{S}$. In biological terms, the solution is the

age at which an individual matured that is presently an adult of age a and that experienced the food history ψ. Under constant conditions, the present age is irrelevant. We denote the solution for $\psi = \overline{S}$ and arbitrary a by $\overline{\tau}$, so

$$\xi(\overline{\tau}; a, \overline{S}) = \xi_A \tag{4.18}$$

and $\overline{\tau}$ is the age at which individuals mature under the conditions corresponding to the population steady state.

By the implicit function theorem, (4.17) has a unique solution for $a > \overline{\tau}$ and $\|\psi - \overline{S}\|$ small (uniqueness is global because of the monotonicity of the map $\tau \mapsto \xi(\tau; a, \psi)$). We denote this solution by $\widetilde{\tau}(a, \psi)$. So

$$\xi(\widetilde{\tau}(a, \psi); a, \psi) = \xi_A \tag{4.19}$$

and by differentiation of this identity with respect to ψ and evaluation of the result in $\overline{S}$, we obtain

$$\frac{\partial \xi}{\partial \tau}(\overline{\tau}; a, \overline{S}) D_2 \widetilde{\tau}(a, \overline{S})\psi + D_3 \xi(\overline{\tau}; a, \overline{S})\psi = 0. \tag{4.20}$$

Hence

$$D_2 \widetilde{\tau}(a, \overline{S})\psi = -\frac{\eta(\overline{\tau}; a, \overline{S}, \psi)}{g(\xi_A -, \overline{S})} \tag{4.21}$$

with η defined by (4.3). (The reason why we should evaluate g at $\xi_A -$, is that the solution of (4.17) does depend only on g for $\xi \leq \xi_A$).

We still define $\eta(\tau; a, \overline{S}, \psi)$ as the solution of (4.3) and do not worry about the discontinuity in the derivative with respect to τ at $\tau = \overline{\tau}$. But, as we will show, (4.2) read from right to left is no longer valid. There is now an additional term, which is a multiple of $H(\tau - \overline{\tau})$, with H the Heaviside function. To derive this, we first observe that (4.2) remains valid as stated for $\tau < \overline{\tau}$. Next, consider $\tau > \overline{\tau}$ and let, for a given $\psi \in Y$, ε be so small that also $\tau > \widetilde{\tau}(a, \overline{S} + \varepsilon\psi)$. Then

$$\begin{aligned}
&\xi(\tau; a, \overline{S} + \varepsilon\psi) - \xi(\tau; a, \overline{S}) = \\
&\int_{\widetilde{\tau}(a, \overline{S}+\varepsilon\psi)}^{\tau} g(\xi(\sigma; a, \overline{S} + \varepsilon\psi), \overline{S} + \varepsilon\psi(-a + \sigma))d\sigma - \int_{\overline{\tau}}^{\tau} g(\xi(\sigma; a, \overline{S}), \overline{S})d\sigma \\
&= \int_{\widetilde{\tau}(a, \overline{S}+\varepsilon\psi)}^{\overline{\tau}} g(\xi(\sigma; a, \overline{S}), \overline{S})d\sigma \\
&\quad + \int_{\widetilde{\tau}(a, \overline{S}+\varepsilon\psi)}^{\tau} \left\{ g(\xi(\sigma; a, \overline{S} + \varepsilon\psi), \overline{S} + \varepsilon\psi(-a + \sigma)) - g(\xi(\sigma; a, \overline{S}), \overline{S}) \right\} d\sigma \\
&= -\varepsilon g(\xi_A +, \overline{S}) D_2 \widetilde{\tau}(a, \overline{S})\psi + o(\varepsilon) + \varepsilon(\eta(\tau; a, \overline{S}, \psi) - \eta(\overline{\tau}; a, \overline{S}, \psi)) + o(\varepsilon).
\end{aligned}$$

Hence we have for $\tau > \overline{\tau}$, because of (4.21), that

$$D_3 \xi(\tau; a, \overline{S})\psi = \eta(\tau) + \left(\frac{g(\xi_A +, \overline{S})}{g(\xi_A -, \overline{S})} - 1 \right) \eta(\overline{\tau}) \tag{4.22}$$

and consequently

$$D_3\xi(\tau;a,\overline{S})\psi = \eta(\tau) + \left(\frac{g(\xi_A+,\overline{S})}{g(\xi_A-,\overline{S})} - 1\right)\eta(\overline{\tau})H(\tau-\overline{\tau}) \tag{4.23}$$

which, in turn, because of (4.4) and (4.5) yields

$$\begin{aligned} D_2\Xi(a;\overline{S})\psi = &\int_0^a K(a,\alpha)\psi(-a+\alpha)d\alpha \\ &+ \left(\frac{g(\xi_A+,\overline{S})}{g(\xi_A-,\overline{S})} - 1\right)\int_0^{\overline{\tau}} K(\overline{\tau},\alpha)\psi(-a+\alpha)d\alpha \cdot H(a-\overline{\tau}). \end{aligned} \tag{4.24}$$

The formula (4.13) likewise needs a Heaviside correction term to incorporate the effects of the jump discontinuity. For (a,ψ) such that $\xi(a;a,\psi) > \xi_A$, we can write

$$\mathcal{F}(a;\psi) = e^{-\int_0^{\widetilde{\tau}(a,\psi)}\mu(\xi(\sigma;a,\psi),\psi(-a+\sigma))d\sigma - \int_{\widetilde{\tau}(a,\psi)}^{a}\mu(\xi(\sigma;a,\psi),\psi(-a+\sigma))d\sigma}$$

which shows that, relative to the smooth situation, there is an extra term

$$(\mu(\xi_A+,\overline{S}) - \mu(\xi_A-,\overline{S}))\mathcal{F}(a;\overline{S})D_2\widetilde{\tau}(a,\overline{S})\psi.$$

Hence

$$\begin{aligned} D_2\mathcal{F}(a,\overline{S})\psi = &\int_0^a L(a,\theta)\psi(-a+\theta)d\theta \\ &- \frac{\mu(\xi_A+,\overline{S}) - \mu(\xi_A-,\overline{S})}{g(\xi_A-,\overline{S})}\overline{\mathcal{F}}(a)\int_0^{\overline{\tau}} K(\overline{\tau},\alpha)\psi(-a+\alpha)d\alpha \cdot H(a-\overline{\tau}). \end{aligned} \tag{4.25}$$

Finally, we reconsider (2.11). Let $\overline{a} = \overline{a}(\psi)$ be the age of the individuals that mature exactly at the present time, given that the food history is ψ. In mathematical terms $\overline{a}$ is the solution of the equation

$$\widetilde{\tau}(a,\psi) = a \tag{4.26}$$

or, equivalently, of the equation

$$\Xi(a;\psi) = \xi_A. \tag{4.27}$$

Note that

$$\overline{a}(\overline{S}) = \overline{\tau}. \tag{4.28}$$

Since juveniles do not reproduce, we replace the first equation of (2.11) with

$$b(t) = \int_{\overline{a}(S_t)}^{\infty} b(t-a)\beta(\Xi(a;S_t),S(t))\mathcal{F}(a;S_t)da. \tag{4.29}$$

In the linearised equation (the first equation of (3.1)) this yields, apart from the contributions of the Heaviside terms in (4.24) and (4.25), an extra term

$$-\overline{b}\beta(\xi_A+,\overline{S})\overline{\mathcal{F}}(\overline{\tau})D\overline{a}(\overline{S})\psi.$$

Similarly the second equation of (3.1) should get an extra term

$$(\gamma(\xi_A+,\overline{S})-\gamma(\xi_A-,\overline{S}))\overline{b}\mathcal{F}(\overline{\tau})D\overline{a}(\overline{S})\psi.$$

By implicit differentiation of (4.27) we obtain

$$D_1\Xi(\overline{\tau};\overline{S})D\overline{a}(\overline{S})\psi+D_2\Xi(\overline{\tau};\overline{S})\psi=0$$

which can be written as

$$g(\xi_A-;\overline{S})D\overline{a}(\overline{S})\psi+\eta(\overline{\tau};\overline{\tau},\overline{S},\psi)=0$$

to deduce that

$$D\overline{a}(\overline{S})\psi=-\frac{\int_0^{\overline{\tau}}K(\overline{\tau},\alpha)\psi(-\overline{\tau}+\alpha)d\alpha}{g(\xi_A-,\overline{S})}. \tag{4.30}$$

