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On periodic cohort solutions of a size-structured population model

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Abstract. We consider a size-structured population model with discontinuous reproduction and feedback through the environmental variable 'substrate'. The model admits solutions with finitely many cohorts and in that case the problem is described by a system of ODEs involving a bifurcation parameter β. Existence of nontrivial periodic n-cohort solutions is investigated. Moreover, we discuss the question whether n cohorts ($n \geq 2$) with small size differences will tend to a periodic one-cohort solution as $t \to \infty$.

Key words: Size-structured populations – Discontinuous reproduction – Variable environment – Periodic cohort solutions – Stability

1. Introduction

Reproduction is an event in the life of individuals. When there is quite some variation in the individual states at which such events occur, a formal appeal to the law of large numbers allows one to model reproduction by rates at the population level. When reproduction occurs upon reaching a specified individual state, one can still work with rates at the population level provided the distribution of the population with respect to individual state is smooth (i.e. absolutely continuous). However, when 'giving birth' is restricted to specific individual states and, in addition, the population is concentrated in some (moving) individual states, reproduction is an event even at the population level. The aim of this paper is to initiate the study of models incorporating these two features.

We consider a size-structured population model of this type, i.e. the state of an individual is characterised by its size. The individuals are born at size x_α, and when they reach size x_ω ($x_\omega > x_\alpha > 0$), they produce k offspring of size x_α and die (or, equivalently, split into k equal parts). There is feedback through the environment, i.e. the growth rate g depends on the food density S. The mortality rate μ is assumed to be a positive constant. Some information on suicide reproduction can be found in [5], and size-structured population models with binary fission into two equal or unequal parts are analysed in [6], [5], [4] and [3], for example.

We are interested in the special case that the population consists of finitely many cohorts. A cohort refers to a group of individuals of exactly the same state (i.e. size in the present context) and is mathematically described by a measure concentrated in a point, i.e. a Dirac measure. The underlying biology of single cohort solutions is very simple and therefore such models come natural to the biological mind. In models with sharply pulsed reproduction such as models for fish populations the population tends to be composed of distinguishable cohorts and periodic one-cohort solutions might be the dominating feature of the dynamics; cf. [7]. The full problem is described by an abstract renewal equation with a measure on $[x_\alpha, x_\omega)$ as initial condition and a feedback law (cf. the 'cumulative' formulation of [1] and [2]), but in the case of finitely many cohorts it reduces to a system of coupled ordinary differential equations. If we start with n cohorts, we shall have n cohorts all the time. Let N_i denote the population number of cohort i and x_i the corresponding size. In the case of n cohorts the model equations read

$$\begin{cases} \dfrac{dN_i}{dt} = -\mu N_i, \quad i = 1, \dots, n, \\ \dfrac{dx_i}{dt} = g(S, x_i), \quad i = 1, \dots, n, \\ \dfrac{dS}{dt} = h(S, \beta) - \displaystyle\sum_{i=1}^{n} \gamma(S, x_i) N_i \\ + \text{ initial conditions and jumps in } N_i \text{ and } x_i \text{ at times } t \\ \text{such that } x_i(t) = x_\omega \text{ for some } i. \end{cases} \tag{1.1}$$

The function h describes the dynamics of the unstructured variable S in the absence of a consumer, and γ is the consumption rate. We want to study the asymptotic behaviour and, in particular, the existence and stability of periodic n-cohort solutions. This behaviour might change if certain parameters in the model equations are varied. We assume that the function h also depends on a scalar parameter β that will be the bifurcation parameter for our problem. The following assumptions on the functions g, h and γ are used throughout this paper:

(H_g) $g \in C([0, \infty) \times [x_\alpha, x_\omega]; \mathbb{R})$, for each $x \in [x_\alpha, x_\omega]$ there exists an $S_x \geq 0$ such that $g(S, x) > 0$ for $S > S_x$ and $g(S, x) = 0$ for $0 \leq S \leq S_x$, g is decreasing in x, strictly increasing in S on $[S_x, \infty)$ for all $x \in [x_\alpha, x_\omega]$ and twice continuously differentiable at those (S, x) for which $g(S, x) > 0$.

(H_h) $h \in C^1([0, \infty) \times (0, \infty); \mathbb{R})$, h is strictly increasing in β, for each $\beta > 0$ there exists a unique $\tilde{S}_\beta > 0$ such that $h(\tilde{S}_\beta, \beta) = 0$ and $\frac{\partial h}{\partial S}(\tilde{S}_\beta, \beta) =: -d_\beta < 0$.

(H_γ) $\gamma \in C^1([0, \infty) \times [x_\alpha, x_\omega]; \mathbb{R})$, $\gamma(0, x) = 0$ for $x \in [x_\alpha, x_\omega]$ and $\gamma > 0$ elsewhere, γ is increasing in S and x.

Moreover, we consider only values of β for which

$(\mathrm{H}_\beta)\quad \tilde{S}_\beta > S_{x_\omega}$.

The typical growth rates we have in mind are the so-called growth rates of von Bertalanffy type (cf. [6, p. 22] and [5], for example)

$$g(S,x) = c(f(S) - x)^+, \tag{1.2}$$

where $c > 0$, $z^+ := \max(0,z)$, f is a continuously differentiable, strictly increasing function of S with $f(0) = 0$ and $\lim_{S\to\infty} f(S) > x_\omega$, and x is of dimension 'length'. In this case we have $S_x = f^{-1}(x)$, and there is no growth if food becomes too scarce. The condition (H_h) implies that a larger value of β favours the abundance of food. We have $h(S,\beta) > 0$ for $0 < S < \tilde{S}_\beta$, $h(S,\beta) < 0$ for $S > \tilde{S}_\beta$ and $\tilde{S}_\beta$ is strictly increasing in β. Moreover, $\tilde{S}_\beta$ is the only stable biologically meaningful (i.e. nonnegative) equilibrium of S for fixed β in the absence of a consumer. Typical examples are $h(S,\beta) = \beta - S$ (constant inflow of fresh, nonreproducing food particles combined with a constant food deterioration) and $h(S,\beta) = S(1 - S/\beta)$ (logistic growth). The assumption (H_γ) reflects some biologically intuitive facts: if food is more abundant, more can be consumed (and in particular there cannot be any consumption in the absence of food), and larger individuals consume more. The condition (H_β) ensures that size x_ω is reached under the food conditions $S \equiv \tilde{S}_\beta$; otherwise size x_ω would never be reached for initial data $S(0) \le \tilde{S}_\beta$ and the population would become extinct.

We consider n cohorts (that we assume to be arranged according to size; without loss of generality we can also assume that the first cohort is a cohort of newborns) and associate a mapping (discrete time dynamical system) with the ODE system. Let $n \in \mathbb{N}$, $\beta > 0$ with (H_β), $x_\alpha = x_{1,0} \le x_{2,0} \le \ldots \le x_{n,0} \le x_\omega$, $0 < S_0 \le \tilde{S}_\beta$, $N_{i,0} \ge 0$ for $i = 1,\ldots,n$, and solve the equations

$$\begin{cases} \dfrac{dx_i}{dt} = g(S,x_i), \quad x_i(0) = x_{i,0}, \quad i = 1,\ldots,n, \\ \dfrac{dS}{dt} = h(S,\beta) - \mathrm{e}^{-\mu t} \displaystyle\sum_{i=1}^{n} \gamma(S,x_i) N_{i,0}, \quad S(0) = S_0. \end{cases} \tag{1.3}$$

Remark 1.1. a) (H_h) implies that it is necessary to choose $S_0 \in (0,\tilde{S}_\beta]$ in order to possibly obtain a periodic solution.
b) We have to extend the mapping artificially to the case that the initial sizes can become x_ω in order to be able to deal with the degenerate case that $x_{i,0} = x_{i+1,0}$ for some i. In this case, as well as in the case where $N_{i,0} = 0$ for some i, we actually have less than n cohorts.

We define a mapping $F_n : \mathbb{R}^{2n} \to \mathbb{R}^{2n}$, $(S_0, N_{1,0}, \ldots, N_{n,0}, x_{2,0}, \ldots, x_{n,0}) \mapsto (S_0', N_{1,0}', \ldots, N_{n,0}', x_{2,0}', \ldots, x_{n,0}')$ as follows. Let $T = T(S_0, N_{1,0}, \ldots, N_{n,0}, x_{2,0}, \ldots, x_{n,0}) \ge 0$ be such that $x_n(T) = x_\omega$, $x_n(t) < x_\omega$ for $0 \le t < T$ (if $x_{n,0} = x_\omega$, we have $T = 0$), and set

$$\begin{cases} S_0' := S(T), \\ N_{1,0}' := k N_{n,0} \mathrm{e}^{-\mu T}, \\ N_{i,0}' := N_{i-1,0} \mathrm{e}^{-\mu T}, \quad i = 2,\ldots,n, \\ x_{i,0}' := x_{i-1}(T), \quad i = 2,\ldots,n. \end{cases} \tag{1.4}$$

T is well-defined because of assumptions (H_β), (H_h) and (H_γ), and we have $S_0' > 0$, $S_0' \in [S_{x_\omega}, \tilde{S}_\beta]$, $N_{i,0} \geq 0$ for $i = 1, \dots, n$ and $x_\alpha \leq x_{2,0}' \leq \dots \leq x_{n,0}' \leq x_\omega$. The iterates of F_n give the food density, population numbers and corresponding sizes of the cohorts at the instants of reproduction, and a periodic point of F_n thus corresponds to a periodic n-cohort solution.

Remark 1.2. Since the size growth is not necessarily strictly monotonous, the mappings F_n might have discontinuities if $S_0' = S_{x_\omega} > 0$, $\dot{S}(T-) < 0$. (If $S(T) = S_{x_\omega}$, $\dot{S}(T-) = 0$, then $\ddot{S}(T-) = \mu e^{-\mu T} \sum_{i=1}^n \gamma(S_{x_\omega}, x_i) N_{i,0} > 0$, i.e. S would have a local minimum at $t = T$ if there were no jumps, and this case is all right.)

In Sect. 2 the mapping F_1 is investigated. We assume that the trivial fixed point $(\tilde{S}_\beta, 0)$ becomes unstable at $\beta = 1$, and existence of a stable nontrivial fixed point of F_1 (resp. a periodic one-cohort solution of Eq. (1.1)) is proved for $1 < \beta < \beta_1$ for some $\beta_1 > 1$. In Sect. 3 a criterion is derived to determine whether for $1 < \beta < \beta_1$, β sufficiently close to 1, the iterations of F_2 will converge to the nontrivial fixed point $(\bar{S}_0(\beta), \bar{N}_0(\beta))$ of F_1 for $(S_0, N_{1,0} + N_{2,0}, x_{2,0})$ sufficiently close to $(\bar{S}_0(\beta), \bar{N}_0(\beta), x_\alpha)$, i.e. whether the periodic one-cohort solution is stable with respect to splitting into two cohorts. The same criterion applies to splitting into n cohorts for all $n \geq 2$, and the proof of this statement can be found in the Appendix. Moreover, local existence of nontrivial fixed points of F_n (i.e. periodic n-cohort solutions) is proved for $n \geq 2$. In Sect. 4 we present some numerical examples that show that both stability and instability of the fixed point of F_1 with respect to cohort splitting can occur in the case of linear growth rates (1.2).

2. The one-cohort problem

We consider now the special case $n = 1$, $F_1 =: F$, and we drop the indices. Let $\beta > 0$ be such that (H_β) is satisfied. We have to solve the coupled ODE system

$$\begin{cases} \dfrac{dx}{dt} = g(S, x), \quad x(0) = x_\alpha, \\ \dfrac{dS}{dt} = h(S, \beta) - N_0 e^{-\mu t} \gamma(S, x), \quad S(0) = S_0. \end{cases} \tag{2.1}$$

If $T = T(S_0, N_0) > 0$ is such that $x(T) = x_\omega$, $x(t) < x_\omega$ for $0 \leq t < T$, the mapping $F : (S_0, N_0) \mapsto (S_0', N_0')$ is given by

$$\begin{cases} S_0' := S(T), \\ N_0' := k N_0 e^{-\mu T}. \end{cases} \tag{2.2}$$

Remark 2.1. We have $T(S_0, N_0) > T(S_0, 0)$ for all $S_0 \in (0, \tilde{S}_\beta]$, $N_0 > 0$ (if there is no consumption, the food density is larger and consequently the individuals reach x_ω more quickly), and $S_0 \mapsto T(S_0, 0)$ is strictly decreasing on $(0, \tilde{S}_\beta]$. If

$$T(\tilde{S}_\beta, 0) \geq \frac{1}{\mu} \ln k,$$

we have $\lim_{t \to \infty} N(t) = 0$ and $\lim_{t \to \infty} S(t) = \tilde{S}_\beta$ for all choices of (S_0, N_0), and F has only the trivial fixed point $(S_0, N_0) = (\tilde{S}_\beta, 0)$.

