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On circulant populations. I. The algebra of semelparity

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Abstract

We consider a class of nonlinear Leslie matrix models, describing the population dynamics of an age-structured semelparous species. Semelparous species are those whose individuals reproduce only once and die afterwards. Competitive interaction between individuals is modelled via a one-dimensional environmental quantity. Age classes are characterised by their impact on, and their sensitivity to, the environment. We do not restrict ourselves to some particular form of functional dependence and keep the model otherwise as general as possible.

The system possesses a cyclic symmetry. Due to the symmetry it exhibits so-called vertical bifurcations, where a manifold filled with periodic orbits appears in the phase space for specific parameter combinations. This bifurcation serves as a switch between the main types of behaviour: coexistence of all year classes or a periodic regime with some year classes missing. In particular, the vertical bifurcation takes place when a certain circulant matrix is singular.

We also analyse the local stability of the unique coexistence equilibrium state and derive a characteristic equation for it. The dynamics of populations with two and, especially, with three age classes are analysed in detail.

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1. Introduction

A semelparous organism reproduces only once in its life, as reproduction has death as an inevitable consequence. Examples include many plants, Pacific salmon, cicada's and many other species. If ever one speaks about the life *cycle*, it should be for these organisms.

If seasonal variations allow for only one reproduction opportunity per year, the length of the life cycle is an integer number of years. This is the situation considered in this paper: we strictly fix the period in between being born and going to reproduce at k years. All individuals born in some year then mate and reproduce k years later, so are *reproductively isolated* from individuals born in other years. Consequently we distinguish k subpopulations, called *year classes*, according to the year of birth modulo k.

Year classes are, in general, not independent from one another, as they may influence each others living conditions, e.g., by competition for food. Once a year class is extinct, it stays extinct, because of the assumed strictness of the length of the life cycle. So year classes may be *missing*, i.e., have density zero. *Periodical insects* [2] are characterized by the fact that all but one year classes are missing. The most famous example are certain cicada species in North America, some of which have $k = 13$ while others have $k = 17$ (see e.g., [1] and the references in there).

The general aim of our investigation is to understand, in terms of a submodel for interaction (i.e., density dependence), when we should expect to find coexistence of year classes (as, e.g., in salmon) and when competitive exclusion (as in the periodical insects)? When does one year class tune the environmental conditions such that other year classes, when low in abundance, are driven to extinction? And when, on the other hand, can a missing year class invade successfully? How many year classes persist? What pattern in fluctuations of cohort sizes should we expect? How do the answers to these questions depend on k?

The structure of the paper is as follows. In Section 2 we introduce notation and formulate a *linear* Leslie matrix model. In this case survival probabilities and the number of offspring are density independent. We introduce a compound parameter R_0, called the *basic reproduction ratio*. The dynamics of the model is fully characterized by R_0: the population grows if $R_0 > 1$ and declines if $R_0 < 1$, while the relative proportions of the age classes cycle with period k.

We also notice that the linear model possesses a cyclic symmetry which extends to a nonlinear model which we introduce in Section 3, see also [10]. The density dependence is incorporated via an *environmental quantity* I, which we assume to be one-dimensional (it is a linear combination of age class numbers). We define the impact of age classes on the environment and the sensitivity to it. Furthermore, we perform a scaling of the nonlinear model which simplifies the further investigations and the presentation of results. Also in Section 3 we find a unique steady state with all year classes present (to which we refer both as the coexistence steady state/equilibrium and as the internal steady state/equilibrium).

In Section 4 we begin the analysis of the nonlinear model. We look for k-periodic orbits. The environmental quantity I is then also k-periodic and takes values $I_0, \dots, I_{k-1}$ which should be solutions of a *nonlinear circulant* system. In the case with all I_i equal, the relation between I and the age class numbers N_i is given by a *linear circulant* system. If the corresponding circulant matrix is singular, there is a whole family of k-cycles with all year classes present. In this section we consider the most degenerate situation when all impacts are equal (*uniform impact* case). An analogue of that, but for the nonlinear circulant, is when all sensitivity functions are the same. In that case we speak about *uniform sensitivity*. In both cases there is a manifold in the phase space filled with periodic orbits. If such a phenomenon is observed for some particular parameter combination in a model, we call it a *vertical bifurcation*.

In Section 5 we derive a detailed list of conditions for the singularity of a circulant matrix, as a generalization of the uniform impact case described in Section 4. In Section 6 we describe manifolds (which are just simplices) filled with k-cycles corresponding to different cases of singularity of the circulant.

In Section 7 we look for families of k-cycles if the environmental quantity is not constant, i.e. the nonlinear circulant system has nonuniform solutions. In fact, we generalize the uniform sensitivity case of Section 4.

In Section 8 we write down a characteristic equation corresponding to the internal steady state. Though we are not able to perform a full linear stability analysis, we show that eigenvalues of the internal steady state are on the unit circle under the conditions for the vertical bifurcations found in Sections 5 and 7. It leads us to conjecture that the vertical bifurcations serve as a switch between the stability of the internal steady state and the stability of a cycle with some year classes missing.

In Section 9 we consider the other extreme, a k-cycle with only one year class present. We call this case Single Year Class (SYC) dynamics [8,23,25]. We show, in particular, that a SYC-cycle is stable in a special case when the impact on the environment is a decreasing function of age while the sensitivity increases with age.

Section 10 is devoted to biennials ($k = 2$). It is a short section, because this case is already analysed in detail in [8], see also [5,21]. In fact we focus on the effect of different nonlinearities in survival probability functions. We choose them so that the ratio is nonmonotone. The consequence is that a generic period doubling bifurcation of the internal steady state occurs, instead of the vertical bifurcation.

In the long Section 11 we deal with $k = 3$. We construct a bifurcation diagram for the stability of the internal steady state. Then we consider the specific case that only the survival probability of the youngest year class is density dependent. In this particular case we make a rather detailed bifurcation analysis of the model: we analyse stability of the internal steady state, of single year class equilibria and stability of multiple year class equilibria and make a combined bifurcation diagram.

2. The linear model

In this section we consider a k-dimensional linear recursion

$$N(t+1) = L(h)N(t). \tag{2.1}$$

We number the *age classes* from 0 to $k-1$. A component $N_i(t)$ of the vector $N(t)$ denotes the number of individuals in the ith age class. Time is measured in years, $t \in \mathbb{Z}$. The symbol h denotes the k-vector with components $h_i > 0$ where, for $i = 0, \ldots, k-2$, h_i is the *survival probability* of an i-years old individual in some year to an $(i+1)$-years old individual in the next year, and h_{k-1} is the *expected number of offspring* of a $(k-1)$-years old individual *in the next year*. We use $L(h)$ to denote the Leslie matrix corresponding to h. So, explicitly we have

$$L(h) = \begin{pmatrix} 0 & 0 & \cdots & 0 & h_{k-1} \\ h_0 & 0 & \cdots & 0 & 0 \\ 0 & h_1 & \cdots & 0 & 0 \\ \cdots & & & & \\ 0 & 0 & \cdots & h_{k-2} & 0 \end{pmatrix}. \tag{2.2}$$

Adopting (throughout the paper!) the convention that indices are considered modulo k, we can express the solution to (2.1) explicitly in terms of the initial condition by the formula

$$N_i(t) = \left(\prod_{j=0}^{t-1} h_{i-t+j} \right) N_{i-t}(0).$$

Putting $t = k$ we find in particular

$$N_i(k) = R_0 N_i(0) \tag{2.3}$$

with R_0 the so-called *basic reproduction ratio* defined by

$$R_0 = \prod_{i=0}^{k-1} h_i. \tag{2.4}$$

So the dynamics is a superposition of a cyclic shift and growth (if $R_0 > 1$) or decline (if $R_0 < 1$). Under the constant (by assumption) environmental conditions all year classes have the same per generation growth factor R_0 and the relative proportions in which they occur return to the initial values after every k years.