This ends the preparations and we are ready to formulate the final results. But first we recall the notation χ_ω for the characteristic function of the set ω. In particular

$$\chi_{[0,\overline{\tau}]}(a)=\begin{cases}1 & \text{for} \quad 0\le a\le\overline{\tau}\\ 0 & \text{otherwise.}\end{cases}$$

$$\begin{aligned}
&k_{12}(a)=\\
&\overline{b}\int_{\max\{0,\overline{\tau}-a\}}^{\infty}\left\{\beta(\overline{\xi}(a+\theta),\overline{S})L(a+\theta,\theta)+\frac{\partial\beta}{\partial\xi}(\overline{\xi}(a+\theta),\overline{S})K(a+\theta,\theta)\overline{\mathcal{F}}(a+\theta)\right\}d\theta\\
&+\chi_{[0,\overline{\tau}]}(a)\overline{b}\int_{\overline{\tau}}^{\infty}\frac{\partial\beta}{\partial\xi}(\overline{\xi}(\sigma),\overline{S})\overline{\mathcal{F}}(\sigma)d\sigma\left(\frac{g(\xi_A+,\overline{S})}{g(\xi_A-,\overline{S})}-1\right)K(\overline{\tau},\overline{\tau}-a)\\
&+\overline{b}\frac{\mu(\xi_A-,\overline{S})-\mu(\xi_A+,\overline{S})}{g(\xi_A-,\overline{S})}\int_{\max\{0,\overline{\tau}-a\}}^{\overline{\tau}}\beta(\overline{\xi}(a+\theta),\overline{S})\overline{\mathcal{F}}(a+\theta)K(\overline{\tau},\theta)d\theta\\
&+\chi_{[0,\overline{\tau}]}(a)\overline{b}\frac{\beta(\overline{\xi}_A+,\overline{S})\overline{\mathcal{F}}(\overline{\tau})}{g(\xi_A-,\overline{S})}K(\overline{\tau},\overline{\tau}-a).
\end{aligned} \tag{4.31}$$

$$\begin{aligned}
&k_{22}(a)=\\
&-\overline{b}\int_{0}^{\infty}\left\{\gamma(\overline{\xi}(a+\theta),\overline{S})L(a+\theta,\theta)+\frac{\partial\gamma}{\partial\xi}(\overline{\xi}(a+\theta),\overline{S})K(a+\theta,\theta)\overline{\mathcal{F}}(a+\theta)\right\}d\theta\\
&-\chi_{[0,\overline{\tau}]}(a)\overline{b}\int_{\overline{\tau}}^{\infty}\frac{\partial\gamma}{\partial\xi}(\overline{\xi}(\sigma),\overline{S})\overline{\mathcal{F}}(\sigma)d\sigma\left(\frac{g(\xi_A+,\overline{S})}{g(\xi_A-,\overline{S})}-1\right)K(\overline{\tau},\overline{\tau}-a)\\
&-\overline{b}\frac{\mu(\xi_A-,\overline{S})-\mu(\xi_A+,\overline{S})}{g(\xi_A-,\overline{S})}\int_{\max\{0,\overline{\tau}-a\}}^{\overline{\tau}}\gamma(\overline{\xi}(a+\theta),\overline{S})\overline{\mathcal{F}}(a+\theta)K(\overline{\tau},\theta)d\theta\\
&-\chi_{[0,\overline{\tau}]}(a)\overline{b}\frac{\gamma(\overline{\xi}_A+,\overline{S})-\gamma(\overline{\xi}_A-,\overline{S})}{g(\xi_A-,\overline{S})}\overline{\mathcal{F}}(\overline{\tau})K(\overline{\tau},\overline{\tau}-a).
\end{aligned} \tag{4.32}$$

5 How to analyse the characteristic equation : some didactical examples

In this section we illustrate how one can use the characteristic equation (3.3) to find stability boundaries in parameter space.

5.1 A stage structured model

Motivated by the work of Gurney and Nisbet [10], see also Chapter 5 of [30], and that of de Roos and Persson [33], we consider a stage structured population. Here the word "stage" is used to express that g, μ, β and γ are independent of ξ on the juvenile interval $\xi_b \leq \xi < \xi_A$) and on the adult interval $\xi > \xi_A$. Since the juvenile growth rate depends on the food concentration, there is a variable maturation delay. Our purported aim is to investigate how the density dependence of this maturation delay can lead to population cycles.

We denote the per capita death rate and the per capita consumption rate by μ_1, $\gamma_1(S)$ when $\xi < \xi_A$ and by μ_2, $\gamma_2(S)$ for $\xi \geq \xi_A$, respectively. In contrast to [33] we restrict our attention to death rates that are independent of the resource concentration. By $g(S)$ we denote the growth rate of juveniles and by $\beta(S)$ the reproduction rate of adults (there is no need for an index here, as juveniles do not reproduce and the size of adults is irrelevant).

If g is bounded away from zero, the equation in τ

$$\int_{-\tau}^{0} g(\psi(\theta))d\theta = \xi_A - \xi_b \tag{5.1}$$

has a unique solution which we denote by

$$\tau = \tau_m(\psi). \tag{5.2}$$

Biologically $\tau_m(\psi)$ is the age of individuals that mature at the present time, given that the food history is ψ. If g can become zero or even negative for low resource concentrations, one needs restrictions on ψ to guarantee the solvability of (5.1). Close to population steady state such restrictions are automatically satisfied and hence we refrain from any attempt at giving more precise formulations.

For $a > \tau_m(\psi)$ we can also consider the equation

$$\int_{0}^{\tau} g(\psi_{-a}(\theta))d\theta = \xi_A - \xi_b \tag{5.3}$$

to find the age at maturation of an individual that presently has age a (and is an adult since $a > \tau_m(\psi)$). We denote the unique solution by

$$\tau = \widetilde{\tau}_m(a, \psi), \quad a > \tau_m(\psi). \tag{5.4}$$

Note that the identity

$$\widetilde{\tau}_m(\tau_m(\psi), \psi) = \tau_m(\psi)$$

holds. Moreover $\widetilde{\tau}_m(a+t,S_t)$ is constant, i.e., $\widetilde{\tau}_m$ is independent of t. The point of introducing τ_m and $\widetilde{\tau}_m$ is that we can now reformulate (2.11) for the present situation in explicit detail:

$$b(t) = \beta(S(t)) \int_{\tau_m(S_t)}^{\infty} b(t-a) e^{-\mu_1 \widetilde{\tau}_m(a,S_t) - \mu_2(a - \widetilde{\tau}_m(a,S_t))} da \tag{5.5}$$

$$\begin{aligned} \frac{dS}{dt}(t) =& f(S(t)) - \gamma_1(S(t)) \int_0^{\tau_m(S_t)} b(t-a) e^{-\mu_1 a} da \\ & - \gamma_2(S(t)) \int_{\tau_m(S_t)}^{\infty} b(t-a) e^{-\mu_1 \widetilde{\tau}_m(a,S_t) - \mu_2(a - \widetilde{\tau}_m(a,S_t))} da. \end{aligned} \tag{5.6}$$

The steady state condition $R_0(\overline{S}) = 1$, cf. (2.13), amounts to

$$\beta(\overline{S}) e^{-\mu_1 \overline{\tau}} \frac{1}{\mu_2} = 1 \tag{5.7}$$

as follows at once from (5.5). Here $\overline{\tau}$ is the common steady state value of τ_m and $\widetilde{\tau}_m$, so $\overline{\tau}$ depends on $\overline{S}$ and is given explicitly by

$$\overline{\tau} = \frac{\xi_A - \xi_b}{g(\overline{S})}. \tag{5.8}$$

This allows us to rewrite (5.7) in the form

$$\frac{g(\overline{S})}{\mu_1} \log \frac{\beta(\overline{S})}{\mu_2} = \xi_A - \xi_b. \tag{5.9}$$

Whenever g and β are monotone increasing, the left hand side of (5.9) is monotone increasing and so there is a unique solution provided the left hand side is smaller than the right hand side for small $\overline{S}$ and larger for large $\overline{S}$. From (5.6) we obtain

$$\overline{b} = \frac{f(\overline{S})}{\gamma_1(\overline{S}) \frac{1 - e^{-\mu_1 \overline{\tau}}}{\mu_1} + \gamma_2(\overline{S}) \frac{e^{-\mu_1 \overline{\tau}}}{\mu_2}} \tag{5.10}$$

as the corresponding steady consumer population birth rate, cf. (2.14).

At population steady state, the size of a juvenile of age a is given by

$$\overline{\xi}(a) = \xi_b + g(\overline{S}) a, \quad 0 \le a < \overline{\tau} \tag{5.11}$$

and the survival probability as a function of age by

$$\overline{\mathcal{F}}(a) = \begin{cases} e^{-\mu_1 a}, & 0 \le a \le \overline{\tau} \\ e^{-\mu_1 \overline{\tau}} e^{-\mu_2(a - \overline{\tau})}, & a \ge \overline{\tau}. \end{cases} \tag{5.12}$$

5.2 The characteristic equation for purely imaginary λ

We recall that the characteristic equation (3.3) is given by

$$\left\{1-\widehat{k}_{11}(\lambda)\right\}\left\{\lambda-c_2-\widehat{k}_{22}(\lambda)\right\}-\widehat{k}_{21}(\lambda)\left\{c_1+\widehat{k}_{12}(\lambda)\right\}=0, \tag{5.13}$$

where

$$\widehat{k}_{ij}(\lambda)=\int_0^\infty k_{ij}(a)e^{-\lambda a}da, \quad (i,j=1,2). \tag{5.14}$$

Combining (3.5) with (5.7) we find

$$\widehat{k}_{11}(\lambda)=\frac{\mu_2}{\mu_2+\lambda}e^{-\lambda\overline{\tau}}. \tag{5.15}$$

Directly from (3.6) we obtain

$$\widehat{k}_{21}(\lambda)=\gamma_1(\overline{S})\frac{e^{-(\mu_1+\lambda)\overline{\tau}}-1}{\mu_1+\lambda}-\gamma_2(\overline{S})\frac{e^{-(\mu_1+\lambda)\overline{\tau}}}{\mu_2+\lambda}, \tag{5.16}$$

while (3.7) and (3.8) lead to

$$c_1=\overline{b}\beta'(\overline{S})\frac{e^{-\mu_1\overline{\tau}}}{\mu_2}=\overline{b}\frac{\beta'(\overline{S})}{\beta(\overline{S})} \tag{5.17}$$

$$c_2=f'(\overline{S})-\overline{b}\gamma_1'(\overline{S})\frac{1-e^{-\mu_1\overline{\tau}}}{\mu_1}-\overline{b}\frac{\gamma_2'(\overline{S})}{\beta(\overline{S})} \tag{5.18}$$

where we have used (5.7) twice more.