Notation 2.2. We introduce the abbreviations

$$\tilde{T}_\beta := T(\tilde{S}_\beta, 0)$$

and

$$\bar{T} := \frac{1}{\mu} \ln k,$$

i.e. $\bar{T}$ is the time it takes to reduce the population number to one kth of its initial value if there is no reproduction. Note that $\tilde{T}_\beta$ is strictly decreasing in β.

Remark 2.3. a) If the food density is constant $S(t) \equiv S > S_{x_\omega}$, a population of newborns will reach size x_ω at time

$$\bar{t}(S) := \int_{x_\alpha}^{x_\omega} \frac{dx}{g(S,x)}.$$

The population will go extinct if $\bar{t}(S) < \bar{T}$ and increase unboundedly if $\bar{t}(S) > \bar{T}$. For $\bar{t}(S) = \bar{T}$ the number of offspring from the surviving members of an initial population N_0 is just N_0 and thus the population number is periodic with period $\bar{T}$. The hypothesis (H_g) implies that $\bar{t}$ is strictly decreasing on (S_{x_ω}, ∞) and therefore there exists at most one value S such that $\bar{t}(S) = \bar{T}$.
b) Remark 1.2 implies that discontinuities might occur if $S(T) = S_0' = S_{x_\omega} > 0$, $\dot{S}(T-) < 0$, i.e.

$$h(S_{x_\omega}, \beta) - N_0 \mathrm{e}^{-\mu T} \gamma(S_{x_\omega}, x_\omega) < 0$$

or

$$N_0 > \frac{\mathrm{e}^{\mu T}}{\gamma(S_{x_\omega}, x_\omega)} h(S_{x_\omega}, \beta).$$

Since $T > \tilde{T}_\beta$ for $N_0 > 0$, the mapping is in particular continuously differentiable (differentiability of ODE solutions with respect to initial conditions and parameters) in the neighbourhood of (S_0, N_0) with $S_0 \in (0, \tilde{S}_\beta]$ and

$$0 \leq N_0 \leq \frac{\mathrm{e}^{\mu \tilde{T}_\beta}}{\gamma(S_{x_\omega}, x_\omega)} h(S_{x_\omega}, \beta).$$

At the points where F is differentiable we have

$$\begin{cases} \dfrac{\partial S_0'}{\partial S_0} = \dfrac{\partial S}{\partial S_0}(T) + \dot{S}(T) \dfrac{\partial T}{\partial S_0}, \\ \dfrac{\partial S_0'}{\partial N_0} = \dfrac{\partial S}{\partial N_0}(T) + \dot{S}(T) \dfrac{\partial T}{\partial N_0}, \\ \dfrac{\partial N_0'}{\partial S_0} = -\mu \dfrac{\partial T}{\partial S_0} k \mathrm{e}^{-\mu T} N_0, \\ \dfrac{\partial N_0'}{\partial N_0} = -\mu \dfrac{\partial T}{\partial N_0} k \mathrm{e}^{-\mu T} N_0 + k \mathrm{e}^{-\mu T}. \end{cases}$$

We have to compute the eigenvalues of the Jacobi matrix of F in order to determine the stability of the trivial fixed point $(0, \tilde{S}_\beta)$. To this end we first evaluate the derivatives of x and S with respect to initial data and parameters at $(S_0, N_0) = (\tilde{S}_\beta, 0)$.

Lemma 2.4. *Let (x,S) be the solution of Eq. (2.1), and let $\bar{x}$ be the solution of*

$$\frac{d\bar{x}}{dt} = g(\bar{x},\tilde{S}_\beta), \quad \bar{x}(0) = x_\alpha.$$

Then we have at $(S_0,N_0) = (\tilde{S}_\beta,0)$

$$\frac{\partial S}{\partial S_0}(t) = \mathrm{e}^{-d_\beta t}, \tag{2.3}$$

$$\frac{\partial x}{\partial S_0}(t) = \int_0^t \exp\left(\int_\tau^t \frac{\partial g}{\partial x}(\tilde{S}_\beta,\bar{x}(\sigma))\,d\sigma\right)\frac{\partial g}{\partial S}(\tilde{S}_\beta,\bar{x}(\tau))\mathrm{e}^{-d_\beta\tau}\,d\tau, \tag{2.4}$$

$$\frac{\partial S}{\partial N_0}(t) = -\mathrm{e}^{-d_\beta t}\int_0^t \mathrm{e}^{(d_\beta-\mu)\tau}\gamma(\tilde{S}_\beta,\bar{x}(\tau))\,d\tau, \tag{2.5}$$

$$\frac{\partial x}{\partial N_0}(t) = \int_0^t \exp\left(\int_\tau^t \frac{\partial g}{\partial x}(\tilde{S}_\beta,\bar{x}(\sigma))\,d\sigma\right)\frac{\partial g}{\partial S}(\tilde{S}_\beta,\bar{x}(\tau))\frac{\partial S}{\partial N_0}(\tau)\,d\tau, \tag{2.6}$$

$$\frac{\partial S}{\partial \beta}(t) = \frac{1}{d_\beta}\frac{\partial h}{\partial \beta}(\tilde{S}_\beta,\beta)(1-\mathrm{e}^{-d_\beta t}), \tag{2.7}$$

$$\frac{\partial x}{\partial \beta}(t) = \int_0^t \exp\left(\int_\tau^t \frac{\partial g}{\partial x}(\tilde{S}_\beta,\bar{x}(\sigma))\,d\sigma\right)\frac{\partial g}{\partial S}(\tilde{S}_\beta,\bar{x}(\tau))\frac{\partial S}{\partial \beta}(\tau)\,d\tau. \tag{2.8}$$

Moreover we have at $(S_0,N_0) = (\tilde{S}_\beta,0)$

$$\frac{\partial T}{\partial \alpha} = -g(\tilde{S}_\beta,x_\omega)^{-1}\frac{\partial x}{\partial \alpha}(\tilde{T}_\beta) \tag{2.9}$$

for $\alpha = S_0$, N_0 and β.

Proof. Application of theorems about differentiability of ODE solutions with respect to initial data and parameters yields Eqs. (2.3)–(2.8), and by differentiating the relationship $x(T) = x_\omega$ we obtain Eq. (2.9). □

In particular the quantities (2.3)–(2.9) have the biologically obvious signs: the larger the initial value S_0, the larger S at later times (for $N_0 = 0$) and consequently the individuals grow more quickly; a larger value of the bifurcation parameter β has a similar effect, but setting the initial population to a small positive value (and thus adding consumption to the food dynamics) has the opposite effect.

The following lemma shows that the stability of the trivial fixed point of F is as we might expect from Remarks 2.1 and 2.3, a), i.e., the population will go extinct if the unexploited equilibrium food density $\tilde{S}_\beta$ is too small but that will not happen if $\tilde{S}_\beta$ is large enough.

Lemma 2.5. *The Jacobi matrix of F at the trivial fixed point $(S_0,N_0) = (\tilde{S}_\beta,0)$ reads*

$$(DF)(\tilde{S}_\beta,0) = \begin{pmatrix} \mathrm{e}^{-d_\beta\tilde{T}_\beta} & \frac{\partial S}{\partial N_0}(\tilde{T}_\beta) \\ 0 & k\mathrm{e}^{-\mu\tilde{T}_\beta} \end{pmatrix}$$

and has the two real positive eigenvalues $\lambda_1 = \mathrm{e}^{-d_\beta\tilde{T}_\beta} < 1$ and $\lambda_2 = k\mathrm{e}^{-\mu\tilde{T}_\beta}$. The trivial fixed point is stable if $\lambda_2 < 1$ or $\tilde{T}_\beta > \bar{T}$ and unstable if $\lambda_2 > 1$ or $\tilde{T}_\beta < \bar{T}$, where $\tilde{T}_\beta$ and $\bar{T}$ are defined in Notation 2.2.

We want to discuss the existence of nontrivial fixed points of F for $\tilde{T}_\beta < \bar{T}$. The mapping F can be extended to $S_0 > \tilde{S}_\beta$ and $N_0 < 0$, but the case $N_0 < 0$ has no biological meaning.

Definition 2.6. Let $\beta_0 \geq 0$ such that (H_β) is satisfied for $\beta > \beta_0$. Then we can define a mapping $G : (0,\infty) \times (-\infty,\infty) \times (\beta_0,\infty) \to \mathbb{R}^2$ by

$$\begin{cases} G_1(S_0, N_0, \beta) := S(T) - S_0, \\ G_2(S_0, N_0, \beta) := k\mathrm{e}^{-\mu T} - 1, \end{cases}$$

where S is the solution of the second equation of (2.1) and $T = T(S_0, N_0, \beta)$ is defined as before.

By Eq. (2.2) we must have $G(S_0, N_0, \beta) = 0$ if (S_0, N_0) is a nontrivial fixed point of F pertaining to the parameter value β, and in particular $T(S_0, N_0, \beta) = \bar{T}$. Without loss of generality we assume that the trivial fixed point becomes unstable at $\beta = 1$, i.e.

$$\tilde{T}_1 = \bar{T}. \tag{2.10}$$

Since $\tilde{T}_1 = T(0, \tilde{S}_1) = \int_{x_\alpha}^{x_\omega} \frac{dx}{g(\tilde{S}_1, x)}$, Remark 2.3, a) implies that $\tilde{S}_1$ is just the unique value such that $\bar{t}(\tilde{S}_1) = \bar{T}$. Moreover, we assume henceforth

$$d_1 = 1, \tag{2.11}$$

which can be achieved by scaling the time variable and serves to simplify notation.

Theorem 2.7. *Assume that* (2.10) *and* (2.11) *are satisfied. Then there exist a neighbourhood U of* 1 *in* $(0,\infty)$ *and a neighbourhood V of* $(\tilde{S}_1, 0)$ *in* $\mathbb{R}^2$ *such that for each $\beta \in U$ there exists a unique* $(S_0, N_0) \in V$ *with* $G(S_0, N_0, \beta) = 0$. *Moreover, for $\beta \in U$ with $\beta < 1$ we have $S_0 > \tilde{S}_\beta$, $N_0 < 0$, and for $\beta \in U$ with $\beta > 1$ we have $S_0 < \tilde{S}_\beta$, $N_0 > 0$, i.e. only the second case yields a biologically meaningful nontrivial fixed point of F resp. a periodic one-cohort solution of Eq.* (1.1).

Proof. By Eq. (2.10) we have $T(\tilde{S}_1, 0, 1) = \bar{T}$ and $G(\tilde{S}_1, 0, 1) = 0$, and there exists a neighbourhood W of $(\tilde{S}_1, 0, 1)$ such that G is continuously differentiable on W. Let $y := (S_0, N_0)$. Then we have

$$(D_y G)(y, \beta) = \begin{pmatrix} \frac{\partial S}{\partial S_0}(T) + \dot{S}(T)\frac{\partial T}{\partial S_0} - 1 & \frac{\partial S}{\partial N_0}(T) + \dot{S}(T)\frac{\partial T}{\partial N_0} \\ -\mu k\mathrm{e}^{-\mu T}\frac{\partial T}{\partial S_0} & -\mu k\mathrm{e}^{-\mu T}\frac{\partial T}{\partial N_0} \end{pmatrix},$$

and in particular

$$(D_y G)(\tilde{S}_1, 0, 1) = \begin{pmatrix} k^{-\frac{1}{\mu}} - 1 & \frac{\partial S}{\partial N_0}(\bar{T}) \\ -\mu\frac{\partial T}{\partial S_0} & -\mu\frac{\partial T}{\partial N_0} \end{pmatrix}. \tag{2.12}$$

The determinant of this matrix is

$$\Delta := \det(D_y G)(\tilde{S}_1, 0, 1) = \mu\frac{\partial T}{\partial N_0}(1 - k^{-\frac{1}{\mu}}) + \mu\frac{\partial T}{\partial S_0}\frac{\partial S}{\partial N_0}(\bar{T}), \tag{2.13}$$

which is positive by Lemma 2.4 and assumptions (H_g) and (H_γ). The Implicit Function Theorem implies that there exist neighbourhoods U of 1 and V of $(\tilde{S}_1, 0)$ and a C^1-function $H : U \to V$ such that $V \times U \subset W$ and $G(H(\beta), \beta) = 0$ for all $\beta \in U$. Moreover, for $\beta \in U$ the equation $G(y, \beta) = 0$ possesses one and only one solution $y = H(\beta)$ in V.