Thus we obtained a complete description of the dynamics in the case of independent year classes, but we add some observations for future use. The matrix $L(h)$ with positive components h_i is irreducible but not primitive. In fact it has period k [22], which is reflected in the characteristic equation

$$\lambda^k = R_0$$

and its roots, which are the $R_0^{\frac{1}{k}}$ multiples of the kth roots of unity.

Let **1** denote the k-vector with all components equal to 1, then

$$S = L(\mathbf{1}) = \begin{pmatrix} 0 & \cdots & 0 & 1 \\ 1 & \cdots & 0 & 0 \\ & \cdots & & \\ 0 & \cdots & 1 & 0 \end{pmatrix} \tag{2.5}$$

is the cyclic forward shift on $\mathbb{R}^k$

$$S \begin{pmatrix} x_0 \\ x_1 \\ \cdots \\ x_{k-1} \end{pmatrix} = \begin{pmatrix} x_{k-1} \\ x_0 \\ \cdots \\ x_{k-2} \end{pmatrix}.$$

The transpose S^{T} equals the inverse S^{-1}, which is the cyclic backward shift. Moreover, as a straightforward calculation shows, one has the following two results.

Lemma 2.1. $SL(h)S^{-1} = L(Sh)$.

Corollary 2.2. *The recursion* (2.1) *is invariant under the transformation* $N \mapsto SN$, $h \mapsto Sh$.

3. Formulation and scaling of the nonlinear model

We next introduce density dependence (nonlinearity) in a two step procedure. First, we assume that the positive quantities h_i, defined in the previous section, depend on a variable I describing the *environmental condition*. Throughout this paper we restrict ourselves to the case that I is a one-dimensional real variable. (We assume also that the functions $h_i(I)$ are decreasing and smooth enough, so if we deal with derivatives $h_i'(I)$, we choose these functions to be C^1 etc.) Typical examples of the kind of dependence are provided by the Ricker family

$$h_i(I) = \sigma_i \mathrm{e}^{-g_i I} \tag{3.1}$$

and the Beverton–Holt family

$$h_i(I) = \frac{\sigma_i}{1 + g_i I}. \tag{3.2}$$

In the second step of the model construction, we formulate a feedback law that relates the environmental condition I to the population size and composition N. Specifically we postulate the linear relation

$$I = c \cdot N = \sum_{i=0}^{k-1} c_i N_i.$$

The underlying idea is that I should be such that individuals are independent from one another when I is given (prescribed) and that this independence extends to the feedback. More details on the notion of I and on the general modelling philosophy can be found in [11,12].

We shall use the following terminology: c_i is the age-specific *impact* on the environmental condition, and the functions $h_i(I)$ are the age-specific *sensitivity to the environment*; in cases like (3.1) and (3.2), the parameters g_i are also called the sensitivity to the environment. (The quantities σ_i featuring in (3.1) and (3.2) are of minor importance, as we will show below that they can be eliminated by an appropriate scaling.)

The term “sensitivity” is already used in the literature on matrix population models [3]. The sensitivity of a quantity $f(x)$ to x is just the derivative $f'(x)$. But it is more convenient for our purposes to call the functions $h_i(I)$ *sensitivity functions*. This reflects the fact that the survival probabilities and/or number of offspring depend on the environment or, in other words, they are *sensitive* to the environment.

Very often we want sensitivity to be a parameter, not a function. If the functions $h_i(I)$ are chosen from the same two-parameter family $\sigma H(gI)$, as indeed in the Ricker (3.1) and Beverton–Holt (3.2) cases, $h_i(I)$ can be written in the form

$$h_i(I) = \sigma_i H(g_i I), \tag{3.3}$$

where the function H is normalized so that

$$H(0) = |H'(0)| = 1. \tag{3.4}$$

(These equalities are indeed satisfied for the Ricker and Beverton–Holt families.) But, in general, we do not put this restriction on the functions h_i and only use it whenever useful.

So, the object of our study is the dynamical system generated by the nonlinear recursion

$$\begin{aligned} N(t+1) &= L(h(I(t)))N(t), \\ I(t) &= c \cdot N(t). \end{aligned} \tag{3.5}$$

Since $c \cdot N = Sc \cdot SN$ (recall that $S^{\mathrm{T}} = S^{-1}$!) there is an analogue to Corollary 2.2.

Lemma 3.1. *The recursion* (3.5) *is invariant under the transformation* $N \mapsto SN$, $h \mapsto Sh$, $c \mapsto Sc$.

(Here we take the notational freedom of denoting the “lift” of S from $\mathbb{R}^k$ to $\mathbb{R}^k$-valued functions by the same symbol.)

When I is constant we are back to the linear setting of the preceding section. Motivated by (2.3) and (2.4) we notice that $N_i(k) = N_i(0)$ if

$$\prod_{i=0}^{k-1} h_i(I) = 1. \tag{3.6}$$

The basic reproduction ratio R_0 now corresponds to the virgin environment $I = 0$ and is given by

$$R_0 := \prod_{i=0}^{k-1} h_i(0). \tag{3.7}$$

We assume that

(i) $R_0 > 1$;
(ii) $\prod_{i=0}^{k-1} h_i(I)$ is a strictly decreasing continuous function of I;
(iii) $\lim_{I\to\infty} \prod_{i=0}^{k-1} h_i(I) < 1$.

The consequence is that (3.6) has a unique positive solution, which we denote by $\overline{I}$. So the *steady environmental condition* $\overline{I}$ is such that under this condition the population will neither grow nor decline, but just cycle with period k. Technically we have

$$\prod_{i=0}^{k-1} h_i(\overline{I}) = 1. \tag{3.8}$$

Even though $\overline{I}$ is only implicitly determined, we use it to perform a scaling of N, h and c. We stress that this scaling has miraculous effects in simplifying the subsequent analysis (having struggled a lot with messy calculations before discovering this scaling, we feel entitled to do so)!