In order to compute $\widehat{k}_{12}$ and $\widehat{k}_{22}$, we first observe that (4.5) reduces to

$$K(\tau,\alpha)=g'(\overline{S}) \quad \text{for} \quad 0\le\alpha<\overline{\tau} \quad \text{(and zero otherwise)} \tag{5.19}$$

while (4.12) yields

$$L(\tau,\theta)=0. \tag{5.20}$$

It is now a straightforward matter to deduce from (4.31) and (4.32) that

$$\widehat{k}_{12}(\lambda)=\overline{b}\frac{g'(\overline{S})}{g(\overline{S})}\left\{\frac{\mu_1}{\lambda}+\frac{\mu_2-\mu_1}{\mu_2+\lambda}\right\}(1-e^{-\lambda\overline{\tau}}). \tag{5.21}$$

$$\widehat{k}_{22}(\lambda)=\overline{b}\frac{g'(\overline{S})}{g(\overline{S})}e^{-\mu_1\overline{\tau}}\left\{\frac{1-e^{-\lambda\overline{\tau}}}{\lambda}\left(\gamma_1(\overline{S})-\gamma_2(\overline{S})\frac{\mu_1}{\mu_2}\right)-\gamma_2(\overline{S})\frac{1-\mu_1/\mu_2}{\mu_2+\lambda}(1-e^{-\lambda\overline{\tau}})\right\}. \tag{5.22}$$

If we substitute $\lambda=i\omega$ into (5.13) and rewrite the complex equation as two real equations we obtain

$$\begin{aligned}
&\Re\widehat{k}_{11}\Re\widehat{k}_{22}-\Im\widehat{k}_{11}\Im\widehat{k}_{22}-c_1\Re\widehat{k}_{21}-c_2(1-\Re\widehat{k}_{11})-\Re\widehat{k}_{22}+\omega\Im\widehat{k}_{11}\\
&-(\Re\widehat{k}_{21}\Re\widehat{k}_{12}-\Im\widehat{k}_{21}\Im\widehat{k}_{12})=0,\\
&\Re\widehat{k}_{11}\Im\widehat{k}_{22}+\Im\widehat{k}_{11}\Re\widehat{k}_{22}-c_1\Im\widehat{k}_{21}+c_2\Im\widehat{k}_{11}-\Im\widehat{k}_{22}+\omega(1-\Re\widehat{k}_{11})\\
&-(\Re\widehat{k}_{12}\Im\widehat{k}_{21}+\Im\widehat{k}_{12}\Re\widehat{k}_{21})=0.
\end{aligned} \tag{5.23}$$

The symbols $\Re$ and $\Im$ denote the real and imaginary part of a complex number, respectively. If we define $\varphi = \varphi(\mu, \omega)$ by requiring that

$$\cos\varphi = \frac{\mu}{\sqrt{\mu^2+\omega^2}} \text{ and } \sin\varphi = \frac{\omega}{\sqrt{\mu^2+\omega^2}},$$

then we can write

$$\frac{1}{\mu+i\omega} = \frac{\mu-i\omega}{\mu^2+\omega^2} = \frac{1}{\sqrt{\mu^2+\omega^2}} e^{-i\varphi(\mu,\omega)}.$$

It follows that

$$\begin{aligned}
\widehat{k}_{11}(i\omega) =& \frac{\mu_2}{\sqrt{\mu_2^2+\omega^2}} e^{-i(\omega\overline{\tau}+\varphi(\mu_2,\omega))},\\
\widehat{k}_{12}(i\omega) =& \overline{b}\frac{g'(\overline{S})}{g(\overline{S})}\left(\frac{\mu_1}{i\omega} + \frac{\mu_2-\mu_1}{\sqrt{\mu_2^2+\omega^2}} e^{-i\varphi(\mu_2,\omega)}\right)(1-e^{-i\omega\overline{\tau}}),\\
\widehat{k}_{21}(i\omega) =& \frac{\gamma_1(\overline{S})}{\sqrt{\mu_1^2+\omega^2}}\left(e^{-\mu_1\overline{\tau}-i(\omega\overline{\tau}+\varphi(\mu_1,\omega))} - e^{-i\varphi(\mu_1,\omega)}\right) - \frac{\gamma_2(\overline{S})}{\sqrt{\mu_2^2+\omega^2}} e^{-\mu_1\overline{\tau}-i(\omega\overline{\tau}+\varphi(\mu_2,\omega))},\\
\widehat{k}_{22}(i\omega) =& \overline{b}\frac{g'(\overline{S})}{g(\overline{S})} e^{-\mu_1\overline{\tau}}\left\{\frac{1-e^{-i\omega\overline{\tau}}}{i\omega}\left(\gamma_1(\overline{S}) - \gamma_2(\overline{S})\frac{\mu_1}{\mu_2}\right)\right.\\
& \left. -\gamma_2(\overline{S})\left(1-\frac{\mu_1}{\mu_2}\right)\frac{1}{\sqrt{\mu_2^2+\omega^2}} e^{-i\varphi(\mu_2,\omega)}(1-e^{-i\omega\overline{\tau}})\right\}.
\end{aligned}$$

We can use (5.23) to find stability boundaries in parameter space. An effective way is to single out two parameters and to use ω to parametrise the curve in the corresponding parameter plane at which a Hopf bifurcation occurs (see [4, 35] for details). In principle one can determine by way of additional analytic computations whether the Hopf bifurcation is sub- or supercritical. By implementing the corresponding algorithm, a useful tool for numerical bifurcation analysis is obtained (see [14], which builds on [16,23,21,22]). As the tool is not yet available in a user friendly form, we report some numerical experiments that provide information concerning the direction of bifurcation in Section 6.

5.3 Analytical results

When does maturation delay lead to population cycles? This question is not precise enough to allow a clear-cut answer (for instance, oscillations may arise by the combined effect of several mechanisms and then, of course, it makes no sense to call a single one of these the cause). Yet, in order to understand complex phenomena it may help (to try) to disentangle the various mechanisms by analysing limiting cases that are relatively simple. In that spirit we shall in the present subsection present some analytical results and in the next section some numerical studies.

What follows is a telegram style preview of this section. Note that the conclusions are based on a local stability analysis of the steady-state, but that the choice of wording does not reflect this limitation. (Note also that in the Hopf Bifurcation Theorem one of the conditions states that the eigenvalues should pass the imaginary axis with positive speed if the scalar parameter passes the critical value. In terms of the stability boundary this requires that when we implicitly consider a one parameter path in two parameter space, this path is supposed to cross the stability boundary transversally.)

Consumer-resource cycles may occur in unstructured models as a result of a hump-shaped resource growth function $f(S)$. We call these classical predator-prey cycles. If f is a decreasing function of S, one may still have cycles in case of maturation delay. We shall, for ease of formulation, call these 'delayed negative feedback' cycles.

Delayed negative feedback cycles will not occur if there are no differences between juvenile and adult consumers in either resource ingestion rate or mortality. If only adults exploit the resource, cycles are possible, but not unless near the steady state a small relative increase of food leads to a large relative increase in reproduction. If cycles occur, their period at 'birth' is in between two and four times the duration of the juvenile period, at least in a quasi-steady-state-approximation. If only juveniles exploit the substrate, cycles are also possible. They are promoted by a high reproduction rate. At 'birth' their period is between one and two times the duration of the juvenile period, at least in a quasi-steady-state-approximation.

5.3.1 Nothing but a growth-reproduction transition

Assume that there is neither a change in the death rate μ nor in the consumption rate $\gamma(S)$ at ξ_A. We will show that the (in)stability is closely related to that of the steady state of the corresponding unstructured model

$$\begin{aligned} \frac{dS}{dt} &= f(S) - \gamma(S)P, \\ \frac{dP}{dt} &= \beta(S)P - \mu P. \end{aligned} \tag{5.24}$$

We shall briefly review the stability of (5.24). There exists a positive equilibrium of (5.24), denoted by $(\overline{S}, \overline{P})$, if there exists a positive constant $\overline{S}$ such that $\beta(\overline{S}) = \mu$ and, moreover, $f(\overline{S}) > 0$. The characteristic equation defined for the linearized equations for (5.24) around the positive equilibrium is given by

$$\lambda^2 + c_2\lambda + f(\overline{S})\beta'(\overline{S}) = 0, \tag{5.25}$$

where c_2 is given by $c_2 = f'(\overline{S}) - \frac{\gamma'(\overline{S})}{\gamma(\overline{S})} f(\overline{S})$. System (5.24) undergoes a Hopf bifurcation if and only if c_2 passes 0. So a necessary condition for Hopf bifurcation to be possible is that f is increasing on part of its domain.

For the structured model (2.11), we concentrate on the special case

$$\mu = \mu_1 = \mu_2, \quad \gamma(S) = \gamma_1(S) = \gamma_2(S). \tag{5.26}$$

This means that when juveniles turn into adults there is no change in uptake rate nor in death rate. By substituting the explicit expressions for $\widehat{k}_{ij}(i\omega)$ and c_i $(i,j=1,2)$ into the characteristic equation (5.23), we can derive that for $i\omega$ to be a root necessarily $p(\omega^2)=0$ should hold, where

$$p(\omega^2) := (\omega^2 - \gamma(\overline{S})c_1)^2 + c_2^2\omega^2 + 2\gamma(\overline{S})\mu c_2\left(\overline{b}\frac{g'(\overline{S})}{g(\overline{S})} - c_1\right) \tag{5.27}$$

(the details of the derivation are presented in the Appendix). We now have

$$c_1 = \overline{b}\frac{\beta'(\overline{S})}{\beta(\overline{S})}, \quad c_2 = f'(\overline{S}) - \frac{\gamma'(\overline{S})}{\gamma(\overline{S})}f(\overline{S}). \tag{5.28}$$

If $p(\omega^2)=0$ has no positive real root, there exist no purely imaginary roots of (5.23). By substituting the explicit expression for c_1 we find $\overline{b}\frac{g'(\overline{S})}{g(\overline{S})} - c_1 = \overline{b}\left(\frac{g'(\overline{S})}{g(\overline{S})} - \frac{\beta'(\overline{S})}{\beta(\overline{S})}\right)$. Note that if g and β are proportional, then necessarily

$$\frac{g'(\overline{S})}{g(\overline{S})} - \frac{\beta'(\overline{S})}{\beta(\overline{S})} = 0.$$

So in this case we find, exactly as for the unstructured model, that a Hopf bifurcation occurs if and only if $c_2=0$, where c_2 is given by the same formula $c_2 = f'(\overline{S}) - \{\gamma'(\overline{S})/\gamma(\overline{S})\}f(\overline{S})$ in both cases (concerning the 'if' part, note that in the Appendix we show that for $c_2=0$ there is indeed a pair of roots on the imaginary axis). Hence, if adults and juveniles only differ in that juveniles convert substrate into growth and adults convert it into offspring, with fixed conversion factors, then the stability properties of that model exactly mimick those of an unstructured model. As a corollary we conclude that the maturation delay on its own cannot lead to oscillations.