Only three kinds of choices for (S_0, N_0) are possible such that S might return to its initial value: a) $S_0 > \tilde{S}_\beta$, $N_0 < 0$; b) $S_0 = \tilde{S}_\beta$, $N_0 = 0$; c) $S_0 < \tilde{S}_\beta$, $N_0 > 0$. Let $\beta > 1$. Then $T(S_0, N_0) \leq \tilde{T}_\beta < \bar{T}$ for $S_0 \geq \tilde{S}_\beta$, $N_0 \leq 0$, i.e. we must have case c). Analogously, case a) applies to $\beta < 1$. □

The fact that a nontrivial biologically meaningful fixed point of F can only exist for $\beta > 1$ can also be derived from the following heuristic considerations. If we add a very small number of individuals to a food population which is at its own dynamical equilibrium $\tilde{S}_\beta$, the dynamics of the consumer population will, initially at least, conform approximately to the assumption of a constant food density. Remark 2.3, a) and assumption (2.10) then tell us that the population will go extinct whenever $\tilde{S}_\beta < \tilde{S}_1$ (resp. $\beta < 1$) and will start to grow when $\tilde{S}_\beta > \tilde{S}_1$ (resp. $\beta > 1$).

The principle of exchange of stability (cf. [8, p. 93, Theorem 5.1], for example) implies

Theorem 2.8. *Let the assumptions of Theorem 2.7 be satisfied. If U is chosen sufficiently small, the biologically meaningful nontrivial fixed point of F for $\beta \in U \cap (1, \infty)$ is stable.*

We assume in the following that U is chosen sufficiently small such that the conclusion of Theorem 2.8 holds.

3. The n-cohort problem for $n \geq 2$

In this section we address the following question: If we start with $n \geq 2$ cohorts with small size differences, will these differences be larger after all n cohorts have reproduced, or will they be smaller and eventually tend to zero? Will the solution of the n-cohort problem converge to a periodic solution of the one-cohort problem? This phenomenon cannot occur in the case of a constant food density or if the growth rate is independent of S since then the size differences always stay the same. First we consider the case $n = 2$, i.e. for $(S_0, N_1, N_2, x_0) \in (0, \tilde{S}_\beta] \times [0, \infty) \times [0, \infty) \times [x_\alpha, x_\omega]$, $\beta > 0$, we solve

$$\left\{ \begin{aligned} &\frac{dx_1}{dt} = g(S, x_1), \quad x_1(0) = x_\alpha, \\ &\frac{dx_2}{dt} = g(S, x_2), \quad x_2(0) = x_0, \\ &\frac{dS}{dt} = h(S, \beta) - \mathrm{e}^{-\mu t}(N_1 \gamma(S, x_1) + N_2 \gamma(S, x_2)), \quad S(0) = S_0, \end{aligned} \right. \tag{3.1}$$

where we again assume that (H_β), (2.10) and (2.11) are satisfied. The mapping $F_2 : (S_0, N_1, N_2, x_0) \mapsto (S_0', N_1', N_2', x_0')$ is defined by

$$\begin{cases} S_0' := S(T), \\ N_1' := kN_2\mathrm{e}^{-\mu T}, \\ N_2' := N_1\mathrm{e}^{-\mu T}, \\ x_0' := x_1(T), \end{cases} \tag{3.2}$$

where $T = T(S_0, N_1, N_2, x_0) \geq 0$ is such that $x_2(T) = x_\omega$, $x_2(t) < x_\omega$ for $0 \leq t < T$.

Notation 3.1. For $\beta \in U$ we use the abbreviations

$$\begin{cases} \bar{S}_0(\beta) := H_1(\beta), \\ \bar{N}_0(\beta) := H_2(\beta), \end{cases}$$

where H is defined by Theorem 2.7 (see the proof), i.e. $(\bar{S}_0(\beta), \bar{N}_0(\beta))$ is the nontrivial biologically meaningful fixed point of F_1 for $\beta \in U \cap (1, \infty)$. Moreover, we denote the solution of Eq. (2.1) corresponding to $S_0 = \bar{S}_0(\beta)$, $N_0 = \bar{N}_0(\beta)$ with $(\bar{x}_\beta, \bar{S}_\beta)$.

The nontrivial fixed point $(\bar{S}_0(\beta), \bar{N}_0(\beta))$ of F_1 for $\beta \in U \cap (1, \infty)$ can be viewed as a periodic point (S_0, N_1, N_2, x_0) of period two of F_2 with $S_0 = \bar{S}_0(\beta)$, $N_1 + N_2 = \bar{N}_0(\beta)$, $x_0 = x_\alpha$ (or $N_1 + kN_2 = \bar{N}_0(\beta)$, $x_0 = x_\omega$), i.e. the artificial splitting of one cohort into two cohorts is not unique and instead of a fixed point of F_1 we obtain a family of periodic points of period two of F_2. In order to investigate the 'stability' of these periodic points of period two, we have to consider the second iterate $F_2^2 =: K : (S_0, N_1, N_2, x_0) \mapsto (S_0'', N_1'', N_2'', x_0'')$. If $T_1 := T(S_0, N_1, N_2, x_0)$ and $T_2 := T(F_2(S_0, N_1, N_2, x_0))$, we have $N_1'' = kN_1\mathrm{e}^{-\mu(T_1+T_2)}$ and $N_2'' = kN_2\mathrm{e}^{-\mu(T_1+T_2)}$, i.e. the quotient $\frac{N_1}{N_2}$ or $\frac{N_2}{N_1}$ remains invariant under K if the denominator is not zero. (Biologically obvious: Since the mortality rate is constant and the individuals produce a fixed number of offspring, the ratios between the population numbers of the cohorts stay the same in later generations.) This allows us to restrict K to any set $N_2 = \eta N_1$, η a positive constant, and thus to reduce the problem by one dimension. Let $K_\eta : (S_0, N_0, x_0) \mapsto (S_0'', N_0'', x_0'')$ be defined by

$$\big(S_0'', \frac{1}{1+\eta}N_0'', \frac{\eta}{1+\eta}N_0'', x_0''\big) := K\big(S_0, \frac{1}{1+\eta}N_0, \frac{\eta}{1+\eta}N_0, x_0\big).$$

The nontrivial fixed point $(\bar{S}_0(\beta), \bar{N}_0(\beta))$ of F_1 for $\beta \in U \cap (1, \infty)$ corresponds to the fixed point $(\bar{S}_0(\beta), \bar{N}_0(\beta), x_\alpha)$ (or $(\bar{S}_0(\beta), \frac{1+\eta}{1+k\eta}\bar{N}_0(\beta), x_\omega)$) of K_η. The Jacobi matrix of K_η at the point $(\bar{S}_0(\beta), \bar{N}_0(\beta), x_\alpha)$ is

$$(DK_\eta)(\bar{S}_0(\beta), \bar{N}_0(\beta), x_\alpha) = \begin{pmatrix} \multicolumn{2}{c}{\multirow{2}{*}{A}} & * \\ & & * \\ 0 & 0 & \frac{\partial x_0''}{\partial x_0} \end{pmatrix}, \tag{3.3}$$

where

$$A := (DF_1)(\bar{S}_0(\beta), \bar{N}_0(\beta)) \tag{3.4}$$

is the (2×2)-Jacobi matrix of F_1 evaluated at its stable fixed point $(\bar{S}_0(\beta), \bar{N}_0(\beta))$ and '$*$' denotes a not so interesting number. Note that $x_0''(S_0, N_0, x_\alpha) = x_\alpha$ for all S_0, N_0, which accounts for the two zeros in the third row of the matrix (3.3).

Thus the eigenvalues of the Jacobi matrix (3.3) are given by the eigenvalues of A and

$$\lambda := \frac{\partial x_0''}{\partial x_0}\big(\bar S_0(\beta), \frac{1}{1+\eta}\bar N_0(\beta), \frac{\eta}{1+\eta}\bar N_0(\beta), x_\alpha\big), \tag{3.5}$$

where x_0'' now again denotes the fourth component of the mapping K. The former are of absolute value < 1 by assumption, and the stability of the fixed point $(\bar S_0(\beta), \bar N_0(\beta), x_\alpha)$ of K_η depends on the value of λ, which has to be nonnegative since $x_0'' > x_\alpha$ for $x_0 > x_\alpha$.

Lemma 3.2. *The eigenvalue* λ *defined by* (3.5) *is independent of* η *and given by*

$$\lambda(\beta) = \frac{g(\bar S_0(\beta), x_\alpha)}{g(\bar S_0(\beta), x_\omega)} \exp\left(\int_0^{\bar T} \frac{\partial g}{\partial x}(\bar S_\beta(t), \bar x_\beta(t))\, dt\right), \tag{3.6}$$

where $\bar S_0(\beta)$, $\bar S_\beta(t)$ *and* $\bar x_\beta(t)$ *are defined by Notation 3.1 and* $\bar T$ *is given by Notation 2.2. In particular, for a growth rate of the form* (1.2) λ *reads*

$$\lambda(\beta) = \frac{f(\bar S_0(\beta)) - x_\alpha}{f(\bar S_0(\beta)) - x_\omega} \mathrm{e}^{-c\bar T} = \frac{f(\bar S_0(\beta)) - x_\alpha}{f(\bar S_0(\beta)) - x_\omega} k^{-\frac{\varepsilon}{\mu}}. \tag{3.7}$$

Proof. In order to compute λ, we first have to solve the following ODE system:

$$\begin{cases} \dfrac{dx_1}{dt} = g(S, x_1), \quad x_1(0) = x_\alpha, \\ \dfrac{dx_2}{dt} = g(S, x_2), \quad x_2(0) = x_0, \\ \dfrac{dS}{dt} = h(S,\beta) - \dfrac{\bar N_0(\beta)}{1+\eta}\mathrm{e}^{-\mu t}(\gamma(S,x_1) + \eta\gamma(S,x_2)), \quad S(0) = \bar S_0(\beta). \end{cases} \tag{3.8}$$

Let $T_1 \geq 0$ be such that $x_2(T_1) = x_\omega$, $x_2(t) < x_\omega$ for $0 \leq t < T_1$. We set $S_0' := S(T_1)$, $x_0' := x_1(T_1)$, $N_0' := \mathrm{e}^{-\mu T_1}\bar N_0(\beta)$ and solve

$$\begin{cases} \dfrac{d\tilde x_1}{dt} = g(\tilde S, \tilde x_1), \quad \tilde x_1(0) = x_\alpha, \\ \dfrac{d\tilde x_2}{dt} = g(\tilde S, \tilde x_2), \quad \tilde x_2(0) = x_0', \\ \dfrac{d\tilde S}{dt} = h(\tilde S,\beta) - \dfrac{N_0'}{1+\eta}\mathrm{e}^{-\mu t}(k\eta\gamma(\tilde S,\tilde x_1) + \gamma(\tilde S,\tilde x_2)), \quad \tilde S(0) = S_0'. \end{cases}$$

Let $T_2 \geq 0$ be such that $\tilde x_2(T_2) = x_\omega$, $\tilde x_2(t) < x_\omega$ for $0 \leq t < T_2$, and define $x_0'' := \tilde x_1(T_2)$. Then x_0'' is differentiable with respect to x_0 for $0 \leq x_0 - x_\alpha < \varepsilon$, $\varepsilon > 0$ suitably chosen, where the derivative is replaced with the right-hand derivative at $x_0 = x_\alpha$. For $x_0 = x_\alpha$ we have $T_1 = \bar T$, $T_2 = 0$, $S_0' = \bar S_0(\beta)$, $x_0' = x_\omega$, and we obtain

$$\frac{dx_0''}{dx_0}(x_\alpha) = \dot{\tilde x}_1(0)\frac{dT_2}{dx_0}(x_\alpha) = g(\bar S_0(\beta), x_\alpha)\frac{dT_2}{dx_0}(x_\alpha),$$

where we have used $\frac{\partial \tilde x_1}{\partial x_0'}(0) = \frac{\partial \tilde x_1}{\partial S_0'}(0) = \frac{\partial \tilde x_1}{\partial N_0'}(0) = 0$. Differentiation of the relationship $\tilde x_2(T_2) = x_\omega$ with respect to x_0 yields at $x_0 = x_\alpha$

$$\dot{\tilde{x}}_2(0)\frac{dT_2}{dx_0}(x_\alpha)+\frac{\partial\tilde{x}_2}{\partial x_0'}(0)\frac{dx_0'}{dx_0}(x_\alpha)=g(\bar{S}_0(\beta),x_\omega)\frac{dT_2}{dx_0}(x_\alpha)+\frac{dx_0'}{dx_0}(x_\alpha)=0,$$

and we obtain

$$\frac{dT_2}{dx_0}(x_\alpha)=-\frac{1}{g(\bar{S}_0(\beta),x_\omega)}\frac{dx_0'}{dx_0}(x_\alpha)$$

and

$$\lambda=\frac{dx_0''}{dx_0}(x_\alpha)=-\frac{g(\bar{S}_0(\beta),x_\alpha)}{g(\bar{S}_0(\beta),x_\omega)}\frac{dx_0'}{dx_0}(x_\alpha).$$