Theorem 3.2. *Consider the system* (3.5). *By scaling one can achieve that*

$$\begin{aligned} &h_i(\overline{I}) = 1 \quad \textit{for } i = 0, \dots, k-1, && \text{(a)} \\ &\sum_{i=0}^{k-1} c_i = 1. && \text{(b)} \end{aligned} \tag{3.9}$$

Proof. Below the upper index "s" denotes "scaled" variables and "u" denotes "unscaled" variables. Let for $i = 0, \dots, k-1$

$$\begin{aligned} N_i^s &= \theta_i^{-1} N_i^u, \\ h_i^s(I) &= \frac{\theta_i}{\theta_{i+1}} h_i^u(I), \\ c_i^s &= \theta_i c_i^u, \end{aligned} \tag{3.10}$$

where

$$\theta_{i+1} = \theta_i \, h_i^u(\overline{I}) = \theta_0 \prod_{j=0}^{i} h_j^u(\overline{I}),$$

$$\theta_0 = \left(\sum_{i=0}^{k-1} c_i^u \prod_{j=0}^{i-1} h_j^u(\overline{I}) \right)^{-1}.$$

The system (3.5) is invariant under this transformation and the properties (3.9) are satisfied for h_i^s and c_i^s. □

Remark. Under the scaling (3.10)

$$h_i^s(I) = \frac{h_i^u(I)}{h_i^u(\overline{I})}.$$

In particular, if the functions $h_i^u(I)$ belong to a two-parameter family (3.3), we have for the new functions

$$h_i^s(I) = \frac{H(g_i I)}{H(g_i \overline{I})}. \tag{3.11}$$

Under the scaling the Ricker family and the Beverton–Holt family look, respectively, as follows:

$$h_i(I) = \mathrm{e}^{-g_i(I-\overline{I})}, \tag{3.12}$$

$$h_i(I) = \frac{1 + g_i \overline{I}}{1 + g_i I}. \tag{3.13}$$

One can notice that the scaling (3.10) is not complete, there is still some freedom, as we have not scaled I, we have only fixed relative scales of N_i for different i. Now we choose an absolute scale for N.

Theorem 3.3. *If the scaled functions $h_i(I)$ belong to the family* (3.11), *by another scaling one can achieve that*

$$\sum_{i=0}^{k-1} g_i = 1 \tag{3.14}$$

without destroying the properties (3.9) *and* (3.11).

Proof. The scaling is given by

$$N^{ss} = N^s \sum_{i=0}^{k-1} g_i^u,$$

$$g_i^s = \frac{g_i^u}{\sum_{i=0}^{k-1} g_i^u},$$

where the index "ss" denotes doubly scaled N. Then the properties (3.14) and (3.9) hold. Since

$$I^s = I^u \sum_{i=0}^{k-1} g_i^u$$

we notice that $g_i I$ is invariant under the scaling for all i. Hence the functions $h_i^s(I)$ do not change and still have the form (3.11). □

In the rest of the paper we consider the situation after scaling, i.e., we deal with N^{ss}, c^s, g^s and h^s, but still use the symbols N, c, g and h without "s", just like we did in (3.5). If (3.11) does not apply, we do not perform the second scaling and deal with N^s (or adopt the convention $N^{ss} = N^s$).

A first advantage of the proposed scaling is demonstrated by the very simple form in which the unique coexistence steady state of (3.5) appears.

Corollary 3.4

$$L(h(\overline{I})) = L(\mathbf{1}) = S.$$

Theorem 3.5. *The nonlinear recursion* (3.5) *has a unique nontrivial steady state*

$$\overline{N} = \mathbf{1}\overline{I}. \tag{3.15}$$

4. In search for *k*-periodic orbits with all year classes present

As k-periodicity is inherent in the life cycle, it is natural to look for k-periodic orbits of (3.5). We first look for conditions on the values I_i that the environmental condition takes. So assume $t \mapsto N(t)$ is k-periodic and define $I_i = c \cdot N(i)$ then necessarily

$$N_j(k) = \left(\prod_{i=0}^{k-1} h_{j+i}(I_i) \right) N_j(0) \tag{4.1}$$

(this is just the time-inhomogeneous analogue of (2.3)). So either the jth year class is missing or we need to have that

$$\prod_{i=0}^{k-1} h_{j+i}(I_i) = 1. \tag{4.2}$$

If we want all of the year classes to be present we therefore need to solve the system of k equations:

$$\begin{array}{lllll} h_0(I_0) & h_1(I_1) & \cdots & h_{k-1}(I_{k-1}) & = 1, \\ h_{k-1}(I_0) & h_0(I_1) & \cdots & h_{k-2}(I_{k-1}) & = 1, \\ \cdots & & & & \\ h_1(I_0) & h_2(I_1) & \cdots & h_0(I_{k-1}) & = 1 \end{array} \tag{4.3}$$

for the k unknowns $I_0, I_1, \ldots, I_{k-1}$. By analogy with a circulant matrix (see Section 5), we call the left-hand side of (4.3) a *nonlinear circulant* (and (4.3) itself a nonlinear circulant (system of) equation(s)). The relation between $\mathbf{I}$ and N is given implicitly by the equation:

$$\begin{pmatrix} c_0 & \cdots & c_{k-1} \\ c_1 h_0(I_0) & \cdots & c_0 h_{k-1}(I_0) \\ \cdots & \cdots & \cdots \\ c_{k-1} h_{k-2}(I_{k-2}) \cdots h_0(I_0) & \cdots & c_{k-2} h_{k-3}(I_{k-2}) \cdots h_0(I_1) h_{k-1}(I_0) \end{pmatrix} N = \mathbf{I}. \tag{4.4}$$

If $I_i = \overline{I}$ for $i = 0, \ldots, k-1$, then (4.3) is just a k-fold repetition of (3.8) and therefore satisfied. So we know already one solution of (4.3); we call this solution *uniform*, and before embarking on the question whether there are any other (*nonuniform*) solutions, we consider the second step of the construction of k-periodic orbits, which consists of determining one or more initial conditions that yield the correct sequence of I-values. When $I_i = \overline{I}$ we can exploit Corollary 3.4 to deduce that our task is to determine $N \in \mathbb{R}^k$ such that

$$\overline{I} = c \cdot S^i N = S^{-i} c \cdot N \quad \text{for } i = 0, \ldots, k-1$$

or, written out in detail,

$$\begin{array}{l} c_0 N_0 + c_1 N_1 + \cdots + c_{k-1} N_{k-1} = \overline{I}, \\ c_{k-1} N_0 + c_0 N_1 + \cdots + c_{k-2} N_{k-1} = \overline{I}, \\ \cdots \\ c_1 N_0 + c_2 N_1 + \cdots + c_0 N_{k-1} = \overline{I} \end{array} \tag{4.5}$$

and, in more symbolic form,

$$CN = \mathbf{1}\overline{I}, \tag{4.6}$$

where C is the *circulant matrix* [6] generated by the vector c (see Section 5):

$$C = \begin{pmatrix} c_0 & c_1 & \cdots & c_{k-1} \\ c_{k-1} & c_0 & \cdots & c_{k-2} \\ \cdots & & & \\ c_1 & c_2 & \cdots & c_0 \end{pmatrix}. \tag{4.7}$$