5.3.2 Substrate serves for reproduction, not for growth

Motivated by earlier work of Gurney & Nisbet [10] and by the observation above, we next consider the case that the growth rate g is independent of S. For consistency we assume that the juveniles have a different food source and do not consume the substrate. So we have $g'=0$ and $\gamma_1=0$. Note that the maturation delay is now fixed rather than variable.

We now have

$$\overline{b} = \frac{\beta(\overline{S})f(\overline{S})}{\gamma_2(\overline{S})}, \quad c_1 = \frac{\beta'(\overline{S})f(\overline{S})}{\gamma_2(\overline{S})}, \quad c_2 = f'(\overline{S}) - \frac{\gamma_2'(\overline{S})f(\overline{S})}{\gamma_2(\overline{S})}, \tag{5.29}$$

and the characteristic equation is given by

$$\left(1 - \frac{\mu_2}{\lambda+\mu_2}e^{-\lambda\overline{\tau}}\right)\left(\lambda - f'(\overline{S}) + \frac{\gamma_2'(\overline{S})}{\gamma_2(\overline{S})}f(\overline{S})\right) + \frac{\mu_2}{\lambda+\mu_2}\frac{\beta'(\overline{S})}{\beta(\overline{S})}f(\overline{S})\mathrm{e}^{-\lambda\overline{\tau}} = 0. \tag{5.30}$$

By reorganizing a bit we can bring this equation in the form

$$\frac{\mu_2}{\lambda+\mu_2}\,\mathrm{e}^{-\lambda\overline{\tau}}\;\frac{\lambda - f'(\overline{S}) + \frac{\gamma_2'(\overline{S})}{\gamma_2(\overline{S})}f(\overline{S}) - \frac{\beta'(\overline{S})}{\beta(\overline{S})}f(\overline{S})}{\lambda - f'(\overline{S}) + \frac{\gamma_2'(\overline{S})}{\gamma_2(\overline{S})}f(\overline{S})} = 1. \tag{5.31}$$

Taking the square of the absolute value of both sides of (5.31) we obtain, after some rearranging, the equation

$$\omega^4 + c_2^2\omega^2 - \mu_2^2 c_3(2c_2 + c_3) = 0, \tag{5.32}$$

where

$$c_3 := \frac{\beta'(\overline{S})}{\beta(\overline{S})}f(\overline{S}). \tag{5.33}$$

This is a quadratic equation for ω^2 which has a positive root iff

$$(2c_2 + c_3)c_3 > 0.$$

For increasing beta we have $c_3 > 0$ and then this condition translates into

$$2\frac{f'(\overline{S})}{f(\overline{S})} - 2\frac{\gamma_2'(\overline{S})}{\gamma_2(\overline{S})} + \frac{\beta'(\overline{S})}{\beta(\overline{S})} > 0. \tag{5.34}$$

If f is decreasing and β is proportional to γ_2, (5.34) is false and hence we know for sure that the steady state is stable. By writing (5.34) in the form

$$2\frac{f'(\overline{S})}{f(\overline{S})} - \frac{\gamma_2'(\overline{S})}{\gamma_2(\overline{S})} + \frac{d}{dS}\ln\frac{\beta(S)}{\gamma_2(S)}\bigg|_{S=\overline{S}} > 0 \tag{5.35}$$

we see that, for decreasing f and increasing γ_2, destabilization requires that the conversion efficiency increases rapidly with S near $\overline{S}$. This may happen in an energy budget model of the net-production type (in which reproduction is proportional to the difference between the ingestion rate and maintenance costs) if at equilibrium β is small, so that a small relative increase in ingestion can lead to a rather large relative increase in reproduction.

To gain more insight about the possibility of destabilization we take a drastic step and delete λ in the second factor of equation (5.30). The underlying idea is that, when both f and γ_2 are large relative to β, g, and μ_2, the food dynamics is fast relative to both maturation and demographic turnover of the consumer population. The corresponding quasi-steady state assumption amounts to replacing dS/dt at the left hand side of the second equation of (2.11) with zero. At the level of the characteristic equation this amounts to removing the term λ in (5.31). The technical way of relating results of the reduced characteristic equation to results for the full characteristic equation is as follows. If f has a factor ε^{-1} then we can multiply (5.31) with ε, and next obtain the reduced equation by putting $\varepsilon = 0$. The implicit function theorem then can be used to show that if the reduced equation has roots in the right half plane, so has the full equation for ε positive but small.

If we multiply the reduced equation with $\lambda+\mu_2$, reorganise a bit, and scale λ with a factor $\overline{\tau}$, we obtain

$$\lambda = \alpha_1 + \alpha_2 e^{-\lambda} \tag{5.36}$$

with

$$\alpha_1 = -\mu_2\overline{\tau}, \quad \alpha_2 = \mu_2\overline{\tau}\left(\frac{f'(\overline{S})}{f(\overline{S})} - \frac{\gamma_2'(\overline{S})}{\gamma_2(\overline{S})} + \frac{\beta'(\overline{S})}{\beta(\overline{S})}\right)\left(\frac{f'(\overline{S})}{f(\overline{S})} - \frac{\gamma_2'(\overline{S})}{\gamma_2(\overline{S})}\right)^{-1}. \tag{5.37}$$

This equation is analysed in great detail in [4, Section XI.2]. The most relevant information is summarized in Figure 1, where α_1 and α_2 are considered as free parameters. Since in the case of (5.37) $\alpha_1 < 0$, we can infer from Figure 1 that destabilization occurs if α_2 becomes sufficiently negative. We already know that this cannot happen if β is proportional to γ_2 and f is decreasing. Reassuringly we find that $\alpha_2 > 0$ in this case. The condition that α_2 be sufficiently negative translates, in fact, again into the requirement that the conversion efficiency increases rapidly with S near $\overline{S}$. The extra information we now have is that destabilization is indeed possible and that $\pi/2 < \omega < \pi$ (see Figure 1), which means that the period of the limit cycle is at its 'birth' by Hopf bifurcation between two and four times the juvenile delay $\overline{\tau}$, just as it is in Nicholson's blowfly model of Gurney *et al* [11], also see Thieme [39, Section 16].

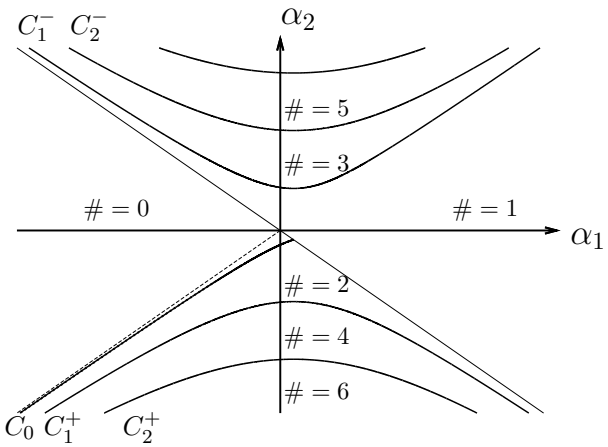

Fig. 1 The equation (5.36) has a real root $\lambda = 0$ along the line $\alpha_2 = -\alpha_1$ and purely imaginary roots along the curves C_0 and $C_k^{\pm}$. The numbers "# =" indicate the number of roots in the right half plane. So C_0 is the stability boundary. Along the curve C_0 ω increases from 0 at the starting point on the line $\alpha_2 = -\alpha_1$ to $\omega = \pi/2$ where C_0 intersects the negative α_2-axis to π in the limit where C_0 touches the line $\alpha_2 = \alpha_1$.

The information about how the position of the roots of (5.36) depends on the two parameters α_1 and α_2 can be used to deduce biologically interpretable

conclusions by exploiting the explicit expression (5.37). For example, if we choose

$$g(S) = g_0, \quad \gamma_2(S) = \theta S, \quad f(S) = D, \quad \beta(S) = \varphi S - \nu \text{ and } \mu_1 = \mu_2 = \mu,$$

then we have that by the inverse transformation

$$\mu\overline{\tau} = -\alpha_1, \quad \nu\overline{\tau} = -\alpha_2 e^{-\alpha_1}.$$

Hence we can translate information from the third quadrant of Figure 1 to Figure 2. Figure 2 reveals that population cycles do occur when the loss rate of maintenance is large relative to the loss rate of mortality. Note that the

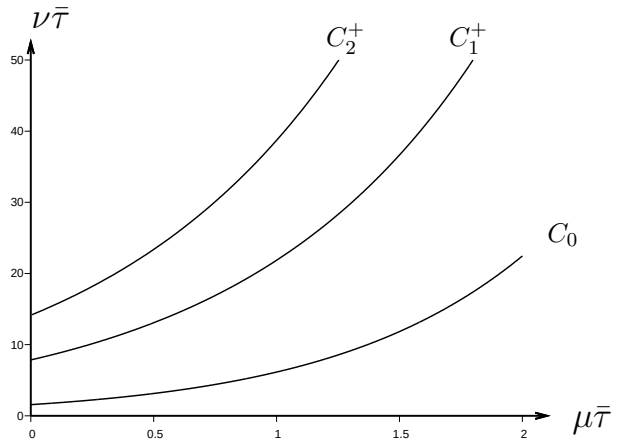

Fig. 2 Stability boundary in the $(\mu\overline{\tau}, \nu\overline{\tau})$-plane. C_0, C_1^+ and C_2^+ are the images of the corresponding curves in Figure 1. Note that along C_0, ω ranges from $\pi/2$ at the vertical axis to π at infinity.

quasi-steady state assumption potentially leads to the disappearance of cycles, as was indicated in [33, subsection 3.4 and Figure 8].