We have

$$\frac{dx_0'}{dx_0}=\frac{\partial x_1}{\partial x_0}(T_1)+\dot{x}_1(T_1)\frac{dT_1}{dx_0},$$

and for $x_0=x_\alpha$ we obtain similarly as above, using the definition of T_1 and the fact that $T_1(x_\alpha)=\bar{T}$,

$$\frac{dx_0'}{dx_0}(x_\alpha)=\frac{\partial x_1}{\partial x_0}(\bar{T})-\frac{\partial x_2}{\partial x_0}(\bar{T}).$$

If we differentiate the solutions of Eq. (3.8) with respect to the initial condition x_0 at $x_0=x_\alpha$, we obtain the differential equations

$$\begin{cases}\dfrac{d}{dt}\dfrac{\partial x_1}{\partial x_0}=\dfrac{\partial g}{\partial x}(\bar{S}_\beta,\bar{x}_\beta)\dfrac{\partial x_1}{\partial x_0}+\dfrac{\partial g}{\partial S}(\bar{S}_\beta,\bar{x}_\beta)\dfrac{\partial S}{\partial x_0}, & \dfrac{\partial x_1}{\partial x_0}(0)=0,\\ \dfrac{d}{dt}\dfrac{\partial x_2}{\partial x_0}=\dfrac{\partial g}{\partial x}(\bar{S}_\beta,\bar{x}_\beta)\dfrac{\partial x_2}{\partial x_0}+\dfrac{\partial g}{\partial S}(\bar{S}_\beta,\bar{x}_\beta)\dfrac{\partial S}{\partial x_0}, & \dfrac{\partial x_2}{\partial x_0}(0)=1,\end{cases}$$

which implies that $z(t):=\frac{\partial x_2}{\partial x_0}(t)-\frac{\partial x_1}{\partial x_0}(t)$ is the solution of the equation

$$\frac{dz}{dt}=\frac{\partial g}{\partial x}(\bar{S}_\beta,\bar{x}_\beta)z,\quad z(0)=1.$$

From this we infer

$$\frac{\partial x_2}{\partial x_0}(t)-\frac{\partial x_1}{\partial x_0}(t)=\exp\left(\int_0^t\frac{\partial g}{\partial x}(\bar{S}_\beta(\tau),\bar{x}_\beta(\tau))\,d\tau\right),$$

and Eqs. (3.6) and (3.7) follow. □

Remark 3.3. The eigenvalue $\lambda(\beta)$ given by Eq. (3.6) can be biologically interpreted as the ratio between the flux of individuals from size x_α at $t=0$ and the influx to size x_ω at time $t=\bar{T}$ if the food density is given by $S(t)=\bar{S}_\beta(t)$ for $0\le t\le\bar{T}$ and mortality is ignored. This makes biological sense: if the influx to x_ω at $t=\bar{T}$ is larger than the flux from x_α at $t=0$, the individuals of the first cohort can only grow from x_α to $x_0''<x_0$ while the individuals of the second cohort grow from x_0' to x_ω (in the notation of the proof of Lemma 3.2) for $0<x_0-x_\alpha$ infinitesimally small. This corresponds to the case of an eigenvalue $\lambda(\beta)\in(0,1)$ and stability of the periodic one-cohort solution with respect to splitting into two cohorts. Likewise the case $\lambda(\beta)>1$ has a biologically meaningful interpretation.

The equations $\frac{d\bar{x}_\beta}{dt} = g(\bar{S}_\beta, \bar{x}_\beta)$, $\bar{x}_\beta(0) = x_\alpha$ and $\bar{x}_\beta(\bar{T}) = x_\omega$ yield

$$\begin{aligned}\frac{g(\bar{S}_0(\beta), x_\alpha)}{g(\bar{S}_0(\beta), x_\omega)} &= \exp\left(-\int_0^{\bar{T}} \frac{d}{dt} \ln g(\bar{S}_0(\beta), \bar{x}_\beta(t))\, dt\right) \\ &= \exp\left(-\int_0^{\bar{T}} \frac{\partial g}{\partial x}(\bar{S}_0(\beta), \bar{x}_\beta(t)) \frac{g(\bar{S}_\beta(t), \bar{x}_\beta(t))}{g(\bar{S}_0(\beta), \bar{x}_\beta(t))}\, dt\right),\end{aligned}$$

and we obtain the useful representation

$$\lambda(\beta) = \exp\left(\int_0^{\bar{T}} \left(\frac{\partial g}{\partial x}(\bar{S}_\beta(t), \bar{x}_\beta(t)) - \frac{\partial g}{\partial x}(\bar{S}_0(\beta), \bar{x}_\beta(t)) \frac{g(\bar{S}_\beta(t), \bar{x}_\beta(t))}{g(\bar{S}_0(\beta), \bar{x}_\beta(t))}\right) dt\right). \tag{3.9}$$

For $\beta = 1$ we have by assumption (2.10) $\bar{S}_1(t) \equiv \bar{S}_0(1) = \tilde{S}_1$, and Eq. (3.9) immediately implies

$$\lambda(1) = 1.$$

In particular we obtain for a linear growth rate from Eq. (3.7)

$$\frac{f(\tilde{S}_1) - x_\alpha}{f(\tilde{S}_1) - x_\omega} k^{-\frac{c}{\mu}} = 1. \tag{3.10}$$

Corollary 3.4. *a) If in addition to* (H_g) *we have*

$$S \mapsto \frac{\partial}{\partial x}(\ln g(S,x)) \text{ is strictly increasing in } S \text{ for } S > S_x,\ x \in [x_\alpha, x_\omega], \tag{3.11}$$

and

$$\bar{S}_0(\beta) = \max_{t \geq 0} \bar{S}_\beta(t) \tag{3.12}$$

for a $\beta \in U \cap (1, \infty)$*, then the nontrivial fixed point* $(\bar{S}_0(\beta), \bar{N}_0(\beta), x_\alpha)$ *of* K_η *is stable for all* $\eta > 0$.
b) In case of a linear growth rate (1.2) *the nontrivial fixed point* $(\bar{S}_0(\beta), \bar{N}_0(\beta), x_\alpha)$ *of* K_η *is stable for all* $\eta > 0$ *for a* $\beta \in U \cap (1, \infty)$ *if and only if* $\bar{S}_0(\beta) > \tilde{S}_1$.

Proof. The assertion a) follows from the representation (3.9) and the assumptions (H_g), (3.11) and (3.12).

In the case of a linear growth rate (1.2), Eqs. (3.7) and (3.10) and the strict monotony of f imply that $\lambda(\beta) < 1$ if and only if $\bar{S}_0(\beta) > \tilde{S}_1$, which proves statement b). □

Corollary 3.4, b) says that for von Bertalanffy growth rates (1.2) the nontrivial periodic one-cohort solution is stable with respect to splitting into two cohorts if and only if the value of the food density is 'large enough' (namely larger than $\tilde{S}_1$) at the instants of reproduction.

Remark 3.5. In numerical computations of nontrivial periodic one-cohort solutions for growth rates (1.2), linear h, consumption rates as in Sect. 4 and conservation of mass (cf. Sect. 4) S did attain its maximum at the instants of reproduction. However, we do not know if the property (3.12) was a just a peculiarity of our examples or if it may also occur for growth rates that satisfy (3.11) but are not of type (1.2).

We have $\operatorname{sign}(\lambda(\beta)-1)=\operatorname{sign}\lambda'(1)$ for $\beta>1$ sufficiently close to 1, and the stability of the fixed point $(\bar{S}_0(\beta),\bar{N}_0(\beta),x_\alpha)$ of K_η depends on the sign of $\lambda'(1)$. In order to compute $\lambda'(1)$, we need the following lemma.

Lemma 3.6. *Let (x,S) be the solution of Eq. (2.1), let T be defined as in Sect. 2, and let $\bar{S}_0(\beta)$ and $\bar{N}_0(\beta)$ be defined by Notation 3.1. Then the derivatives with respect to β at $\beta=1$ are given by*

$$\frac{d}{d\beta}\bar{S}_0(1)=\frac{\mu}{\Delta}\left((1-k^{-\frac{1}{\mu}})\frac{\partial h}{\partial\beta}(\tilde{S}_1,1)\frac{\partial T}{\partial N_0}-\frac{\partial T}{\partial\beta}\frac{\partial S}{\partial N_0}(\bar{T})\right) \tag{3.13}$$

and

$$\frac{d}{d\beta}\bar{N}_0(1)=-\frac{\mu}{\Delta}(1-k^{-\frac{1}{\mu}})\left(\frac{\partial h}{\partial\beta}(\tilde{S}_1,1)\frac{\partial T}{\partial S_0}+\frac{\partial T}{\partial\beta}\right), \tag{3.14}$$

where Δ is defined by Eq. (2.13), $\bar{T}$ is defined by Notation 2.2 and all partial derivatives are evaluated at $(S_0,N_0,\beta)=(\tilde{S}_1,0,1)$.

Proof. If G is given by Definition 2.6 and H and U are defined as in the proof of Theorem 2.7, differentiation of the relationship $G(H(\beta),\beta)=0$, $\beta\in U$, with respect to β yields

$$(D_yG)(H(\beta),\beta)\frac{dH}{d\beta}(\beta)+\frac{\partial G}{\partial\beta}(H(\beta),\beta)=0,\quad \beta\in U.$$

Since the matrix $(D_yG)(\tilde{S}_1,0,1)$ (cf. (2.12)) is invertible, we obtain in particular

$$\begin{aligned}\frac{dH}{d\beta}(1)&=\begin{pmatrix}\frac{d}{d\beta}\bar{S}_0(1)\\ \frac{d}{d\beta}\bar{N}_0(1)\end{pmatrix}=-((D_yG)(\tilde{S}_1,0,1))^{-1}\frac{\partial G}{\partial\beta}(H(1),1)\\ &=-\frac{1}{\Delta}\begin{pmatrix}-\mu\frac{\partial T}{\partial N_0} & -\frac{\partial S}{\partial N_0}(\bar{T})\\ \mu\frac{\partial T}{\partial S_0} & k^{-\frac{1}{\mu}}-1\end{pmatrix}\begin{pmatrix}\frac{\partial S}{\partial\beta}(\bar{T})\\ -\mu\frac{\partial T}{\partial\beta}\end{pmatrix},\end{aligned}$$

where all derivatives are evaluated at $(S_0,N_0,\beta)=(\tilde{S}_1,0,1)$. From Eq. (2.7) and assumption (2.11) we obtain $\frac{\partial S}{\partial\beta}(\bar{T})=\frac{\partial h}{\partial\beta}(\tilde{S}_1,1)(1-k^{-\frac{1}{\mu}})$, which finishes the proof. □

Eq. (3.14), the representations of the derivatives in Lemma 2.4 and the assumptions immediately imply $\frac{d}{d\beta}\bar{N}_0(1)>0$, which reflects the fact that we have $\bar{N}_0(\beta)>0$ for $\beta\in U\cap(1,\infty)$ and $\bar{N}_0(\beta)<0$ for $\beta\in U\cap(0,1)$. The sign of $\frac{d}{d\beta}\bar{S}_0(\beta)$, however, is a more complicated matter; cf. Lemma 3.9.