Again we already know a solution, viz. (3.15). But is it the only solution? It is if C is non-singular and it is not if C is singular, so we reformulate the question as: *when is a nonnegative circulant matrix singular*? The next section is devoted to answering this question. But before being systematic we study the most singular case, which obviously corresponds to all c_i being equal. In that case (4.5) is simply the k-fold repetition of the equation $c \cdot N = \overline{I}$. In combination with Corollary 3.4 this observation immediately leads to

Theorem 4.1 (uniform impact). *If* $c = \mathbf{1}\frac{1}{k}$ *the simplex*

$$\left\{ N : c \cdot N = \frac{1}{k} \sum_{i=0}^{k-1} N_i = \overline{I} \right\} \tag{4.8}$$

is invariant under the nonlinear recursion (3.5) *and every point on this simplex is* k*-periodic.*

So under a rather restrictive condition on c we find a plenitude of k-periodic orbits, filling a $(k-1)$-dimensional "flat" subset of the positive cone. Inspired by this result we now return to the nonlinear circulant equation (4.3). What if the analogue of constant c_i holds, i.e., what if $h_i(I)$ is independent of i?

Theorem 4.2 (uniform sensitivity). *If*

$$h(I) = \mathbf{1}\phi(I)$$

(*and, in particular, in the case* (3.11) *with* $g = \mathbf{1}\frac{1}{k}$) *any positive half-line*

$$X_\sigma = \{N = a\sigma : a \in \mathbb{R}_+\}$$

with $\sigma \in \mathbb{R}^k$, $\sigma_i \geqslant 0$, $\sum_{i=0}^{k-1} \sigma_i = 1$, *is invariant under the kth iterate of the nonlinear recursion* (3.5).

Proof. If $h(I) = \mathbf{1}\phi(I)$ the recursion (3.5) takes the form

$$N(t+1) = \phi(c \cdot N(t))SN(t)$$

(we say that there is a *scalar nonlinearity*). Now put

$$N(t) = a(t)\sigma(t)$$

with $a(t) \in \mathbb{R}_+$ and $|\sigma(t)| = \sum_{i=0}^{k-1} \sigma_i(t) = 1$, so that σ specifies the direction and a the magnitude. Then

$$\sigma(t+1) = S\sigma(t)$$

and

$$a(t+1) = \phi(a(t)c \cdot \sigma(t))a(t). \tag{4.9}$$

Hence $\sigma(t+k) = \sigma(t)$ or, in words, the positive cone decomposes into a collection of invariant k-tuples of half-lines which are cyclically mapped into each other. □

Note that the coordinate axes form the outer extreme of these k-tuples and that these are mapped cyclically into each other even if sensitivity is non-uniform. In the “middle” there is the invariant half-line spanned by **1**, which forms a degenerate k-tuple.

Proposition 4.3. *Let* $R_0 > 1$ (R_0 *is given by* (3.7)) *and let the matrix* C, *given by* (4.7), *be non-singular. Assume uniform sensitivity, then the one-dimensional map* $a(t) \mapsto a(t+k)$ *generated by* (4.9) *has at least one fixed point for any given* σ, *if* ϕ *is a decreasing function with* $\lim_{I\to\infty}\phi(I) = 0$.

Proof. To a fixed point of the map $a(t) \mapsto a(t+k)$ corresponds a fixed point of the kth iterate of the original map (3.5), which is a solution of the system (4.4) , provided I satisfies (4.3). In the case of uniform sensitivity (4.4) can be rewritten as a linear system

$$CN = \begin{pmatrix} I_0 \\ \frac{I_{k-1}}{\phi(I_0)\ldots\phi(I_{k-2})} \\ \cdots \\ \frac{I_1}{\phi(I_0)} \end{pmatrix}$$

with C given by (4.7). Clearly, this system has a unique solution for a given combination $(I_0,\ldots,I_{k-1})$ if C is non-singular. So we should prove that there exists a $(I_0,\ldots,I_{k-1})$ combination corresponding to any σ. We substitute $N = a\,\sigma$ in the system above and obtain, by eliminating a via the first equation,

$$I_j = I_0\phi(I_0)\ldots\phi(I_{j-1})\frac{c\cdot S^j\sigma}{c\cdot\sigma}, \quad j = 1,\ldots,k-1.$$

Therefore we have a one-dimensional set of candidate vectors $(I_0,\ldots,I_{k-1})$ with I_0 as a free parameter (if $c\cdot\sigma = 0$ we can write similar relations, but choose I_1 as a free parameter etc.). In addition, we should have

$$\phi(I_0)\cdots\phi(I_{k-1}) = 1$$

in order to satisfy (4.3). This is an equation for I_0. It can be rewritten as

$$R_0H(I_0)\cdots H(I_{k-1}) = 1, \tag{4.10}$$

where $H(I) = \frac{\phi(I)}{\phi(0)} < 1 \forall I > 0$. The left-hand side is equal to $R_0 > 1$ if $I_0 = 0$ and

$$R_0H(I_0)\cdots H(I_{k-1}) \leqslant R_0H(I_0).$$

The right-hand side of this inequality tends to zero as $I_0 \to \infty$, so the left-hand side tends to zero as well and Eq. (4.10) has at least one solution which is positive. □

Corollary 4.4. *Fixed points of the kth iterate of the map* (4.9) *form a* $(k-1)$-*parameter family of k-periodic points of the original map* (3.5) *parameterized by* $\sigma\left(\sum_{j=0}^{k-1}\sigma_j = 1\right)$.

This family is a nonlinear analogue of the simplex (4.8). We refer to [7] for a more systematic study of the $a(t) \mapsto a(t+k)$ map. Also see [8] for a detailed elaboration

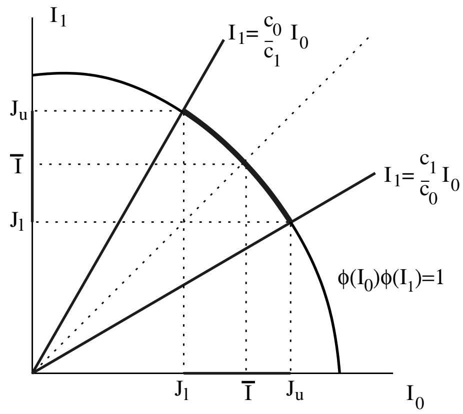

Fig. 1. The region of the (related) parameters I_0 and I_1 which define, for $k = 2$, the family of fixed points of the second iterate of the map (3.5) (see Proposition 4.5). We assume $c_0 > c_1$.

of the case $k = 2$ and h_i of Ricker type (3.1). As an illustration of the results above let us give an explicit expression for the family of 2-periodic points in the case $k = 2$ and uniform sensitivity.