In [27], substrate growth is logistic, so f has a positive derivative for S not too large, and in that case both (5.24) and the model with fixed maturation delay do have a periodic attractor for suitable γ (resp. γ_2) and β. We conclude that the properties of a model with fixed delay to a large extent mimick those of unstructured models. In particular, oscillations are more easily generated by a Rosenzweig-MacArthur type bifurcation of classical prey-predator cycles than by a delayed negative feedback bifurcation. The latter one requires that the conversion efficiency depends rather strongly on the substrate concentration near the equilibrium value.

5.3.3 Substrate serves for growth, not for reproduction

The other extreme is that the birth rate β is independent of S. For consistency we now assume that the adults have a different (and constant) food source and

do not consume the substrate. So we have $\beta' = 0$ and $\gamma_2 = 0$. Note that the maturation delay is now variable, rather than fixed.

We now have

$$\overline{b} = \frac{\mu_1 \beta f(\overline{S})}{\gamma_1(\overline{S})(\beta - \mu_2)}, \qquad c_1 = 0, \qquad c_2 = f'(\overline{S}) - \frac{\gamma_1'(\overline{S}) f(\overline{S})}{\gamma_1(\overline{S})} \tag{5.38}$$

and the characteristic equation is given by

$$\left(1 - \frac{\mu_2}{\lambda + \mu_2} \mathrm{e}^{-\lambda \overline{\tau}}\right) \left(\lambda - f'(\overline{S}) + \frac{\gamma_1'(\overline{S})}{\gamma_1(\overline{S})} f(\overline{S}) - \frac{\mu_1 \mu_2 f(\overline{S})}{\beta - \mu_2} \frac{g'(\overline{S})}{g(\overline{S})} \frac{1 - \mathrm{e}^{-\lambda \overline{\tau}}}{\lambda}\right)$$
$$+ \frac{\beta - \mu_2 \mathrm{e}^{-\lambda \overline{\tau}}}{\lambda + \mu_1} \frac{\mu_1 f(\overline{S})}{\beta - \mu_2} \frac{g'(\overline{S})}{g(\overline{S})} \left(1 - \mathrm{e}^{-\lambda \overline{\tau}}\right) \left(\frac{\mu_1}{\lambda} + \frac{\mu_2 - \mu_1}{\mu_2 + \lambda}\right) = 0. \tag{5.39}$$

We now take the drastic step once again and delete λ in the second factor. If we multiply the reduced equation with $\lambda + \mu_2$, reorganise a bit, and scale λ with a factor $\overline{\tau}$, we obtain

$$\lambda + \alpha_1 \left(1 - \mathrm{e}^{-\lambda}\right) + \alpha_2 \frac{1 - \mathrm{e}^{-\lambda}}{\lambda} = 0 \tag{5.40}$$

with

$$\begin{aligned} \alpha_1 &= \overline{\tau} \mu_2 - \frac{\alpha_2}{\overline{\tau}(\beta - \mu_2)}, \\ \alpha_2 &= \mu_1 \mu_2 \overline{\tau}^2 \frac{g'(\overline{S})}{g(\overline{S})} \frac{\gamma_1(\overline{S}) f(\overline{S})}{\gamma_1'(\overline{S}) f(\overline{S}) - \gamma_1(\overline{S}) f'(\overline{S})}. \end{aligned} \tag{5.41}$$

If we substitute $\lambda = i\omega$ into (5.40), split into real and imaginary part, and solve for (α_1, α_2) we obtain

$$\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} = \frac{1}{2} \begin{pmatrix} -\omega \frac{\cos(\omega/2)}{\sin(\omega/2)} \\ \omega^2 \end{pmatrix}. \tag{5.42}$$

Here we should keep in mind that

$$\overline{\tau} = \frac{\ln \beta - \ln \mu_2}{\mu_1} \qquad \left(\Leftrightarrow \quad \mu_1 \overline{\tau} = \ln \frac{\beta}{\mu_2}\right) \tag{5.43}$$

and

$$\overline{S} = g^{-1} \left(\frac{\xi_A - \xi_b}{\overline{\tau}}\right). \tag{5.44}$$

Let us now concentrate on the special case

$$g(S) = g_0 S, \qquad \gamma_1(S) = \theta S, \qquad f(S) = D - \varepsilon S \tag{5.45}$$

so that

$$\frac{g'(\overline{S})}{g(\overline{S})} \frac{\gamma_1(\overline{S}) f(\overline{S})}{\gamma_1'(\overline{S}) f(\overline{S}) - \gamma_1(\overline{S}) f'(\overline{S})} = 1 - \varepsilon \frac{\overline{S}}{D}$$

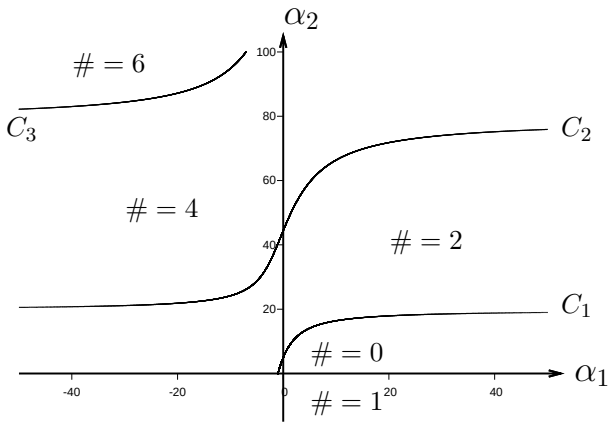

Fig. 3 Stability boundary in the (α_1, α_2)-plane (labelled by C_1) and two more Hopf curves, labelled C_2 and C_3. Numbers "# =" refer to roots in the right half plane.

with

$$\overline{S} = \frac{1}{g_0} \frac{\xi_A - \xi_b}{\overline{\tau}}.$$

It follows that

$$\begin{aligned} \alpha_1 &= \frac{\mu_2}{\mu_1} \ln \frac{\beta}{\mu_2} - \frac{\alpha_2}{\frac{\mu_2}{\mu_1}\left(\frac{\beta}{\mu_2} - 1\right) \ln \frac{\beta}{\mu_2}}, \\ \alpha_2 &= \frac{\mu_2}{\mu_1} \left(\ln \frac{\beta}{\mu_2}\right)^2 \left(1 - \varepsilon \frac{\overline{S}}{D}\right). \end{aligned} \tag{5.46}$$

from which we see that there are three dimensionless parameter combinations that play a role: $\frac{\mu_1}{\mu_2}$, $\frac{\beta}{\mu_2}$, $\varepsilon\frac{\overline{S}}{D}$. If we restrict the attention to $\mu_1 = \mu_2$ only $\frac{\beta}{\mu_2}$ and $\varepsilon\frac{\overline{S}}{D}$ remain. The boundary in parameter space of the region in which the steady state exists is characterized by $\frac{\beta}{\mu} = 1$ or $\varepsilon\frac{\overline{S}}{D} = 1$. If we substitute the stability boundary given by (5.42) into (5.46), it is possible to solve numerically for $\frac{\beta}{\mu}$ and $\varepsilon\frac{\overline{S}}{D}$. As a next step we may then express the result in the primary mechanistic parameters $\frac{\beta}{\mu}$ and $\frac{\varepsilon(\xi_A - \xi_b)\mu}{g_0 D} = \varepsilon\frac{\overline{S}}{D} \ln \frac{\beta}{\mu}$. Note that Figure 4 gives, at just a glance, more information about (in)stability of the steady state than the information presented in [15].

We conclude that a fluctuating length of the juvenile period such that the rate of growing up is negatively related to the juvenile density may on its own lead to cycles. Of course this conclusion is not new (e.g. [10]) but is mathematically rather more neatly brought out by our present calculations.

5.4 Bistability in both reality and a more complex stage structured model

After the finishing of this paper a beautiful paper by McCauley et al appeared [26] in which a generalisation of the stage structured model of this section was

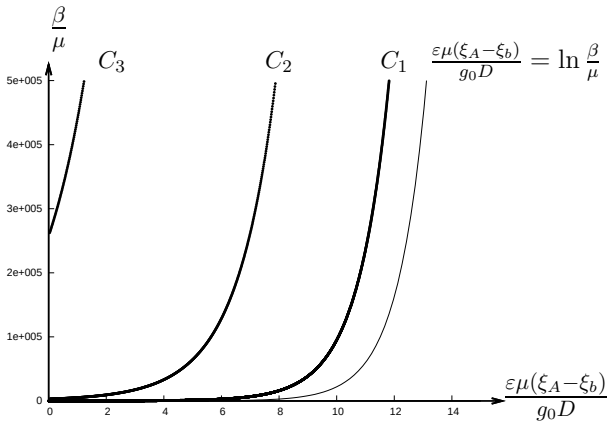

Fig. 4 Stability boundary in the $(\frac{\varepsilon\mu(\xi_A-\xi_b)}{g_0 D}, \frac{\beta}{\mu})$-plane. C_2 and C_3 are the images of the corresponding two curves in Figure 3. Along the stability boundary C_1 we have that $\pi/\overline{\tau} < \omega < 2\pi/\overline{\tau}$ and so the period of the oscillations is between one and two times the length of the juvenile period at their 'birth' by Hopf bifurcation.

analysed by different means. The authors frame their model as a system of delay-differential equations with variable delay, apply an implicit transformation of the time variable to arrive at a fixed delay and approximate the implicit equation for the probability to survive the juvenile period by a finite system of differential equations. The advantage of their technique is that they can then apply the recently developed bifurcation program DDE-BIFTOOLS that also allows them to follow limit cycles, including unstable ones, and their stability switches. (An even better feature of the paper is that the model results are compared with real experimental data, specifically obtained for the purpose!) It seems worth the effort to elaborate in detail the characteristic equation (3.3) for that model and next study it.