Lemma 3.7. *$\lambda'(1)$ is given by*

$$\begin{aligned}\lambda'(1)=-\frac{\mu}{\Delta}&\left(\frac{\partial T}{\partial\beta}+\frac{\partial h}{\partial\beta}(\tilde{S}_1,1)\frac{\partial T}{\partial S_0}\right)\left(\frac{\partial S}{\partial N_0}(\bar{T})\int_0^{\bar{T}}\frac{\frac{\partial g}{\partial S}(\tilde{S}_1,\bar{x}_1(t))}{g(\tilde{S}_1,\bar{x}_1(t))}e^{-t}\,dt\right.\\ &\left.+(1-k^{-\frac{1}{\mu}})\int_0^{\bar{T}}\frac{\frac{\partial g}{\partial S}(\tilde{S}_1,\bar{x}_1(t))}{g(\tilde{S}_1,\bar{x}_1(t))}\left(\frac{\partial S}{\partial N_0}(t)+e^{-\mu t}\gamma(\tilde{S}_1,\bar{x}_1(t))\right)dt\right)\end{aligned} \tag{3.15}$$

and

$$\operatorname{sign}\lambda'(1) = \operatorname{sign}\Bigg(\frac{\partial S}{\partial N_0}(\bar T)\int_0^{\bar T}\frac{\frac{\partial g}{\partial S}(\tilde S_1,\bar x_1(t))}{g(\tilde S_1,\bar x_1(t))}\mathrm{e}^{-t}\,dt + (1-k^{-\frac{1}{\mu}})\int_0^{\bar T}\frac{\frac{\partial g}{\partial S}(\tilde S_1,\bar x_1(t))}{g(\tilde S_1,\bar x_1(t))}\left(\frac{\partial S}{\partial N_0}(t)+\mathrm{e}^{-\mu t}\gamma(\tilde S_1,\bar x_1(t))\right)dt\Bigg), \tag{3.16}$$

where all partial derivatives are evaluated at $(S_0, N_0, \beta) = (\tilde S_1, 0, 1)$.

Proof. We differentiate Eq. (3.9) at $\beta = 1$, and by integration by parts we obtain

$$\begin{aligned}\lambda'(1) &= \int_0^{\bar T}\left(\frac{\partial^2 g}{\partial S\partial x}(\tilde S_1,\bar x_1(t)) - \frac{\partial g}{\partial x}(\tilde S_1,\bar x_1(t))\frac{\frac{\partial g}{\partial S}(\tilde S_1,\bar x_1(t))}{g(\tilde S_1,\bar x_1(t))}\right)\\ &\qquad\times\left(\frac{d\bar S_\beta}{d\beta}\Big|_{\beta=1}(t) - \frac{d}{d\beta}\bar S_0(1)\right)dt\\ &= \int_0^{\bar T}\frac{d}{dt}\left(\frac{\frac{\partial g}{\partial S}(\tilde S_1,\bar x_1(t))}{g(\tilde S_1,\bar x_1(t))}\right)\left(\frac{d\bar S_\beta}{d\beta}\Big|_{\beta=1}(t) - \frac{d}{d\beta}\bar S_0(1)\right)dt\\ &= -\int_0^{\bar T}\frac{\frac{\partial g}{\partial S}(\tilde S_1,\bar x_1(t))}{g(\tilde S_1,\bar x_1(t))}\frac{d}{dt}\left(\frac{d\bar S_\beta}{d\beta}\Big|_{\beta=1}(t)\right)dt,\end{aligned} \tag{3.17}$$

where we have used $\lambda(1) = 1$ and $\dot{\bar x}_1(t) = g(\tilde S_1, \bar x_1(t))$. We have

$$\frac{d\bar S_\beta}{d\beta}\Big|_{\beta=1}(t) = \frac{\partial S}{\partial\beta}(t) + \frac{\partial S}{\partial S_0}(t)\frac{d}{d\beta}\bar S_0(1) + \frac{\partial S}{\partial N_0}(t)\frac{d}{d\beta}\bar N_0(1),$$

where all partial derivatives are evaluated at $(S_0, N_0, \beta) = (\tilde S_1, 0, 1)$, and Eqs. (2.3), (2.5), (2.7) and (2.11) yield

$$\begin{aligned}\frac{d}{dt}\left(\frac{d\bar S_\beta}{d\beta}(t)\right) &= \left(\frac{\partial h}{\partial\beta}(\tilde S_1,1) - \frac{d}{d\beta}\bar S_0(1)\right)\mathrm{e}^{-t}\\ &\qquad - \frac{d}{d\beta}\bar N_0(1)\left(\frac{\partial S}{\partial N_0}(t) + \mathrm{e}^{-\mu t}\gamma(\tilde S_1,\bar x_1(t))\right).\end{aligned} \tag{3.18}$$

Equation (3.13) and the definition of Δ (cf. Eq. (2.13)) imply

$$\frac{\partial h}{\partial\beta}(\tilde S_1,1) - \frac{d}{d\beta}\bar S_0(1) = \frac{\mu}{\Delta}\left(\frac{\partial h}{\partial\beta}(\tilde S_1,1)\frac{\partial T}{\partial S_0} + \frac{\partial T}{\partial\beta}\right)\frac{\partial S}{\partial N_0}(\bar T), \tag{3.19}$$

and by using Eqs. (3.18), (3.19) and (3.14) in Eq. (3.17) we obtain Eq. (3.15).

Equations (2.4) and (2.7)–(2.9) and assumptions (H_g) and (H_h) yield

$$\begin{aligned}&\frac{\partial T}{\partial\beta} + \frac{\partial h}{\partial\beta}(\tilde S_1,1)\frac{\partial T}{\partial S_0}\\ &= -g(\tilde S_1,x_\omega)^{-1}\frac{\partial h}{\partial\beta}(\tilde S_1,1)\int_0^{\bar T}\exp\left(\int_t^{\bar T}\frac{\partial g}{\partial x}(\tilde S_1,\bar x_1(\tau))\,d\tau\right)\frac{\partial g}{\partial S}(\tilde S_1,\bar x_1(t))\,dt < 0,\end{aligned}$$

from which assertion (3.16) follows. □

Remark 3.8. The sign of $\lambda'(1)$ does not depend on the particular shape of h but only on the value of its positive zero at $\beta = 1$.

For a growth rate of the form (1.2) we obtain the following result; cf. Corollary 3.4, b).

Lemma 3.9. *In the special case of a linear growth rate* (1.2) *we have* $\operatorname{sign}\lambda'(1) = -\operatorname{sign}\frac{d}{d\beta}\bar{S}_0(1)$ *and*

$$\begin{aligned}\frac{d}{d\beta}\bar{S}_0(1) = {} & \frac{\mu}{\Delta}(f(\tilde{S}_1) - x_\omega)^{-1} f'(\tilde{S}_1)\frac{\partial h}{\partial \beta}(\tilde{S}_1, 1)k^{-\frac{c}{\mu}} \\ & \times\Big((1 - k^{-\frac{1}{\mu}})\int_0^{\bar{T}} \mathrm{e}^{(c-1)t}\int_0^t \mathrm{e}^{(1-\mu)\tau}\gamma(\tilde{S}_1, \bar{x}_1(\tau))\,d\tau\,dt \\ & \quad -k^{-\frac{1}{\mu}}\int_0^{\bar{T}} \mathrm{e}^{ct}(1 - \mathrm{e}^{-t})\,dt\int_0^{\bar{T}} \mathrm{e}^{(1-\mu)t}\gamma(\tilde{S}_1, \bar{x}_1(t))\,dt\Big),\end{aligned}$$

and consequently

$$\begin{aligned}\operatorname{sign}\lambda'(1) = {} & \operatorname{sign}\Big(k^{-\frac{1}{\mu}}\int_0^{\bar{T}} \mathrm{e}^{ct}(1 - \mathrm{e}^{-t})\,dt\int_0^{\bar{T}} \mathrm{e}^{(1-\mu)t}\gamma(\tilde{S}_1, \bar{x}_1(t))\,dt \\ & - (1 - k^{-\frac{1}{\mu}})\int_0^{\bar{T}} \mathrm{e}^{(c-1)t}\int_0^t \mathrm{e}^{(1-\mu)\tau}\gamma(\tilde{S}_1, \bar{x}_1(\tau))\,d\tau\,dt\Big).\end{aligned}$$

Proof. Eq. (3.7) and the monotony of f imply $\operatorname{sign}\lambda'(1) = -\operatorname{sign}\frac{d}{d\beta}\bar{S}_0(1)$, and we have $\frac{\partial g}{\partial x}(S, x) = -c$ and $\frac{\partial g}{\partial S}(S, x) = cf'(S)$ at those (S, x) for which $f(S) > x$. From Eqs. (2.5)–(2.9) we obtain at $(S_0, N_0, \beta) = (\tilde{S}_1, 0, 1)$

$$\frac{\partial T}{\partial N_0} = \frac{f'(\tilde{S}_1)}{f(\tilde{S}_1) - x_\omega}\mathrm{e}^{-c\bar{T}}\int_0^{\bar{T}} \mathrm{e}^{(c-1)t}\int_0^t \mathrm{e}^{(1-\mu)\tau}\gamma(\tilde{S}_1, \bar{x}_1(\tau))\,d\tau\,dt$$

and

$$\frac{\partial T}{\partial \beta} = -\frac{\partial h}{\partial \beta}(\tilde{S}_1, 1)\frac{f'(\tilde{S}_1)}{f(\tilde{S}_1) - x_\omega}\mathrm{e}^{-c\bar{T}}\int_0^{\bar{T}} \mathrm{e}^{ct}(1 - \mathrm{e}^{-t})\,dt,$$

and Eqs. (3.13), (2.5) and the assumptions on f and h yield the assertions. □

Biological intuition immediately tells us that a nontrivial periodic one-cohort solution is stable with respect to splitting into n cohorts ($n \geq 2$) if and only if this is the case for $n = 2$. Mathematical details are deferred to the Appendix, and we obtain the following result, which shows that the nontrivial periodic one-cohort solution is stable with respect to splitting into n cohorts for $\beta > 1$ sufficiently close to 1 if $\lambda'(1) < 0$.

Theorem 3.10. *Let* $\lambda'(1) < 0$. *Then there exists a* $\beta_1 > 1$ *such that for each* $\beta \in (1, \beta_1)$ *there exist a neighbourhood* V_β *of* $(\bar{S}_0(\beta), \bar{N}_0(\beta))$ *and an* $\varepsilon_\beta > 0$ *such that* $\lim_{k\to\infty} F_n^{nk}(S_0, N_{1,0}, \ldots, N_{n,0}, x_{2,0}, \ldots, x_{n,0}) = (\bar{S}_0(\beta), \frac{N_{1,0}\bar{N}_0(\beta)}{\sum_{i=1}^n N_{i,0}}, \ldots, \frac{N_{n,0}\bar{N}_0(\beta)}{\sum_{i=1}^n N_{i,0}}, x_\alpha, \ldots, x_\alpha)$ *for* $(S_0, \sum_{i=1}^n N_{i,0}) \in V_\beta$, $0 \leq x_{i,0} - x_\alpha < \varepsilon_\beta$ *for* $i = 2, \ldots, n$ *and all* $n \geq 2$.

No general statement can be made about sign $\lambda'(1)$; cf. Sect. 4.

We conclude this section with an investigation of fixed points of F_n for $n \geq 2$. For a fixed point $(S_0, N_{1,0}, \ldots, N_{n,0}, x_{2,0}, \ldots, x_{n,0})$ of F_n we must have $N_{1,0} = k\mathrm{e}^{-\mu T} N_{n,0}$ and $N_{i,0} = \mathrm{e}^{-\mu T} N_{i-1,0}$, $i = 2, \ldots, n$, which implies that either $N_{i,0} = 0$ for $i = 1, \ldots, n$ or

$$T = \frac{1}{n\mu} \ln k = \frac{\bar{T}}{n} \tag{3.20}$$

and

$$N_{i,0} = k^{-(i-1)/n} N_{1,0}, \quad i = 2, \ldots, n, \tag{3.21}$$

where $\bar{T}$ is defined by Notation 2.2. For values of β such that (H_β) is satisfied we define the function $A_\beta : [x_\alpha, x_\omega] \to \mathbb{R}$ by

$$A_\beta(x) := \int_{x_\alpha}^{x} \frac{d\sigma}{g(\tilde{S}_\beta, \sigma)}, \quad x \in [x_\alpha, x_\omega].$$

$A_\beta(x)$ is the time it takes an individual to grow from size x_α to x or, equivalently, the age of an individual of size x if the food density is $\tilde{S}_\beta$. Naturally, A_β is strictly increasing on $[x_\alpha, x_\omega]$, $A_\beta(x_\alpha) = 0$, $A_\beta(x_\omega) = \tilde{T}_\beta$, which implies that $A_\beta^{-1} : [0, \tilde{T}_\beta] \to [x_\alpha, x_\omega]$ exists. The point $(\tilde{S}_\beta, 0, \ldots, 0, x_{2,0}, \ldots, x_{n,0})$ (no population present and the food at its unexploited equilibrium) is a periodic point of period $\leq n$ of F_n for all choices of $x_{i,0}$, $i = 2, \ldots, n$. It is a fixed point of F_n if and only if

$$x_{i,0} = A_\beta^{-1}(\tfrac{i-1}{n} \tilde{T}_\beta), \quad i = 2, \ldots, n,$$

i.e., if the initial sizes are chosen such that the time it takes to grow from $x_{i,0}$ to $x_{i+1,0}$ $(x_{1,0} := x_\alpha)$ is the same for $i = 1, \ldots, n-1$ and equals the time it takes to grow from $x_{n,0}$ to x_ω under food conditions $S \equiv \tilde{S}_\beta$, and this time is necessarily $T = \frac{1}{n} \tilde{T}_\beta$.