Proposition 4.5. *Let $k = 2$ and $h_0(I) = h_1(I) = \phi(I)$ $\forall I \geqslant 0$. Let, in addition, $c_0 \neq c_1$. Then there exists a one-parameter family of fixed points of the second iterate of the map* (3.5) *given explicitly by*

$$\begin{pmatrix} N_0 \\ N_1 \end{pmatrix} = \frac{1}{c_0^2 - c_1^2} \begin{pmatrix} c_0 I_0 - c_1 \frac{I_1}{\phi(I_0)} \\ c_0 \frac{I_1}{\phi(I_0)} - c_1 I_0 \end{pmatrix}$$

with I_0 and I_1 related by

$$\phi(I_0)\phi(I_1) = 1.$$

This implicit relation is symmetric w.r.t. the diagonal $I_0 = I_1$ (Fig. 1). *Moreover, I_1 can be viewed as a decreasing function of I_0 or vice versa, and*

$$(I_0, I_1) \in J,$$

where J is a symmetric region $[J_l, J_u] \times [J_l, J_u]$ containing $(\overline{I}, \overline{I})$ and given implicitly by

$$\phi(J_l)\phi(J_u) = 1 \quad \textit{with } J_u = J_l \max\left\{\frac{c_0}{c_1}, \frac{c_1}{c_0}\right\}.$$

This proposition can be obtained by straightforward computation of solutions of the linear system (4.4) (compare (10.4) below). Values of the environmental

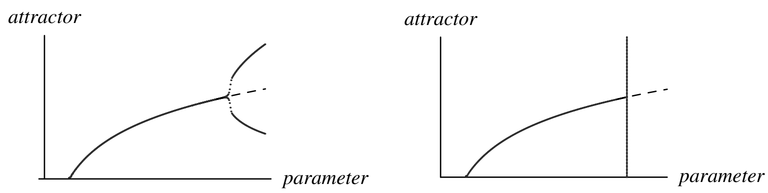

Fig. 2. A standard bifurcation diagram with a period doubling and a vertical bifurcation, in which a family of 2-cycles occurs for one particular (bifurcation) value of the parameter.

quantities I_j which are a family of solutions of the nonlinear circulant, serve themselves as parameters of the family of the fixed points. The boundaries of the regions J correspond to the case when one of the components N_i is zero, inside the region all the components are positive. We notice that in the case $k = 2$ the interval $[J_l, J_u]$ is largest if one of the parameters c_0 or c_1 is zero and that this interval degenerates to the point $\overline{I}$ if $c_0 = c_1$. So in the case of uniform impact there exists only one biologically relevant solution of the nonlinear circulant which is in fact the uniform solution. But a whole family of fixed points of the second iterate of the map corresponds to this solution (see Theorem 4.1).

If a dynamical system possesses, for special parameter values, an invariant manifold in the phase space filled with periodic points, we call this phenomenon a *vertical bifurcation*. The motivation for that is the following. Imagine a standard bifurcation diagram for a period-doubling (Fig. 2). For a particular value of a bifurcation parameter a fixed point branches into two period-2 points. In the case of the vertical bifurcation the whole family of 2-cycles occurs for one particular (bifurcation) value of the parameter, so that we see a *vertical* line of periodic points on the bifurcation diagram. In the system (3.5) we indeed have such a situation: in Section 8 we show that eigenvalues of the internal steady state are on the unit circle under the parameter conditions for a vertical bifurcation.

Theorems 4.1 and 4.2 involve $k - 1$ conditions on the parameters, so refer to a rather non-generic situation (a bifurcation of codimension $k - 1$) especially for $k > 2$. But they inspire results in Sections 5–7 that deal with less degenerate situations (bifurcations of codimension 1 and 2). A more ambitious aim would be to try to obtain a complete unfolding of the "uniform impact and sensitivity" case, while respecting the model structure.

5. Singular circulants

Now we come back to the question formulated in the previous section: when is a circulant matrix singular? By answering this question we find conditions for vertical bifurcations which generalise those of the *uniform impact* case of Theorem 4.1.

First, we need several formal notions. The definitions and lemmas below till and including Lemma 5.4 are summarized from [6, pp. 66–68, 88–89].

Definition 5.1. A matrix

$$C = \operatorname{circ}(c_0, \ldots, c_{k-1}) = \begin{pmatrix} c_0 & c_1 & \cdots & c_{k-1} \\ c_{k-1} & c_0 & \cdots & c_{k-2} \\ \cdots & & & \\ c_1 & c_2 & \cdots & c_0 \end{pmatrix} \tag{5.1}$$

is called a circulant matrix of order k or a circulant of order k.

A matrix is called *uniform* if all its entries are equal. A uniform matrix is, of course, circulant.

Lemma 5.2. *A circulant C can be represented as*

$$C = c_0 E + c_1 S^{-1} + \cdots + c_{k-1} S^{-(k-1)},$$

where S is the shift defined in (2.5) *and E is the identity matrix of order k.*

Definition 5.3. The polynomial

$$p(z) = c_0 + c_1 z + \cdots + c_{k-1} z^{k-1} \tag{5.2}$$

is called the representer of the circulant C.

The eigenvalues of the shift S are the kth roots of unity

$$\lambda_{n,k} = \mathrm{e}^{n\frac{2\pi \mathrm{i}}{k}}, \quad n = 0, 1, \ldots, k-1$$

and the corresponding eigenvectors are

$$\xi_{n,k} = \begin{pmatrix} 1 \\ \lambda_{n,k}^{-1} \\ \cdots \\ \lambda_{n,k}^{-k+1} \end{pmatrix}. \tag{5.3}$$

From Lemma 5.2 one can see that

$$C\xi_{n,k} = p(\lambda_{n,k}^{-1})\xi_{n,k}, \tag{5.4}$$

i.e. $\xi_{n,k}$ are also eigenvectors of C with corresponding eigenvalues $p(\lambda_{n,k}^{-1})$. Hence we have the following lemma, which gives the answer to the question in the beginning of the section.

Lemma 5.4. *A circulant C is singular if and only if a kth root of unity is a zero of its representer $p(z)$, i.e. there exists an n such that*

$$p(\lambda_{n,k}^{-1}) = 0, \tag{5.5}$$

or, in other words,

$$c \cdot \xi_{n,k} = 0. \tag{5.6}$$

Remark. Without loss of generality we can consider n in the interval $[0, \frac{k}{2}]$, because all other values of n give the same or complex conjugated roots.

To illustrate the lemma, we consider several special cases of singular circulants and then formulate a general theorem.

Proposition 5.5. *If the sum of the entries* $c_0 + \cdots + c_{k-1}$ *of a circulant is zero, the circulant is singular.*

This is the most simple case which, however, is uninteresting for us because we deal with nonnegative circulants. If the sum of all entries is zero, we have just a matrix consisting of all zeros, which we call a *trivial circulant*.

Proposition 5.6. *A nontrivial nonnegative circulant of order* 2 *or* 3 *is singular if and only if it is uniform.*

Therefore, if the system (3.5) is low-dimensional ($k = 2$ or 3), it possesses a k-cycle, with all year-classes present and constant environmental condition $\overline{I}$, only in the case of *uniform impact* (cf. Theorem 4.1).