6 Numerical studies

In this section, we continue to investigate under what conditions density dependence in the maturation delay leads to population cycles. We do this by numerically determining when the characteristic equation (3.3) has a root exactly on the imaginary axis. In addition, we do some numerical simulations, using the Escalator Boxcar Train method (see [32]), to determine the direction of the Hopf-bifurcation.

We make the following choices for the ingredients of (5.5) and (5.6): The uptake of resources by adults is assumed to be proportional to the concentration of the substrate. The juveniles are assumed to spend a fraction $1-\alpha$ of their time on exploiting a fixed alternative food supply, denoted by A, and a fraction α on exploiting the substrate, leading to per capita uptake rates for adults and juveniles of $\gamma_2(S) = \theta S$ and $\gamma_1(S) = \alpha\theta S$, respectively. The growth rate of juveniles $g(S)$ is determined by their total resource uptake. Hence the

growth of juveniles is independent of the substrate when $\alpha = 0$ whereas juveniles completely depend on the substrate for their growth when $\alpha = 1$. In particular, $g(S)$ is given by $g(S) = g_0((1-\alpha)A+\alpha S)$, where g_0 is a conversion constant transforming food intake into growth/maturation. We allow for unequal mortality rates for the juveniles and adults, parametrised as $\mu_1 = q\mu$ and $\mu_2 = \mu$, respectively. The per capita reproduction rate is proportional to the per capita resource intake, $\beta(S) = \beta_0 S$. The dynamics of the substrate in the absence of consumers is given by $f(S) = D - \varepsilon S$. The number of parameters can be reduced by scaling. By a scaling of time, i-size, birth rate and S we fix the parameters μ, $\xi_A - \xi_b$, θ and D to 1. The other six parameters α, A, β_0, g_0, ε and q can vary. Hereafter the latter parameters will be referred to as the "free parameters". The relation between the scaled and unscaled parameters is indicated by denoting the unscaled parameter by the same symbol as the corresponding scaled parameter but equipped with a tilde.

$$
\begin{aligned}
&t = \mu\widetilde{t},\ \xi = \frac{\widetilde{\xi}}{\xi_A - \xi_b},\ b = \frac{\theta}{\mu^2}\widetilde{b},\ S = \frac{\mu}{D}\widetilde{S},\\
&\mu = 1, \xi_A - \xi_b = 1,\ \theta = 1, D = 1,\\
&\varepsilon = \frac{1}{\mu}\widetilde{\varepsilon},\ A = \frac{\mu}{D}\widetilde{A},\ \alpha = \widetilde{\alpha},\ g_0 = \frac{D}{\mu^2(\xi_A - \xi_b)}\widetilde{g_0},\ q = \widetilde{q},\ \beta_0 = \frac{D}{\mu^2}\widetilde{\beta_0}.
\end{aligned}
$$

The default values of the potentially free parameters are $\varepsilon = 0.1$, $A = 1$, $\alpha = 1$, $g_0 = 0.025$, $q = 0.1$ and $\beta_0 = 5.0$, when they are not varied.

We start our discussion by showing some simulation results. When varying the parameters we always observed two qualitatively different types of asymptotic behaviour, convergence to a steady state, illustrated in the left panel of Figure 6, and to periodic oscillations (population cycles), shown in the right panel of Figure 6.

Since there are six parameters ε, A, α, g_0, q and β_0, we have fifteen options for drawing one-dimensional stability boundaries. For $\alpha = 0$ we have a fixed maturation delay and model ingredients that fulfill the conditions for stability as derived in subsection 5.3.2. This indicates that larger values of α are required for population cycles and it makes α a good choice for one of the two free parameters.

Figure 5 shows numerically calculated stability boundaries for different values of ε in the (α, β_0)-plane (left panel of Figure 5) and for different values of β_0 in the (α, g_0)-plane (right panel of Figure 5). For the discussion we shall distinguish two qualitatively different types of boundaries, parabola-like ones, in which there is only one stability switch in the α-direction for all values of the second parameter, and boot-like ones in which there occur two such switches for increasing α. In the left panel of Figure 5, the cycle regions are boot-like for the lower ε-values, for higher values they are parabola-like. The instability regions shrink when ε becomes larger and have disappeared by the time that $\varepsilon = 0.25$. Population cycles are absent for sufficiently small α, with the stable region increasing with ε. This strongly suggests that the density dependence in maturation time brings about the qualitative change

of the dynamics, but that a delayed impact of this density dependence due to slow substrate dynamics is essential for cycles to occur, as also concluded by [33, subsection 3.4]. The other stability boundaries for different values of ε in the (α, β_0)-plane, of q in the (α, β_0)-plane, of ε in the (α, g_0)-plane and of q in (α, g_0)-plane show essentially the same features as in the left panel of Figure 5 (results not shown). This is also the case for different values of β_0 in the (α, g_0)-plane ($\beta_0 = 5.0$, $\beta_0 = 1.5$ and $\beta_0 = 1.15$, results also not shown). For these lower values of β_0, however, the instability region does not always provide a complete picture of the parameter combinations for which population cycles occur. Numerical studies reveal that population cycles occur for parameter combinations well into the stable region, in particular at the upper boundary of the parabola-like instability regions in the (α, g_0)-plane. This suggests that for these low values of β_0 the bifurcation at this particular part of the stability boundary is subcritical. Furthermore, for high values of β_0 ($\beta_0 = 10$ and $\beta_0 = 20$) two stability boundaries are found for the same value of β_0, corresponding to two different pairs of characteristic roots crossing the imaginary axis. These two stability boundaries suggest that different types of population cycles may branch of the equilibrium (see below).

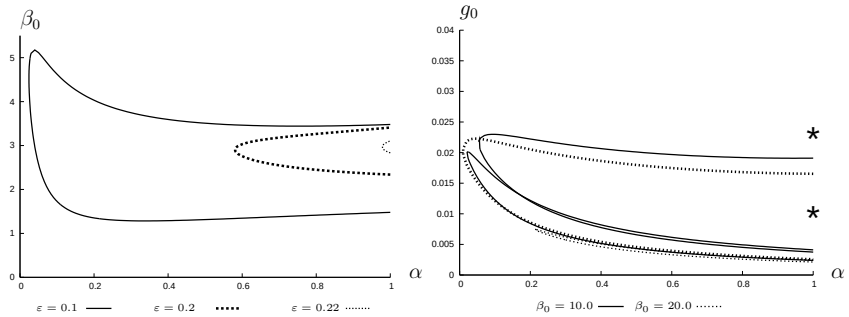

Fig. 5 Left panel: stability boundaries in the (α, β_0)-plane, α the relative dependence on the dynamic substrate, β_0 the conversion constant of food into offspring, for three different values of ε, the autonomous decay rate of the food; solid: $\varepsilon = 0.1$; dashed: $\varepsilon = 0.2$; dotted: $\varepsilon = 0.22$ ($A = 1$, $q = 0.1$ and $g_0 = 0.025$). The cycle region shrinks and eventually vanishes as ε increases. When ε is large population cycles are not induced for small α (that is, when juveniles are weakly dependent on the substrate for their growth). For the lower ε-values the cycle regions are boot-like, for higher values they are parabola-like. Right panel: stability boundaries in the (α, g_0)-plane, g_0 the conversion constant transforming food into growth (maturation), for different values of β_0; solid $\beta_0 = 10$, dashed $\beta_0 = 20$ ($A = 1$, $q = 0.1$, $\varepsilon = 0.1$). For the same β_0 two different sets of purely imaginary roots of the characteristic equation are found.

Figure 6 shows the results of numerical simulations at the parameter values indicated by stars in the right panel of Figure 5. For $g_0 = 0.025$ the population density converges to the steady state via a long and somewhat complicated transient (left panel of Figure 6), corroborating that for the corresponding point in Figure 6 all characteristic roots indeed lie in the left half of the complex plane. The simulation results for $g_0 = 0.011$ exhibit an additional interesting

phenomenon (right panel of Figure 6). The population density first appears to approach the steady state in an oscillatory manner only to move off again to end up on a limit cycle with a different period. This saddle-like behaviour of the steady state can be tentatively understood from the stability diagram in Figure 5. From the fact that the parameter point under consideration is near the second stability boundary one may infer that the slowest submanifold of the stable manifold of the steady state is tangent to the eigenspace of the characteristic root that is about to pass through the imaginary axis. When g_0 is decreased this slowest submanifold links at the lower stability boundary to the center manifold containing the limit cycle. So in the oscillatory approach to the steady state one sees the ghost of the cycle that is about to branch of at the lower of the two stability boundaries. After having approached the steady state, the trajectory slowly diverges along the unstable manifold that brings it to the limit cycle springing from the Hopf-bifurcation on the upper stability boundary.