In order to investigate the existence of nontrivial fixed points of F_n, $n \geq 2$, we define a mapping similarly to Definition 2.6 and again call it G.

Definition 3.11. Let $W \subset \mathbb{R}^{n+1}$ an appropriately chosen neighbourhood of $(\tilde{S}_1, 0, \bar{x}_{2,0}, \ldots, \bar{x}_{n,0}, 1)$, where

$$\bar{x}_{i,0} := A_1^{-1}(\tfrac{i-1}{n} \bar{T}), \quad i = 2, \ldots, n. \tag{3.22}$$

For $(S_0, N_0, x_{2,0}, \ldots, x_{n,0}, \beta) \in W$ we solve the ODE system

$$\begin{cases} \dfrac{dx_1}{dt} = g(S, x_1), \quad x_1(0) = x_\alpha, \\ \dfrac{dx_i}{dt} = g(S, x_i), \quad x_i(0) = x_{i,0}, \quad i = 2, \ldots, n, \\ \dfrac{dS}{dt} = h(S, \beta) - N_0 \mathrm{e}^{-\mu t} \displaystyle\sum_{i=1}^{n} k^{-(i-1)/n} \gamma(S, x_i), \quad S(0) = S_0. \end{cases} \tag{3.23}$$

Let $T \geq 0$ be such that $x_n(T) = x_\omega$, $x_n(t) < x_\omega$ for $0 \leq t < T$. Then we define $G : W \to \mathbb{R}^n$ by

$$\begin{cases} G_1(S_0, N_0, x_{2,0}, \ldots, x_{n,0}, \beta) := S(T) - S_0, \\ G_2(S_0, N_0, x_{2,0}, \ldots, x_{n,0}, \beta) := k\mathrm{e}^{-n\mu T} - 1, \\ G_i(S_0, N_0, x_{2,0}, \ldots, x_{n,0}, \beta) := x_{i-2}(T) - x_{i-1,0}, \quad i = 3, \ldots, n+1. \end{cases} \tag{3.24}$$

If W is chosen sufficiently small, G is continuously differentiable in W, and Eqs. (2.10) and (3.22) imply $G(\tilde{S}_1, 0, \bar{x}_{2,0}, \dots, \bar{x}_{n,0}, 1) = 0$. In view of Eqs. (3.20) and (3.21) $(S_0, N_{1,0}, \dots, N_{n,0}, x_{2,0}, \dots, x_{n,0})$ is a nontrivial fixed point of F_n if and only if $N_{i,0} = k^{-(i-1)/n} N_0$, $i = 1, \dots, n$, and $G(S_0, N_0, x_{2,0}, \dots, x_{n,0}, \beta) = 0$.

We want to apply the Implicit Function Theorem to the mapping G. To this end we first compute the derivatives of the solutions of the ODE system (3.23) with respect to initial data and parameters.

Lemma 3.12. *Let $(x_1, \dots, x_n, S)$ be the solution of Eq. (3.23), let T be defined as in Definition 3.11 and $\bar{T}$ by Notation 2.2, and let*

$$\bar{x}_i(t) := A_1^{-1}(t + \tfrac{i-1}{n}\bar{T}), \quad 0 \le t \le \tfrac{n-i+1}{n}\bar{T}, \quad i = 1, \dots, n,$$

i.e. $\bar{x}_i(t)$ is the size at time t of an individual with initial size $\bar{x}_{i,0}$ if the food density is $S \equiv \tilde{S}_1$. Then the partial derivatives at $(S_0, N_0, x_{2,0}, \dots, x_{n,0}, \beta) = (\tilde{S}_1, 0, \bar{x}_{2,0}, \dots, \bar{x}_{n,0}, 1)$ are given by

$$\frac{\partial S}{\partial S_0}(t) = \mathrm{e}^{-t}, \tag{3.25}$$

$$\frac{\partial x_i}{\partial S_0}(t) = \int_0^t \exp\left(\int_\tau^t \frac{\partial g}{\partial x}(\tilde{S}_1, \bar{x}_i(\sigma))\, d\sigma\right) \frac{\partial g}{\partial S}(\tilde{S}_1, \bar{x}_i(\tau))\mathrm{e}^{-\tau}\, d\tau, \quad i = 1, \dots, n, \tag{3.26}$$

$$\frac{\partial S}{\partial x_{j,0}}(t) = 0, \quad j = 2, \dots, n, \tag{3.27}$$

$$\frac{\partial x_i}{\partial x_{j,0}}(t) = 0, \quad i = 1, \dots, n, \quad j = 2, \dots, n, \quad j \neq i, \tag{3.28}$$

$$\frac{\partial x_i}{\partial x_{i,0}}(t) = \exp\left(\int_0^t \frac{\partial g}{\partial x}(\tilde{S}_1, \bar{x}_i(\tau))\, d\tau\right), \quad i = 2, \dots, n, \tag{3.29}$$

$$\frac{\partial S}{\partial N_0}(t) = -\mathrm{e}^{-t} \sum_{i=1}^n k^{-(i-1)/n} \int_0^t \mathrm{e}^{(1-\mu)\tau} \gamma(\tilde{S}_1, \bar{x}_i(\tau))\, d\tau, \tag{3.30}$$

$$\frac{\partial x_i}{\partial N_0}(t) = \int_0^t \exp\left(\int_\tau^t \frac{\partial g}{\partial x}(\tilde{S}_1, \bar{x}_i(\sigma))\, d\sigma\right) \frac{\partial g}{\partial S}(\tilde{S}_1, \bar{x}_i(\tau)) \frac{\partial S}{\partial N_0}(\tau)\, d\tau, \quad i = 1, \dots, n, \tag{3.31}$$

$$\frac{\partial T}{\partial \alpha} = -g(\tilde{S}_1, x_\omega)^{-1} \frac{\partial x_n}{\partial \alpha}\left(\frac{1}{n}\bar{T}\right) \text{ for } \alpha = S_0, N_0 \text{ and } x_{i,0},\ i = 2, \dots, n, \tag{3.32}$$

and in particular

$$\frac{\partial T}{\partial x_{j,0}} = 0, \quad j = 2, \dots, n-1. \tag{3.33}$$

The following theorem is an analogue to Theorem 2.7 for F_n, $n \ge 2$. It shows that for each $n \ge 2$ there exists, for $\beta > 1$ sufficiently close to 1, a nontrivial periodic n-cohort solution whose period is just one nth of that of the periodic one-cohort solution. Moreover, the individuals of cohort i reach the initial body size of the individuals of cohort $i+1$, $i = 1, \dots, n-1$, at the instance when the individuals of cohort n reproduce.

Theorem 3.13. *Let $n \geq 2$. There exists a $\beta_1 > 1$ such that for each $\beta \in (1, \beta_1)$ there exists a fixed point $(S_0, N_{1,0}, \ldots, N_{n,0}, x_{2,0}, \ldots, x_{n,0})$, $N_{i,0} = k^{-(i-1)/n} N_0$, $i = 1, \ldots, n$, of F_n with $N_0 > 0$.*

Proof. We apply the Implicit Function Theorem to the function G given by Definition 3.11. Let $y := (S_0, N_0, x_{2,0}, \ldots, x_{n,0})$ and $\bar{y} := (\tilde{S}_1, 0, \bar{x}_{2,0}, \ldots, \bar{x}_{n,0})$. Then the Jacobi matrix $(D_y G)(\bar{y}, 1)$ reads

$$\begin{pmatrix}
\frac{\partial G_1}{\partial S_0} & \frac{\partial G_1}{\partial N_0} & 0 & \cdots & \cdots & \cdots & \cdots & \cdots & 0 \\
\frac{\partial G_2}{\partial S_0} & \frac{\partial G_2}{\partial N_0} & 0 & \cdots & \cdots & \cdots & \cdots & 0 & \frac{\partial G_2}{\partial x_{n,0}} \\
\frac{\partial G_3}{\partial S_0} & \frac{\partial G_3}{\partial N_0} & -1 & 0 & \cdots & \cdots & \cdots & 0 & \frac{\partial G_3}{\partial x_{n,0}} \\
\frac{\partial G_4}{\partial S_0} & \frac{\partial G_4}{\partial N_0} & \frac{\partial G_4}{\partial x_{2,0}} & -1 & \ddots & & & \vdots & \vdots \\
\frac{\partial G_5}{\partial S_0} & \frac{\partial G_5}{\partial N_0} & 0 & \frac{\partial G_5}{\partial x_{3,0}} & \ddots & \ddots & & \vdots & \vdots \\
\vdots & \vdots & \vdots & \ddots & \ddots & \ddots & \ddots & \vdots & \vdots \\
\vdots & \vdots & \vdots & & \ddots & \ddots & \ddots & 0 & \frac{\partial G_{n-1}}{\partial x_{n,0}} \\
\vdots & \vdots & \vdots & & & \ddots & \ddots & -1 & \frac{\partial G_n}{\partial x_{n,0}} \\
\frac{\partial G_{n+1}}{\partial S_0} & \frac{\partial G_{n+1}}{\partial N_0} & 0 & \cdots & \cdots & \cdots & 0 & \frac{\partial G_{n+1}}{\partial x_{n-1,0}} & \frac{\partial G_{n+1}}{\partial x_{n,0}}
\end{pmatrix}$$

since Eqs. (3.24), (3.27), (3.28) and (3.33) imply $\frac{\partial G_1}{\partial x_{i,0}} = 0$, $i = 2, \ldots, n$, $\frac{\partial G_2}{\partial x_{i,0}} = 0$, $i = 2, \ldots, n-1$, $\frac{\partial G_{i+1}}{\partial x_{i,0}} = -1$, $i = 2, \ldots, n-1$, and $\frac{\partial G_i}{\partial x_{j,0}} = 0$, $i = 3, \ldots, n$, $j \neq i-2, i-1, n$ at $(y, \beta) = (\bar{y}, 1)$. After a tedious but elementary computation we obtain

$$\begin{aligned}
\det(D_y G)(\bar{y}, 1) \;=\; (-1)^n \sum_{i=3}^{n+1} \Bigg(& \frac{\partial G_1}{\partial S_0} \left(\frac{\partial G_2}{\partial N_0} \frac{\partial G_i}{\partial x_{n,0}} - \frac{\partial G_2}{\partial x_{n,0}} \frac{\partial G_i}{\partial N_0} \right) \\
& - \frac{\partial G_1}{\partial N_0} \left(\frac{\partial G_2}{\partial S_0} \frac{\partial G_i}{\partial x_{n,0}} - \frac{\partial G_2}{\partial x_{n,0}} \frac{\partial G_i}{\partial S_0} \right) \Bigg) \prod_{j=i-1}^{n-1} \frac{\partial G_{j+2}}{\partial x_{j,0}}.
\end{aligned}$$