Proposition 5.7. *Let* C *be a circulant of an even order. It is singular if the sum of its even components is equal to the sum of its odd components, i.e.*

$$\sum_{i=0}^{\frac{k-2}{2}} c_{2i} = \sum_{i=0}^{\frac{k-2}{2}} c_{2i+1}. \tag{5.7}$$

Now we formulate the main theorem.

Theorem 5.8. *For any* k *there exist* $\left[\frac{k}{2}\right]$ *different families of nontrivial nonnegative singular circulants* C *of order* k*, where*

$$\left[\frac{k}{2}\right] := \left[\begin{array}{ll} \frac{k}{2} & k \text{ even} \\ \frac{k-1}{2} & k \text{ odd.} \end{array}\right.$$

Here is the list of these families.

(i) $k = 2, 3$. *A one-parameter family of uniform matrices.*
(ii) $k > 3$ *and* k *is even. A* $(k-1)$*-parameter family of circulants such that the sum of the even entries is equal to the sum of the odd entries* (5.7).

(iii) $k > 3$. *There are* $\left[\frac{k-1}{2}\right]$ *different* $(k-2)$*-parameter families of singular circulants enumerated by* $0 < n < \frac{k}{2}$ *such that*

$$\mathbf{f}_{k,n}(c_0, \dots, c_{k-1}) = 0, \tag{5.8}$$

where $\mathbf{f}_{k,n}(c_0, \dots, c_{k-1})$ *is a linear function* $\mathbb{R}^k \to \mathbb{R}^2$ *given by the following relation*:

$$\mathbf{f}_{k,n}(c_0, \dots, c_k) = \begin{cases} c_0 + (c_1 + c_{k-1}) \cos \frac{2\pi n}{k} + (c_2 + c_{k-2}) \cos \frac{4\pi n}{k} \\ \quad + \dots + \begin{bmatrix} (c_{\frac{k-1}{2}} + c_{\frac{k+1}{2}}) \cos \frac{\pi(k-1)n}{k}, & k \text{ odd} \\ (-1)^n c_{\frac{k}{2}}, & k \text{ even} \end{bmatrix} \\ (c_1 - c_{k-1}) \sin \frac{2\pi n}{k} + (c_2 - c_{k-2}) \sin \frac{4\pi n}{k} \\ \quad + \dots + \begin{bmatrix} (c_{\frac{k-1}{2}} + c_{\frac{k+1}{2}}) \sin \frac{\pi(k-1)n}{k}, & k \text{ odd} \\ (c_{\frac{k-2}{2}} + c_{\frac{k+2}{2}}) \sin \frac{\pi(k-2)n}{k}, & k \text{ even.} \end{bmatrix} \end{cases} \tag{5.9}$$

Proof. Proposition 5.6 gives the statement (5.8) for $k = 2, 3$.

Let $k > 3$. Lemma 5.4 says that a circulant is singular iff (5.5) holds for at least one $n \in \{0, 1, \dots, k-1\}$. We can rewrite this condition in the form (5.8) for $0 \leqslant n \leqslant \frac{k}{2}$. There are three different cases possible:

- $n = 0$ corresponds to 1 being a root of the representer. In this case the circulant is either trivial or has negative entries.
- k is even, $n = \frac{k}{2}$. A root of the representer is -1. The statement (ii) is given by Proposition 5.7. The second condition of (5.8)–(5.9) is trivially fullfilled and so the family of such singular circulants has $(k-1)$ free parameters.
- $0 < n < \frac{k}{2}$. The representer has a complex root $\lambda_{n,k}^{-1}$. Hence the expression (5.5) gives two different conditions on c. These conditions can be written in the form (5.8)–(5.9) noticing that $\left(\lambda_{n,k}^{-1}\right)^{k-m}$ is a complex conjugate to $\left(\lambda_{n,k}^{-1}\right)^{m}$ and also that $\left(\lambda_{n,k}^{-1}\right)^{k/2} = (-1)^n$.

  For any $0 < n < \frac{k}{2}$ we have $k-2$ free c_i. Moreover, the sets given by the different values of n are different because they are orthogonal to different eigenvectors $\xi_{n,k}$ (see (5.6)). There are $\left[\frac{k-1}{2}\right]$ such families. □

In some cases it is possible to rewrite the condition (5.6) using functions with lower values of k and sums of c's as arguments.

Proposition 5.9. *Let* $\frac{n}{k} = \frac{l}{m}$, *where* $l, m \in \mathbb{Z}$, $m < k$. *Then the condition* (5.6) *can be rewritten as*

$$c_\Sigma \cdot \xi_{l,m} = 0,$$

where

$$c_\Sigma = \begin{pmatrix} c_0 + c_m + \cdots + c_{k-m} \\ c_1 + c_{m+1} + \cdots + c_{k-m+1} \\ \cdots \\ c_{m-1} + c_{2m-1} + \cdots + c_{k-1} \end{pmatrix}.$$

Proof. Noticing that $\lambda_{n,k} = \lambda_{l,m}$ and that $\xi_{n,k}$ consists of l copies of $\xi_{l,m}$, i.e. $\xi_{n,k} = (\xi_{l,m}, \xi_{l,m}, \ldots, \xi_{l,m})^{\mathrm{T}}$, the proof is straightforward. □

This proposition is illustrated in Table 1. For example, let $k = 6$ and $n = 2$. Then a common divisor is $m = 2$ and a condition on the c's has the same form as for $k' = 6/2 = 3$ and $n' = 2/2 = 1$, namely $c_0 = c_1 = c_2$, but instead of c_0, c_1 and c_2 we have sums: $c_0 + c_3$, $c_1 + c_4$ and $c_2 + c_5$ respectively. The same analogy we observe for $k = 4$ and $n = 2$, for $k = 6$ and $n = 3$ etc.

Table 1 gives a complete list of families of nontrivial nonnegative singular circulants of order $k = 2, \ldots, 9, 12$. It can be extended to other orders without much difficulty.

6. k-Cycles on affine subsets

In the case of uniform impact we have found a simplex filled with k-cycles (Theorem 4.1). The aim of this section is to find, in each case of a singular circulant, a geometrical object in $\mathbb{R}^k_+$ filled with a family of k-cycles. We show that these are the intersection of either a line or a plane with the positive cone.

Theorem 6.1. *Let $\lambda_{n,k} = \mathrm{e}^{\mathrm{i}\frac{2\pi n}{k}}$ be a root of the representer of a nonnegative singular circulant C of order k with $\sum_{i=0}^{k-1} c_i = 1$.*

(i) *If $\lambda_{n,k} = -1$ (i.e., k is even and $n = \frac{k}{2}$), the line segment $\mathscr{L}_k$ defined by*

$$\mathscr{L}_k = \left\{ N : \begin{matrix} N_{2j} = \overline{I}(1+p) \\ N_{2j+1} = \overline{I}(1-p) \end{matrix} \quad , \quad j = 0, 1, \ldots \frac{k}{2} - 1;\ -1 \leqslant p \leqslant 1 \right\}$$

is both contained in the set $\{N : CN = \mathbf{1}\overline{I}\}$ (i.e. $\mathscr{L}_k$ is a one-parameter family of solutions of the system (4.5)) and invariant under S.