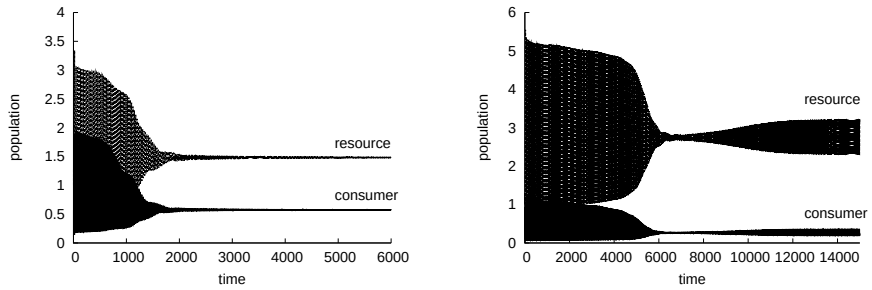

Fig. 6 Numerical simulation results for $A = 1$, $\alpha = 1$, $\beta_0 = 10$, $\varepsilon = 0.1$ and $q = 0.1$. Left: $g_0 = 0.025$. The steady state is approached via a complicated transient. Right: $g_0 = 0.011$. The population density initially approaches the steady state, but eventually ends up cycling.

The main computational results can be summarized as follows. Population cycles occur for parameters within the region of instability of the equilibrium, but cycles may also occur for parameter values for which the equilibrium is locally stable. All instability regions are bounded in the free parameters whenever α is chosen as one of the two parameters. In other words, population cycles can occur only if β_0, g_0 or q are assigned intermediate values. The occurrence of population cycles depends more strongly on α when q and ε are large. The shapes of stability boundaries can be classified into two types. One type are parabola-like curves while another type are boot-like ones. Population cycles are likely not to be induced for small α when the stability boundary is parabola-like. In contrast, population cycles occur even though α is small when the stability boundary is boot-like.

Our numerical results are to a large extent congruent with those presented in [33] for a similar model, which however assumed death rates to depend on substrate density. In [33, subsection 3.2] two broad classes of population cycles were distinguished, referred to as juvenile- and adult-driven cycles, re-

spectively, which occurred when either juveniles or adults had a larger impact on resource levels and hence on population dynamics. The type of population cycles found in our model resemble juvenile-driven cycles, most likely because in our model juveniles are more dominant than adults due to their smaller death rate. In [33] it was shown that juvenile-driven cycles disappear in case of fast substrate dynamics, which is in agreement with our finding that the instability region shrinks for larger values of ε. Furthermore, in [33] two types of juvenile-driven cycles were distinguished on the basis of the ratio between the cycle period and the maturation delay: type I cycles are characterized by a period that is by and large equal to the maturation delay, while type II cycles have a period by and large half that value. The two unstable regions in the right panel of Figure 5 correspond to the occurrence of these two types of juvenile-driven cycles over a considerable range of g_0. By numerical simulations for $\beta_0 = 10$ and $\alpha = 0.2$ we found large-amplitude cycles with a cycle period roughly equal to the maturation delay in the lower of the two instability regions, whereas small-amplitude cycles with a period equal to half the maturation delay occur in the upper unstable region (results not shown). Hence for each β_0, the upper and lower cycle regions are characterized by juvenile-driven type I and type II, respectively.

Juvenile-driven cycles are characterized by the appearance of dominant cohorts in the populations [33]. The birth of such a dominant cohort reduces the resource substantially, leading to retarded growth and dwindling reproduction. Not until the dominant cohort has decreased in abundance due to mortality can resource densities recover again and can a new pulse of offspring be produced. This offspring immediately reduces the resource level and the cycle repeats itself. According to [33], juvenile-driven type I cycles are characterized by a high mean resource density, a short juvenile period, high survival till maturation and a low ratio between juvenile and adult peak densities. Moreover adults have a very short life expectancy and a low fecundity. By comparing two stability boundaries for $\beta_0 = 10$ and $\beta_0 = 20$ we find that the cycle region of juvenile-driven type I for $\beta_0 = 20$ is smaller than that for $\beta_0 = 10$. This observation agrees well with the fact that juvenile-driven type I cycle are likely to occur when adult fecundity is low. Another qualitative difference between juvenile-driven type I and II cycles is that for type I cycles non-negligible quantities of adults are only present in the population during short bouts of time right after maturation of the dominant cohort, whereas for type II cycles adults are always present in the population in non-negligible quantities [33]. According to our numerical computations, qualitative change of population cycles from type I to type II may occur when the resource availability α or the growth speed g_0 cross the boundary between two cycle regions. In particular for $\beta_0 = 10$, this kind of qualitative change can occur for almost all values of α when the growth speed g_0 increases. Hence the growth rate of juveniles may influence the qualitative features of the size distribution. Note that this kind of qualitative change can occur as well when juveniles become less competitive, see [33, Figures 5 and 6].

7 The Kooijman-Metz Model

The modern theory of Dynamic Energy Budget models [18] has its roots in the Kooijman-Metz *Daphnia* model [19], that was designed to extrapolate data on the effect of toxic substances from lab experiments to field situations, with due attention to the various possibilities for the underlying physiological mechanisms (does the chemical impede food uptake, maintenance, growth, survival or reproduction?). In [34] the same model was used to study the ecological implications for prey-predator interaction of delayed maturation of the predator. In that analysis a characteristic equation (equation 17) figured prominently. The aim of this section is to check that equation (3.3) in the present paper translates to (17a) in [34] if we choose ξ, g, μ, β, γ and f in accordance with the Kooijman-Metz model.

While comparing the present formulation with that of [34] one runs into notational problems, as the same symbol may be used in both papers, but with a different meaning. Our strategy is to give the present notation priority and to provide symbols from [34] with an index 0 in case of conflict (this applies in particular to ξ, β, γ and f).

The Kooijman-Metz model also specifies individual behaviour under starvation conditions. For populations close to steady state, such conditions never arise. Therefore we omit this part of the model specification in our description here. We collect a number of observations that will facilitate the comparison

This paper	functional form interpretation	reference [34]
ξ	length	ℓ
S	algal concentration	x
g	$\gamma_0(\ell_m f_0(S) - \xi)$	g
μ	constant	d
β	$r_m f_0(S)\xi^2$	b
γ	$\nu f_0(S)\xi^2$	I
f	$\alpha(S_{max} - S)$ or $\beta_0 S\left(1 - \frac{S}{S_{\max}}\right)$	R
	$\frac{\xi_0 S}{1+\xi_0 S}$: functional response to prey density	f_0

Table 1 The Kooijman-Metz model

of (3.3) (with (3.5)–(3.8) and (4.31), (4.32) as specification of c and k) and (17a) (with (17b)–(17e) as specification of the matrix components).

(i) Since the death rate is constant, $L \equiv 0$, cf. (4.12).

(ii) Since g is linear in ξ and linear in $f_0(S)$,

$$K(\tau, \alpha) = e^{-\gamma_0(\tau-\alpha)}\gamma_0 \ell_m f_0'(\overline{S}), \quad cf.\,(4.5). \tag{7.1}$$

(iii) From (3.7) we deduce that

$$c_1 = \overline{b} r_m f_0'(\overline{S}) \int_{\overline{\tau}}^{\infty} \overline{\xi}^2(a)\overline{\mathcal{F}}(a)da$$

but since (2.13) (which is (11a) in [34]) amounts to

$$1 = r_m f_0(\overline{S}) \int_{\overline{\tau}}^{\infty} \overline{\xi}^2(a)\overline{\mathcal{F}}(a)da$$

this may be rewritten in the form

$$c_1 = \overline{b}\frac{f_0'(\overline{S})}{f_0(\overline{S})}. \tag{7.2}$$

Likewise we deduce from (2.14) and (3.8) that

$$c_2 = f'(\overline{S}) - f(\overline{S})\frac{f_0'(\overline{S})}{f_0(\overline{S})}. \tag{7.3}$$

(iv) Directly from (3.5) and (3.6) we obtain

$$k_{11}(a) = r_m f_0(\overline{S})\overline{\xi}^2(a)e^{-\mu a}H(a-\overline{\tau}), \tag{7.4}$$

$$k_{21}(a) = -\nu f_0(\overline{S})\overline{\xi}^2(a)e^{-\mu a}. \tag{7.5}$$

(v) From (4.31) and (4.32) we deduce

$$\begin{aligned} k_{12}(a) =& 2\overline{b}r_m f_0(\overline{S})\gamma_0\ell_m f_0'(\overline{S})e^{-(\gamma_0+\mu)a}\int_{\max\{0,\overline{\tau}-a\}}^{\infty}\overline{\xi}(a+\theta)e^{-\mu\theta}d\theta \\ &+ \chi_{[0,\overline{\tau}]}(a)\overline{b}\frac{r_m f_0(\overline{S})\xi_A^2 e^{-\mu\overline{\tau}}}{\gamma_0(\ell_m f_0(\overline{S})-\xi_A)}\gamma_0\ell_m f_0'(\overline{S})e^{-\gamma_0 a}, \end{aligned} \tag{7.6}$$

$$k_{22}(a) = -2\overline{b}\nu f_0(\overline{S})\gamma_0\ell_m f_0'(\overline{S})e^{-(\gamma_0+\mu)a}\int_0^{\infty}\overline{\xi}(a+\theta)e^{-\mu\theta}d\theta. \tag{7.7}$$

(vi) By solving

$$\frac{d\overline{\xi}}{da} = g(\overline{\xi},\overline{S}), \quad \overline{\xi}(0) = \xi_b,$$

we obtain

$$\overline{\xi}(a) = \ell_m f_0(\overline{S}) - (\ell_m f_0(\overline{S}) - \xi_b)e^{-\gamma_0 a} \tag{7.8}$$

from which we see that (cf. (11c) in [34])

$$\overline{a} = \frac{1}{\gamma_0}\log\left(\frac{\ell_m f_0(\overline{S})-\xi_b}{\ell_m f_0(\overline{S})-\xi_A}\right). \tag{7.9}$$

The final verification that (3.3) is identical to (17) is now only a matter of computing Laplace transforms, which, in the case of k_{12} and k_{22} involves some changes of the order of integration. All expressions match. At this point the reader has two options: either believe us on our word or perform these final computations himself.