Differentiation of Eq. (3.24) at $(y, \beta) = (\bar{y}, 1)$ yields

$$\frac{\partial G_2}{\partial N_0} \frac{\partial G_i}{\partial x_{n,0}} - \frac{\partial G_2}{\partial x_{n,0}} \frac{\partial G_i}{\partial N_0} = n\mu \left(\frac{\partial T}{\partial N_0} \delta_{i,n+1} + \frac{\partial T}{\partial x_{n,0}} \frac{\partial x_{i-2}}{\partial N_0} (\bar{T}_n) \right)$$

and

$$\frac{\partial G_2}{\partial S_0} \frac{\partial G_i}{\partial x_{n,0}} - \frac{\partial G_2}{\partial x_{n,0}} \frac{\partial G_i}{\partial S_0} = n\mu \left(\frac{\partial T}{\partial S_0} \delta_{i,n+1} + \frac{\partial T}{\partial x_{n,0}} \frac{\partial x_{i-2}}{\partial S_0} (\bar{T}_n) \right)$$

for $i = 3, \ldots, n+1$, where we have used Eq. (2.10), $\bar{T}_n := \frac{1}{n\mu} \ln k$ and δ_{ij} denotes the Kronecker delta, and further

$$\det(D_yG)(\bar{y},1) = (-1)^n n\mu\Bigg(-\left(1-\frac{\partial S}{\partial S_0}(\bar{T}_n)\right)\frac{\partial T}{\partial N_0} - \frac{\partial S}{\partial N_0}(\bar{T}_n)\frac{\partial T}{\partial S_0}$$
$$+\sum_{i=3}^{n+1}\frac{\partial T}{\partial x_{n,0}}\left(-\left(1-\frac{\partial S}{\partial S_0}(\bar{T}_n)\right)\frac{\partial x_{i-2}}{\partial N_0}(\bar{T}_n)\right.$$
$$\left.-\frac{\partial S}{\partial N_0}(\bar{T}_n)\frac{\partial x_{i-2}}{\partial S_0}(\bar{T}_n)\right)\prod_{j=i-1}^{n-1}\frac{\partial x_j}{\partial x_{j,0}}(\bar{T}_n)\Bigg).$$

From Eqs. (3.25), (3.26) and (3.29)–(3.32) and assumptions (H_g) and (H_γ) we infer $\frac{\partial S}{\partial S_0}(\bar{T}_n) < 1$, $\frac{\partial S}{\partial N_0}(\bar{T}_n) < 0$, $\frac{\partial T}{\partial S_0} < 0$, $\frac{\partial T}{\partial N_0} > 0$, $\frac{\partial T}{\partial x_{n,0}} < 0$, $\frac{\partial x_{i-2}}{\partial S_0}(\bar{T}_n) > 0$, $\frac{\partial x_{i-2}}{\partial N_0}(\bar{T}_n) < 0$, $i = 3,\dots,n+1$, and $\frac{\partial x_j}{\partial x_{j,0}}(\bar{T}_n) > 0$, $j = 2,\dots,n$, which implies $\det(D_yG)(\bar{y},1) \neq 0$ and $\mathrm{sign}(\det(D_yG)(\bar{y},1)) = (-1)^{n-1}$. Thus we can apply the Implicit Function Theorem to G and obtain a nontrivial biologically meaningful fixed point of F_n for $\beta \in (1,\beta_1)$, $\beta_1 > 1$ suitably chosen. □

4. Numerical results

In the first example we investigate sign $\lambda'(1)$ numerically for the case of a linear growth rate (1.2) and a particular kind of consumption rate γ.

Example 4.1. We consider a linear growth rate (1.2) and scale the size variable such that $x_\alpha = 1$. Let the consumption rate be given by (cf. [6, p. 21])

$$\gamma(S,x) = f_1(S)x^2, \tag{4.1}$$

where f_1 is a strictly increasing function of S with $f_1(0) = 0$, and assume that the conditions (2.10) and (2.11) are satisfied, i.e.

$$\frac{1}{\mu}\ln k = \frac{1}{c}\ln\frac{f(\tilde{S}_1)-1}{f(\tilde{S}_1)-x_\omega}$$

or

$$f(\tilde{S}_1) = \frac{k^{\frac{c}{\mu}}x_\omega - 1}{k^{\frac{c}{\mu}}-1}.$$

Then we have

$$\bar{x}_1(t) = \frac{k^{\frac{c}{\mu}}x_\omega - 1}{k^{\frac{c}{\mu}}-1} - \mathrm{e}^{-ct}\frac{k^{\frac{c}{\mu}}(x_\omega-1)}{k^{\frac{c}{\mu}}-1}.$$

By Lemma 3.9 the stability of the nontrivial fixed point of the one-cohort problem within the set of n-cohort solutions depends on the sign of the function

$$q(c,\mu,k,x_\omega) := k^{-\frac{1}{\mu}}\int_0^{\frac{1}{\mu}\ln k}\mathrm{e}^{ct}(1-\mathrm{e}^{-t})\,dt$$
$$\times\int_0^{\frac{1}{\mu}\ln k}\mathrm{e}^{(1-\mu)t}\left(\frac{k^{\frac{c}{\mu}}x_\omega-1}{k^{\frac{c}{\mu}}-1}-\mathrm{e}^{-ct}\frac{k^{\frac{c}{\mu}}(x_\omega-1)}{k^{\frac{c}{\mu}}-1}\right)^2dt$$
$$-(1-k^{-\frac{1}{\mu}})\int_0^{\frac{1}{\mu}\ln k}\mathrm{e}^{(c-1)t}\int_0^t\mathrm{e}^{(1-\mu)\tau}\left(\frac{k^{\frac{c}{\mu}}x_\omega-1}{k^{\frac{c}{\mu}}-1}-\mathrm{e}^{-c\tau}\frac{k^{\frac{c}{\mu}}(x_\omega-1)}{k^{\frac{c}{\mu}}-1}\right)^2d\tau dt,$$

where $c > 0$, $\mu > 0$, $k > 1$ and $x_\omega > 1$ and these parameters are in general not connected by any condition and cannot be normalised by any additional scaling.

First we considered the case $kx_\alpha^3 = k = x_\omega^3$ (conservation of mass). The function q was computed for a grid of $(c, \mu, x_\omega) \in [0.001, 100] \times [0.001, 100] \times [1.25, 4.65]$ (i.e. the cases $k = 2$ up to $k = 100$ are included in this set) and the function q was always negative, which means that the fixed point of the one-cohort problem is stable for F_n, $n \geq 2$.

Next we let $k = 2$ fixed (division into two parts) and computed q for a grid of $(c, \mu, x_\omega) \in [0.001, 100] \times [0.001, 100] \times [\sqrt[3]{2}, 10]$ (i.e. $kx_\alpha^3 \leq x_\omega^3$). There exists an increasing function $\mu_1 : [0.001, 100] \to [0.001, 10]$ such that for $(c, \mu) \in [0.001, 100] \times [0.001, 100]$ with $\mu \geq \mu_1(c)$ there exists an $x_1(c, \mu) \in [\sqrt[3]{2}, 10]$ such that $q(c, \mu, x_\omega) \geq 0$ for $x_1(c, \mu) \leq x_\omega \leq 10$ and q negative elsewhere on $[0.001, 100] \times [0.001, 100] \times [\sqrt[3]{2}, 10]$. The function x_1 is decreasing in μ and increasing in c. For other values of k we obtained similar results, i.e. positive values of q could only occur for $kx_\alpha^3 < x_\omega^3$.

The mapping F_n, $n \leq 10$, was iterated numerically for linear growth rates (1.2) and consumption rates (4.1) with

$$f(S) = \frac{c_1 S}{c_2 S + 1}, \quad f_1(S) = \frac{c_3 S}{c_2 S + 1}, \tag{4.2}$$

where c_1, c_2 and c_3 are positive constants (Holling type II functional response, cf. [6]), and linear or logistic h for $kx_\alpha^3 = x_\omega^3$ (i.e. we considered cases where $\lambda'(1) < 1$ according to Example 4.1), $\beta > 1$ and different values of the initial data and the parameters. In all of our examples the iterations converged to a nontrivial fixed point of F_1 even if the initial data were not chosen close to this fixed point.

In the following example we investigate the asymptotic behaviour numerically for a case where the fixed point of the one-cohort problem is not stable for F_n, $n \geq 2$.

Example 4.2. We consider a linear growth rate (1.2) and a consumption rate (4.1) with (4.2), where $c = 1.5$, $c_1 = c_3 = 1$, $c_2 = 0.4$, and let $\mu = 0.5$, $k = 2$, $x_\alpha = 1$, $x_\omega = 2$ and $h(S, \beta) = 15\beta - S$. The trivial fixed point of F_1 becomes unstable at $\beta = 1$ and we have $q(1.5, 0.5, 2, 2) > 0$ (i.e. we chose the parameters such that q is positive). The nontrivial fixed point of F_1 was computed for $\beta = \frac{16}{15}$, $\frac{17}{15}$, $\frac{6}{5}$, $\frac{19}{15}$ and $\frac{4}{3}$ (cf. Table 1). The function $\bar{S}_0$ is strictly decreasing on $[1, \frac{4}{3}]$.

Table 1.

β	$\bar{S}_0(\beta)$	$\bar{N}_0(\beta)$
$\frac{16}{15}$	14.97	0.2392
$\frac{17}{15}$	14.94	0.4782
$\frac{6}{5}$	14.92	0.7170
$\frac{19}{15}$	14.89	0.9556
$\frac{4}{3}$	14.86	1.1939

For $\beta = \frac{19}{15}$ we investigated the asymptotic behaviour of F_n numerically for $n = 2, 3, 4$. Note that the quotients $N_{i,0}/N_{j,0}$ remain invariant under F_n^n.

For $n = 2$ we have after one application of F_2 $N'_{1,0}/N'_{2,0} = kN_{2,0}/N_{1,0}$. We iterated F_2 for different start values and the iterations converged to different periodic points of period two, depending on the start value of $N_{1,0}/N_{2,0}$. In the case that we started with $N_{1,0}/N_{2,0} = \sqrt{k}$ the periodic point of period two degenerated to the fixed point $(14.95, 0.4847, 0.3427, 1.739)$ of F_2. In Table 2 we show some periodic points of period two of F_2. Similarly periodic points of period n were found by iterating F_n for $n = 3, 4$, and these periodic points can again degenerate to fixed points. By replacing h by $h(S, \beta) = S(1 - \frac{S}{15\beta})$ we obtained similar results.

Table 2.

S_0	$N_{1,0}$	$N_{2,0}$	$x_{2,0}$
15.09	0.0814	0.8145	1.222
14.89	0.8748	0.0437	1.966
15.07	0.2960	0.5921	1.330
14.88	0.6632	0.1658	1.942
15.06	0.3534	0.5301	1.383
14.88	0.6074	0.2025	1.928
15.03	0.4345	0.4345	1.515
14.89	0.5304	0.2652	1.883

Example 4.2 suggests that in the 'unstable' case $(\lambda'(1) > 1)$ there exist families of periodic points of period n of F_n, $n \geq 2$, for $1 < \beta < \beta_1$ that can be 'degenerate' (i.e. periodic points of period m, $1 \leq m < n$, m a divisor of n) and belong to the domain of attraction of F_n.

5. Concluding remarks

This simple population model exhibits the feature that cohorts 'synchronise' in the course of time at least for particular choices of the functions, parameters and initial values. This behaviour is well-documented by numerical results. It still remains to determine the domain of attraction in the 'unstable' case $(\lambda'(1) > 0)$. We conjecture that in that case there are families of periodic points of period n (that can be 'degenerate', i.e. periodic points of period m, m a divisor of n) of F_n for all n belonging to the domain of attraction of F_n. Moreover, the results we obtained are only local in nature. Since the mappings F_n might have discontinuities and it is not easy to quantify where they occur, it is difficult to make global statements about the existence and stability of periodic points. However, if $S_x = 0$ for all $x \in [x_\alpha, x_\omega]$ in the condition (H_g), there are no discontinuities.

The robustness of the results with respect to slight changes in the model specification is also still an open problem. For example, it is only an idealisation to say that all individuals reproduce at size x_ω when experimentally they are observed to reproduce at an almost fixed size. When reproduction occurs at a stochastically predetermined size, independent of any characteristics of an individual's forbears, provided it does not die before that time, single cohort solutions do not exist any more and we have to analyse the model by means of the associated renewal equation. We conjecture that, if the 'size at reproduction precluding death' is only a little distributed around x_ω, there exists a periodic solution with one peak instead of a periodic single cohort solution, and this solution will be stable with respect to little perturbations in the initial conditions if $\lambda(\beta) < 1$ for the associated model with reproduction at size x_ω, i.e. if the periodic one-cohort solution of that model is stable with respect to splitting into n cohorts. A few simple numerical experiments seem to support this conjecture.