(ii) *In all other cases the set $\mathscr{P}_{n,k}$ defined by*

$$\mathscr{P}_{n,k} = \{N :\ N = \overline{I}(\mathbf{1} + p\,\mathrm{Re}\,\xi_{n,k} + q\,\mathrm{Im}\,\xi_{n,k}), \text{ where } p \text{ and } q \text{ are real numbers such that } N \text{ is nonnegative}\},$$

(with $\xi_{n,k}$ given by (5.3)), is both contained in $\{N : CN = \mathbf{1}\overline{I}\}$ and invariant under S.

Proof. We begin with the second assertion. The condition for singularity of the circulant is (5.6)

Table 1
A list of conditions for a nontrivial nonnegative circulant of order k to be singular

k	Divisor	n	μ	dim	Family description
2	2	1	-1	0	$c_0 = c_1 = \frac{1}{2}$
3	3	1	$e^{i\frac{2\pi}{3}}$	0	$c_0 = c_1 = c_2 = \frac{1}{3}$
4	2	2	-1	2	$c_0 + c_2 = c_1 + c_3 = \frac{1}{2}$
	4	1	$e^{i\frac{\pi}{2}}$	1	$c_0 = c_2$ $c_1 = c_3 = \frac{1}{2} - c_0$
5	5	1	$e^{i\frac{2\pi}{5}}$	2	$c_0 + (c_1 + c_4)\cos\frac{2\pi}{5} - (c_2 + c_3)\cos\frac{\pi}{5} = 0$ $(c_1 - c_4)\sin\frac{2\pi}{5} + (c_2 - c_3)\sin\frac{\pi}{5} = 0$
	5	2	$e^{i\frac{4\pi}{5}}$	2	$c_0 - (c_1 + c_4)\cos\frac{\pi}{5} + (c_2 + c_3)\cos\frac{2\pi}{5} = 0$ $(c_1 - c_4)\sin\frac{\pi}{5} - (c_2 - c_3)\sin\frac{2\pi}{5} = 0$
6	2	3	-1	4	$\sum c_{2i} = \sum c_{2i+1} = \frac{1}{2}$
	3	2	$e^{i\frac{2\pi}{3}}$	3	$c_0 + c_3 = c_1 + c_4 = c_2 + c_5 = \frac{1}{3}$
	6	1	$e^{i\frac{\pi}{3}}$	3	$(c_0 - c_3) + \frac{1}{2}(c_1 + c_5) - \frac{1}{2}(c_2 + c_4) = 0$ $c_1 + c_2 = c_4 + c_5$
7	7	1	$e^{i\frac{2\pi}{7}}$	4	$c_0 + (c_1 + c_6)\cos\frac{2\pi}{7} - (c_2 + c_5)\cos\frac{3\pi}{7} - (c_3 + c_4)\cos\frac{\pi}{7} = 0$ $(c_1 - c_6)\sin\frac{2\pi}{7} + (c_2 - c_5)\sin\frac{3\pi}{7} + (c_3 - c_4)\sin\frac{\pi}{7} = 0$
	7	2	$e^{i\frac{4\pi}{7}}$	4	$c_0 - (c_1 + c_6)\cos\frac{3\pi}{7} - (c_2 + c_5)\cos\frac{\pi}{7} + (c_3 + c_4)\cos\frac{2\pi}{7} = 0$ $(c_1 - c_6)\sin\frac{3\pi}{7} - (c_2 - c_5)\sin\frac{\pi}{7} - (c_3 - c_4)\sin\frac{2\pi}{7} = 0$
	7	3	$e^{i\frac{6\pi}{7}}$	4	$c_0 - (c_1 + c_6)\cos\frac{\pi}{7} + (c_2 + c_5)\cos\frac{2\pi}{7} - (c_3 + c_4)\cos\frac{3\pi}{7} = 0$ $(c_1 - c_6)\sin\frac{\pi}{7} - (c_2 - c_5)\sin\frac{2\pi}{7} + (c_3 - c_4)\sin\frac{3\pi}{7} = 0$
8	2	4	-1	6	$\sum c_{2i} = \sum c_{2i+1} = \frac{1}{2}$
	4	2	$e^{i\frac{\pi}{2}}$	5	$c_0 + c_4 = c_2 + c_5$ $c_1 + c_6 = c_3 + c_7$
	8	1	$e^{i\frac{\pi}{4}}$	5	$(c_0 - c_4) + \frac{1}{\sqrt{2}}((c_1 + c_7) - (c_3 + c_5)) = 0$ $(c_2 - c_6) + \frac{1}{\sqrt{2}}((c_1 - c_7) + (c_3 - c_5)) = 0$
	8	3	$e^{i\frac{3\pi}{8}}$	5	$c_0 + (c_1 + c_7)\cos\frac{3\pi}{8} - \frac{1}{\sqrt{2}}(c_2 + c_6) - (c_3 + c_5)\cos\frac{\pi}{8} = 0$ $-c_4 + (c_1 - c_7)\sin\frac{3\pi}{8} + \frac{1}{\sqrt{2}}(c_2 - c_6) - (c_3 - c_5)\sin\frac{\pi}{8} = 0$
9	3	3	$e^{i\frac{2\pi}{3}}$	6	$c_0 + c_3 + c_6 = c_1 + c_4 + c_7 = c_2 + c_5 + c_8 = \frac{1}{3}$
	9	1	$e^{i\frac{2\pi}{9}}$	6	$\mathbf{f}_{9,1}(c_0, \ldots, c_8) = 0$
	9	2	$e^{i\frac{4\pi}{9}}$	6	$\mathbf{f}_{9,2}(c_0, \ldots, c_8) = 0$
	9	4	$e^{i\frac{8\pi}{9}}$	6	$\mathbf{f}_{9,4}(c_0, \ldots, c_8) = 0$

(*continued on next page*)

Table 1 (*continued*)

k	Divisor	n	μ	dim	Family description
12	2	6	-1	10	$\sum c_{2i} = \sum c_{2i+1} = \frac{1}{2}$
	3	4	$e^{i\frac{2\pi}{3}}$	9	$\sum c_{3i} = \sum c_{3i+1} = \sum c_{3i+2} = \frac{1}{3}$
	4	3	$e^{i\frac{\pi}{2}}$	9	$\sum c_{4i} = \sum c_{4i+2}$ $\sum c_{4i+1} = \sum c_{4i+3}$
	6	2	$e^{i\frac{\pi}{3}}$	9	$\mathbf{f}_{6,1}(c_0 + c_6, \ldots, c_5 + c_{11}) = 0$
	12	1	$e^{i\frac{\pi}{6}}$	9	$\mathbf{f}_{12,1}(c_0, \ldots, c_{11}) = 0$
	12	5	$e^{i\frac{5\pi}{6}}$	9	$\mathbf{f}_{12,5}(c_0, \ldots, c_{11}) = 0$