We refer to the original paper [34] for an account of the ecological insights that can be obtained by analysing the Kooijman-Metz model.

8 A summary in recipe form

Each of the steps below can be performed either by writing a subroutine that performs the required calculation numerically or (in special cases) analytically in the form of a mathematical formula.

Part 1: Model formulation and finding steady states

Step 1:

specify the individual growth rate g and the per capita death rate μ as a function of size ξ and food concentration S

Step 2:

specify the size at birth ξ_b

for constant S solve, or write an algorithm to solve,

$$\frac{d\xi}{da} = g(\xi, S), \quad \xi(0) = \xi_b,$$
$$\frac{dF}{da} = -\mu(\xi, S)F, \quad F(0) = 1$$

Step 3:

specify the per capita rate of giving birth β as a function of size ξ and food concentration S

Step 4:

solve (2.13)

Step 5:

specify the per capita consumption rate γ as a function of size ξ and food concentration S

specify the rate f of change in S in the absence of consumers

compute the steady population birth rate according to (2.14)

Step 6:

calculate the steady state size-age relation and survival probabilities by substituting the value of S found in Step 4 into the results from Step 2 (cf. (2.15), (2.16))

Part 2: Determining the stability of steady states

Step 1:

define c_1, c_2, k_{11}, k_{21} by (3.5)–(3.8)

Step 2:

define K by (4.5) and L by (4.12)

define k_{12} and k_{22} by (4.31) and (4.32) [note the simplification (4.14), (4.15) for a smooth juvenile-adult transition]

Step 3:

take Laplace transforms of k_{ij}

Step 4:

consider the characteristic equation (3.3):

if at least one root has $\Re\lambda > 0$ then the steady state is unstable

if all roots satisfy $\Re\lambda < 0$ then the steady state is stable

Part 3: Parameter studies

Step 1:
substitute $\lambda = i\omega$ into the characteristic equation (3.3)
select two parameters (start with those that lead to relatively simple calculations)
solve for these parameters as a function of ω
draw stability boundaries (cf. Figures 3, 4 and 5)
Step 2, 3,...:
repeat Step 1, but with another choice of (one or both of the) two parameters

We refer to [17,31] for suggestions concerning the numerical implementation of the computation of (the Laplace transforms of) the kernels k_{ij}. A new edition of the former paper, employing the delay framework of the present paper, is submitted [35].

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Appendix: Derivation of (5.27)

We rewrite the explicit expressions of $\widehat{k}_{ij}(i\omega)$ and c_i $(i,j = 1,2)$ under the assumption (5.26).

$$\begin{aligned}
\widehat{k}_{11}(i\omega) &= \cos\varphi e^{-i(\omega\tau+\varphi)},\\
\widehat{k}_{12}(i\omega) &= -\bar{b}\mu\frac{g'}{g}\frac{1-\cos\omega\tau}{\omega}i + \bar{b}\mu\frac{g'}{g}\frac{\sin\omega\tau}{\omega},\\
\widehat{k}_{21}(i\omega) &= -\frac{\gamma}{\mu}\cos\varphi e^{-i\varphi},\\
\widehat{k}_{22}(i\omega) &= 0.
\end{aligned}$$

The real part of the characteristic equation (5.23) can be rewritten as

$$\begin{aligned}
&c_1\frac{\gamma}{\mu}\cos^2\varphi - c_2 + c_2\cos\varphi\cos(\omega\tau+\varphi) - \omega\cos\varphi\sin(\omega\tau+\varphi)\\
&-\bar{b}\gamma\frac{g'}{g}\cos\varphi\left\{\frac{\sin\varphi}{\omega} - \frac{\sin(\omega\tau+\varphi)}{\omega}\right\} = 0.
\end{aligned} \tag{A.1}$$

In the same way, the imaginary part of (5.23) can be written as

$$\begin{aligned}
&-c_1\frac{\gamma}{\mu}\cos\varphi\sin\varphi + \omega - c_2\cos\varphi\sin(\omega\tau+\varphi) - \omega\cos\varphi\cos(\omega\tau+\varphi)\\
&+\bar{b}\gamma\frac{g'}{g}\cos\varphi\left\{-\frac{\cos\varphi}{\omega} + \frac{\cos(\omega\tau+\varphi)}{\omega}\right\} = 0.
\end{aligned} \tag{A.2}$$

Equations (A.1) and (A.2) read in matrix form:

$$\mathbf{A}(\omega)\begin{bmatrix}\cos(\omega\tau+\varphi)\\ \sin(\omega\tau+\varphi)\end{bmatrix}=\mathbf{b}(\omega), \tag{A.3}$$

where $\mathbf{A}(\omega)=[a_{ij}(\omega)]_{i,j=1,2}$ and $\mathbf{b}(\omega)=[b_j(\omega)]_{j=1,2}$ are given by

$$\mathbf{A}(\omega)=\begin{pmatrix} c_2\cos\varphi & -\omega\cos\varphi+\bar{b}\gamma\frac{g'}{g}\frac{\cos\varphi}{\omega}\\ -\omega\cos\varphi+\bar{b}\gamma\frac{g'}{g}\frac{\cos\varphi}{\omega} & -c_2\cos\varphi\end{pmatrix}$$

and

$$\mathbf{b}(\omega)=\begin{pmatrix} -c_1\frac{\gamma}{\mu}\cos^2\varphi+c_2+\bar{b}\gamma\frac{g'}{g}\cos\varphi\frac{\sin\varphi}{\omega}\\ c_1\frac{\gamma}{\mu}\cos\varphi\sin\varphi-\omega+\bar{b}\gamma\frac{g'}{g}\frac{\cos^2\varphi}{\omega}\end{pmatrix},$$

Note that $a_{11}(\omega)=-a_{22}(\omega)$ and $a_{12}(\omega)=a_{21}(\omega)$. If $c_2=0$, then both $\mathbf{A}(\omega)$ and $\mathbf{b}(\omega)$ are zero for $\omega^2=\bar{b}\gamma g'/g$ if $c_1=\bar{b}g'/g$ and we conclude that in this case the characteristic equation has a root $i\omega$. If

$$\det[\mathbf{A}(\omega)]=-(a_{11}^2+a_{12}^2)=-\cos^2\varphi\left\{c_2^2+\left(\omega-\bar{b}\gamma\frac{g'}{g}\frac{1}{\omega}\right)^2\right\}\neq 0,$$

we find by solving (A.3)

$$\cos(\omega\tau+\varphi)=\frac{a_{11}(\omega)b_1(\omega)+a_{12}(\omega)b_2(\omega)}{a_{11}^2(\omega)+a_{12}^2(\omega)},$$
$$\sin(\omega\tau+\varphi)=\frac{a_{12}(\omega)b_1(\omega)-a_{11}(\omega)b_2(\omega)}{a_{11}^2(\omega)+a_{12}^2(\omega)}.$$

Since $\cos^2(\omega\tau+\varphi)+\sin^2(\omega\tau+\varphi)=1$, $a_{ij}(\omega)$ and $b_j(\omega)$ must satisfy

$$(b_1^2(\omega)+b_2^2(\omega))-(a_{11}^2(\omega)+a_{12}^2(\omega))=0.$$

By using the relation

$$\frac{\cos\varphi}{\mu}=\frac{\sin\varphi}{\omega},$$

$b_1(\omega)$ is rewritten as

$$b_1(\omega)=\frac{\gamma}{\mu}\left(\bar{b}\frac{g'}{g}-c_1\right)\cos^2\varphi+c_2.$$

Since $\cos^2\varphi+\sin^2\varphi=1$, $b_2(\omega)$ is rewritten as follows.

$$b_2(\omega)=-\frac{\gamma}{\mu}\left(\bar{b}\frac{g'}{g}-c_1\right)\cos\varphi\sin\varphi-\omega+\bar{b}\gamma\frac{g'}{g}\frac{1}{\omega}.$$

For convenience of computation, we introduce d_1 and d_2 by

$$d_1=\frac{\gamma}{\mu}\left(\bar{b}\frac{g'}{g}-c_1\right)\text{ and }d_2=-\omega+\bar{b}\gamma\frac{g'}{g}\frac{1}{\omega}.$$

Straightforward calculation yields that

$$
\begin{aligned}
&(b_1^2(\omega) + b_2^2(\omega)) - (a_{11}^2(\omega) + a_{12}^2(\omega)) \\
&= (d_1 \cos^2\varphi + c_2)^2 + (-d_1 \cos\varphi \sin\varphi + d_2)^2 - (c_2 \cos\varphi)^2 - (d_2 \cos\varphi)^2 \\
&= (d_1 \cos\varphi - d_2 \sin\varphi)^2 + c_2^2 \sin^2\varphi + 2 d_1 c_2 \cos^2\varphi \\
&= \frac{1}{\mu^2 + \omega^2} \left\{ (d_1\mu - d_2\omega)^2 + c_2^2\omega^2 + 2 d_1 c_2 \mu^2 \right\} \\
&= \frac{1}{\mu^2 + \omega^2} \left\{ (\omega^2 - \gamma c_1)^2 + c_2^2\omega^2 + 2\gamma\mu c_2 \left(\bar{b}\frac{g'}{g} - c_1 \right) \right\}.
\end{aligned}
$$

Hence we obtain (5.27) as a necessary condition for the possibility that the characteristic equation has a root $i\omega$.

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