6. Appendix: Proof of Theorem 3.10 for $n \geq 3$

Let $n \geq 3$. The nontrivial fixed point $(\bar{S}_0(\beta), \bar{N}_0(\beta))$ of F_1 for $\beta \in U \cap (1, \infty)$ corresponds to a family of periodic points $(S_0, N_{1,0}, \ldots, N_{n,0}, x_{2,0}, \ldots, x_{n,0})$, $S_0 = \bar{S}_0(\beta)$, $\sum_{i=1}^n N_{i,0} = \bar{N}_0(\beta)$, $x_{i,0} = x_\alpha$ for $i = 2, \ldots, n$, of period n of F_n. Let $F_n^n : (S_0, N_{1,0}, \ldots, N_{n,0}, x_{2,0}, \ldots, x_{n,0}) \mapsto (S_0^{(n)}, N_{1,0}^{(n)}, \ldots, N_{n,0}^{(n)}, x_{2,0}^{(n)}, \ldots, x_{n,0}^{(n)})$ and $T_i := T(F_n^{i-1}(S_0, N_{1,0}, \ldots, N_{n,0}, x_{2,0}, \ldots, x_{n,0}))$, $i = 1, \ldots, n$. Then $N_{i,0}^{(n)} = kN_{i,0}\mathrm{e}^{-\mu \sum_{j=1}^n T_j}$, $i = 1, \ldots, n$, so the quotients $N_{i,0}/N_{j,0}$ remain invariant under F_n^n if the denominators are not zero. For a vector $\eta = (\eta_2, \ldots, \eta_n)$, $\eta_i > 0$ for $i = 2, \ldots, n$, we define $K_\eta : (S_0, N_0, x_{2,0}, \ldots, x_{n,0}) \mapsto (S_0^{(n)}, N_0^{(n)}, x_{2,0}^{(n)}, \ldots, x_{n,0}^{(n)})$ by

$$\begin{aligned}\big(S_0^{(n)}, \frac{1}{\zeta}N_0^{(n)}, \frac{\eta_2}{\zeta}N_0^{(n)}, \ldots, \frac{\eta_n}{\zeta}N_0^{(n)}, x_{2,0}^{(n)}, \ldots, x_{n,0}^{(n)}\big) \\ := F_n^n\big(S_0, \frac{1}{\zeta}N_0, \frac{\eta_2}{\zeta}N_0, \ldots, \frac{\eta_n}{\zeta}N_0, x_{2,0}, \ldots, x_{n,0}\big),\end{aligned}$$

where $\zeta := 1 + \sum_{i=2}^n \eta_i$. The Jacobi matrix of K_η at the nontrivial fixed point $(\bar{S}_0(\beta), \bar{N}_0(\beta), x_\alpha, \ldots, x_\alpha)$ equals

$$\begin{pmatrix} \multicolumn{2}{c}{\multirow{2}{*}{A}} & * & \cdots & \cdots & \cdots & * \\ & & * & \cdots & \cdots & \cdots & * \\ 0 & 0 & \frac{\partial x_{2,0}^{(n)}}{\partial x_{2,0}} & 0 & \cdots & \cdots & 0 \\ \vdots & \vdots & 0 & \frac{\partial x_{3,0}^{(n)}}{\partial x_{3,0}} & \ddots & & \vdots \\ \vdots & \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \vdots & \vdots & & \ddots & \ddots & 0 \\ 0 & 0 & 0 & \cdots & \cdots & 0 & \frac{\partial x_{n,0}^{(n)}}{\partial x_{n,0}} \end{pmatrix}, \tag{6.1}$$

where the (2×2)-matrix A is again defined by Eq. (3.4) and the zeros in the last $(n-1)$ rows are due to the fact that $x_{i,0}^{(n)} = x_\alpha$ for $x_{i,0} = x_\alpha$ independent of S_0, N_0 and $x_{j,0}$, $j \neq i$, for $i = 2, \ldots, n$.

The following lemma is a generalisation of Lemma 3.2 to the case $n \geq 3$.

Lemma 6.1. *We have*

$$\frac{\partial x_{i,0}^{(n)}}{\partial x_{i,0}}(\bar{S}_0(\beta), \bar{N}_0(\beta), x_\alpha, \ldots, x_\alpha) = \lambda(\beta), \quad i = 2, \ldots, n,$$

where λ is given by Eq. (3.6).

Proof. Let $n \geq 3$. The quantities $x_{i,0}^{(n)}$ for $S_0 = \bar{S}_0(\beta)$, $N_0 = \bar{N}_0(\beta)$ are obtained by solving the following recursive ODE systems. First solve the system

$$\begin{cases} \dfrac{dx_1^{(1)}}{dt} = g(S^{(1)}, x_1^{(1)}), \quad x_1^{(1)}(0) = x_\alpha, \\ \dfrac{dx_i^{(1)}}{dt} = g(S^{(1)}, x_i^{(1)}), \quad x_i^{(1)}(0) = x_{i,0}, \quad i = 2, \ldots, n, \\ \dfrac{dS^{(1)}}{dt} = h(S^{(1)}, \beta) - \bar{N}_0(\beta)\zeta^{-1}\mathrm{e}^{-\mu t} \displaystyle\sum_{i=1}^{n} \eta_i \gamma(S^{(1)}, x_i^{(1)}), \quad S^{(1)}(0) = \bar{S}_0(\beta), \end{cases}$$

where $\eta_1 := 1$ and $\zeta := \sum_{i=1}^{n} \eta_i$ as before. Let $T_1 \geq 0$ be such that $x_n^{(1)}(T_1) = x_\omega$, $x_n^{(1)}(t) < x_\omega$ for $0 \leq t < T_1$, and set $S_0^{(1)} := S^{(1)}(T_1)$, $N_0^{(1)} := \bar{N}_0(\beta)\mathrm{e}^{-\mu T_1}$ and $x_{i,0}^{(1)} := x_{i-1}^{(1)}(T_1)$, $i = 2, \ldots, n$.

For $j = 2, \ldots, n$ we solve recursively the ODE systems

$$\begin{cases} \dfrac{dx_1^{(j)}}{dt} = g(S^{(j)}, x_1^{(j)}), \quad x_1^{(j)}(0) = x_\alpha, \\ \dfrac{dx_i^{(j)}}{dt} = g(S^{(j)}, x_i^{(j)}), \quad x_i^{(j)}(0) = x_{i,0}^{(j-1)}, \quad i = 2, \ldots, n, \\ \dfrac{dS^{(j)}}{dt} = h(S^{(j)}, \beta) - N_0^{(j-1)}\zeta^{-1}\mathrm{e}^{-\mu t} \left(k \displaystyle\sum_{i=1}^{j-1} \eta_{n+i-j+1} \gamma(S^{(j)}, x_i^{(j)}) \right. \\ \qquad\qquad \left. + \displaystyle\sum_{i=j}^{n} \eta_{i-j+1} \gamma(S^{(j)}, x_i^{(j)}) \right), \quad S^{(j)}(0) = S_0^{(j-1)}. \end{cases}$$

Let $T_j \geq 0$ be such that $x_n^{(j)}(T_j) = x_\omega$, $x_n^{(j)}(t) < x_\omega$ for $0 \leq t < T_j$, and define $S_0^{(j)} := S^{(j)}(T_j)$, $N_0^{(j)} := N_0^{(j-1)}\mathrm{e}^{-\mu T_j}$, $x_{i,0}^{(j)} := x_{i-1}^{(j)}(T_j)$, $i = 2, \ldots, n$.

For $(x_{2,0}, \ldots, x_{n,0}) = (x_\alpha, \ldots, x_\alpha)$ we have $T_1 = \bar{T}$ and $T_j = 0$ for $j = 2, \ldots, n$. Moreover, for $j = 1, \ldots, n$ we have $x_{i,0}^{(j)} = x_\alpha$, $i = 2, \ldots, j$, and $x_{i,0}^{(j)} = x_\omega$, $i = j+1, \ldots, n$. We shall in the following often use the fact that

$$\frac{\partial x_i^{(j)}}{\partial x_{i,0}^{(j-1)}}(0) = 1, \quad i = 2, \ldots, n, \tag{6.2}$$

and

$$\frac{\partial x_i^{(j)}}{\partial N_0^{(j-1)}}(0) = \frac{\partial x_i^{(j)}}{\partial S_0^{(j-1)}}(0) = \frac{\partial x_i^{(j)}}{\partial x_{k,0}^{(j-1)}}(0) = 0, \quad k \neq i, \quad i = 1, \ldots, n, \tag{6.3}$$

for $j = 2, \ldots, n$.

For the remainder of the proof we assume that all partial derivatives are taken at $(x_{2,0}, \ldots, x_{n,0}) = (x_\alpha, \ldots, x_\alpha)$. By differentiating the equations $x_n^{(j)}(T_j) = x_\omega$, $j = 1, \ldots, n$, and by using Eqs. (6.2) and (6.3) we obtain for $i = 2, \ldots, n$

$$\frac{\partial T_1}{\partial x_{i,0}} = -\frac{1}{g(\bar{S}_0(\beta), x_\omega)} \frac{\partial x_n^{(1)}}{\partial x_{i,0}}(\bar{T})$$

and

$$\frac{\partial T_j}{\partial x_{i,0}} = -\frac{1}{g(\bar{S}_0(\beta), x_\omega)} \frac{\partial x_{n,0}^{(j-1)}}{\partial x_{i,0}}, \quad j = 2, \ldots, n.$$

For $j = 2, \ldots, n$, $i = 2, \ldots, n$ we have

$$\frac{\partial x_{2,0}^{(j)}}{\partial x_{i,0}} = \dot{x}_1^{(j)}(0) \frac{\partial T_j}{\partial x_{i,0}} = -\frac{g(\bar{S}_0(\beta), x_\alpha)}{g(\bar{S}_0(\beta), x_\omega)} \frac{\partial x_{n,0}^{(j-1)}}{\partial x_{i,0}} \tag{6.4}$$

and

$$\begin{aligned}\frac{\partial x_{k,0}^{(j)}}{\partial x_{i,0}} &= \dot{x}_{k-1}^{(j)}(0) \frac{\partial T_j}{\partial x_{i,0}} + \frac{\partial x_{k-1,0}^{(j-1)}}{\partial x_{i,0}} = \frac{\partial x_{k-1,0}^{(j-1)}}{\partial x_{i,0}} - \frac{g(\bar{S}_0(\beta), x_{k-1,0}^{(j-1)})}{g(\bar{S}_0(\beta), x_\omega)} \frac{\partial x_{n,0}^{(j-1)}}{\partial x_{i,0}} \\ &= \begin{cases} \dfrac{\partial x_{k-1,0}^{(j-1)}}{\partial x_{i,0}} - \dfrac{g(\bar{S}_0(\beta), x_\alpha)}{g(\bar{S}_0(\beta), x_\omega)} \dfrac{\partial x_{n,0}^{(j-1)}}{\partial x_{i,0}}, & k = 3, \ldots, j, \\ \dfrac{\partial x_{k-1,0}^{(j-1)}}{\partial x_{i,0}} - \dfrac{\partial x_{n,0}^{(j-1)}}{\partial x_{i,0}}, & k = j+1, \ldots, n. \end{cases}\end{aligned} \tag{6.5}$$

The derivatives of $x_{k,0}^{(1)}$ are given by

$$\frac{\partial x_{k,0}^{(1)}}{\partial x_{i,0}} = \dot{x}_{k-1}^{(1)}(\bar{T}) \frac{\partial T_1}{\partial x_{i,0}} + \frac{\partial x_{k-1}^{(1)}}{\partial x_{i,0}}(\bar{T}) = \frac{\partial x_{k-1}^{(1)}}{\partial x_{i,0}}(\bar{T}) - \frac{\partial x_n^{(1)}}{\partial x_{i,0}}(\bar{T}), \quad k, i = 2, \ldots, n. \tag{6.6}$$

From Eqs. (6.4)–(6.6) we obtain recursively

$$\frac{\partial x_{i,0}^{(n)}}{\partial x_{i,0}} = -\frac{g(\bar{S}_0(\beta), x_\alpha)}{g(\bar{S}_0(\beta), x_\omega)} \left(\frac{\partial x_1^{(1)}}{\partial x_{i,0}}(\bar{T}) - \frac{\partial x_i^{(1)}}{\partial x_{i,0}}(\bar{T}) \right), \quad i = 2, \ldots, n.$$

Similarly as in the proof of Lemma 3.2 we have

$$\frac{\partial x_i^{(1)}}{\partial x_{i,0}}(\bar{T}) - \frac{\partial x_1^{(1)}}{\partial x_{i,0}}(\bar{T}) = \exp\left(-\int_0^{\bar{T}} \frac{\partial g}{\partial x}(\bar{S}_\beta(t), \bar{x}_\beta(t))\, dt \right), \quad i = 2, \ldots, n,$$

which finishes the proof. □

Thus the eigenvalues of the Jacobi matrix (6.1) are the eigenvalues of the matrix A and the $(n-1)$-fold eigenvalue λ, which implies that the stability of the nontrivial periodic one-cohort solution with respect to splitting into n cohorts ($n \geq 3$) also only depends on the value of the single quantity $\lambda(\beta)$.

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