'Divisor' is a divisor of k. The number $n = \frac{k}{\text{divisor}} \bmod k$. μ is the corresponding root of the representer, $\mu = e^{i\frac{2\pi n}{k}}$. The function $\mathbf{f}_{k,n}(c_0, \ldots, c_k)$ is given by (5.9). The parameter dim is the dimension of the family, i.e. the number of free components c_i of the circulant (since $\sum_{i=0}^{k-1} c_i = 1$ we have dim is $k-2$ if $\mu = -1$ and $k-3$ otherwise).

$$c \cdot \xi_{n,k} = 0.$$

It is invariant under S, i.e.,

$$S^m c \cdot \xi_{n,k} = 0, \quad m = 0, 1, \ldots, k-1.$$

The equation $CN = \mathbf{1}\overline{I}$ we can write as

$$\begin{aligned} &c \cdot N = \overline{I}, \\ &Sc \cdot N = \overline{I}, \\ &\ldots \\ &S^{k-1} c \cdot N = \overline{I}. \end{aligned}$$

We substitute $N \in \mathscr{P}_{n,k}$ in each of the equations above and get

$$S^m c \cdot \mathbf{1}\overline{I} + p\, S^m c \cdot \operatorname{Re} \xi_{n,k} + q\, S^m c \cdot \operatorname{Im} \xi_{n,k} = \overline{I}.$$

The last two terms vanish and, since the sum of c_i is one, this is indeed a true identity for all m. Hence $\mathscr{P}_{n,k}$ is contained in $\{N : CN = \mathbf{1}\overline{I}\}$.

To show that $\mathscr{P}_{n,k}$ is invariant under S, rewrite the expression for N as

$$N = \overline{I}(\mathbf{1} + \operatorname{Re}(a\, \xi_{n,k})), \tag{6.1}$$

where $a = p - iq$ is a complex number such that N is nonnegative. This is indeed the case if

$$1 + \operatorname{Re}(a\, \lambda_{n,k}^{-j}) \geqslant 0 \quad \text{for all } j = 0, 1, \ldots, k-1. \tag{6.2}$$

Since $\xi_{n,k}$ is the eigenvector of S and $\lambda_{n,k}$ is the corresponding eigenvalue

$$SN = \overline{I}(\mathbf{1} + \operatorname{Re}(b\, \xi_{n,k}))$$

with $b = \lambda_{n,k}\, a$. Clearly, if the conditions (6.2) are satisfied for a, they are also satisfied for b, because we just apply the shift to the system of inequalities (6.2). Indeed,

$$1 + \mathrm{Re}(b\, \lambda_{n,k}^{-j}) = 1 + \mathrm{Re}(a\, \lambda_{n,k}^{-(j-1)}) \geqslant 0.$$

And hence $\mathscr{P}_{n,k}$ is invariant under the shift.

Let now k be even and consider the eigenvalue $\lambda_{k/2,k} = -1$. Then $\mathrm{Im}\, \xi_{k/2} = 0$ and $\mathscr{P}_{n,k}$ reduces to the line segment $\mathscr{L}_k$. □

Corollary 6.2. *Every point on the line segment $\mathscr{L}_k$ is 2-periodic.*

It is rather simple to visualize the line segment $\mathscr{L}_k$. The end points of this segment are two points with coordinates $(0, 2\overline{I}, 0, 2\overline{I}, \ldots, 0, 2\overline{I})$ and $(2\overline{I}, 0, 2\overline{I}, 0, \ldots, 2\overline{I}, 0)$, so each of them lies in a $\frac{k}{2}$-dimensional coordinate hyperplane. We now try to develop a geometric "feeling" concerning the invariant sets $\mathscr{P}_{n,k}$ and the dynamics on them.

Corollary 6.3. *Let $\frac{n}{k} = \frac{l}{m}$, where $\frac{l}{m}$ is the irreducible fraction. Every point N on $\mathscr{P}_{n,k}$ is m-periodic (with m as minimal period). And if we join the points $\{N, SN, \ldots, S^{m-1}N, N\}$ successively by line segments, we obtain a regular polygon with m vertices (a so-called m-gon).*

Proof. We have $S^m N = \overline{I}(\mathbf{1} + \mathrm{Re}\, a\, S^m \xi_{n,k})$ and $S^m \xi_{n,k} = \lambda_{n,k}^m \xi_{n,k} = \mathrm{e}^{\mathrm{i}\frac{2\pi n}{k} m} \xi_{n,k} = \mathrm{e}^{\mathrm{i}\frac{2\pi l}{m} m} \xi_{n,k} = \xi_{n,k}$. Hence $S^m N = N$.

We notice that the distance between two successive points from $\{N, SN, \ldots, S^{m-1}N, N\}$ is determined by differences $|N_i - N_{i+1}|$, with $i = 0, \ldots, k-1$, and thus the same for all pairs $\{S^j N, S^{j+1} N\}$, $j = 0, \ldots, m-1$. □

In the proof of the theorem above we have used the form (6.1) for a point in $\mathscr{P}_{n,k}$. Thus we can rewrite $\mathscr{P}_{n,k}$ as follows:

$$\begin{aligned} \mathscr{P}_{n,k} := \{N :\ & N = \overline{I}(\mathbf{1} + \mathrm{Re}(a\, \xi_{n,k})), \\ & \text{with } a \in \mathbb{C} \text{ such that } N \geqslant 0, \text{ i.e. such that (6.2) holds}\}. \end{aligned} \tag{6.3}$$

If $\frac{n}{k} = \frac{l}{m}$, where $\frac{l}{m}$ is the irreducible fraction, the number of independent inequalities in (6.2) is m. Let us define a set $\mathscr{P}_{n,k}^{\mathbb{C}}$ of all possible values of a:

$$\begin{aligned} \mathscr{P}_{n,k}^{\mathbb{C}} := \big\{ a \in \mathbb{C} :\ & 1 + \mathrm{Re}(a\, \mathrm{e}^{\mathrm{i}\frac{2\pi l}{m}(-j)}) \geqslant 0 \\ & \text{for all } j = 0, 1, \ldots, m-1,\ \tfrac{l}{m} = \tfrac{n}{k} \big\}. \end{aligned} \tag{6.4}$$

The set $\mathscr{P}_{n,k}$ (consisting of k-dimensional vectors) can be obtained by the linear transformation (given in (6.3)) from the set $\mathscr{P}_{n,k}^{\mathbb{C}}$ of complex numbers. We notice that $\mathscr{P}_{n,k}^{\mathbb{C}}$ is a filled regular m-gon in the complex plane. We notice also that the distance between any two points on $\mathscr{P}_{n,k}$ is determined only by the difference between the corresponding a's, and that therefore angles and ratios are preserved under the transformation from $\mathscr{P}^{\mathbb{C}}_{n,k}$ to $\mathscr{P}_{n,k}$. So, we conclude that $\mathscr{P}_{n,k}$ is a filled regular m-gon too.

The boundary of the filled polygon is determined by the fact that at least one or at most two inequalities in (6.4) turn to be equalities. The first case corresponds to an edge of the polygon and the latter to a vertex.

If $\frac{n}{k}$ is irreducible, this translates to the fact that the vertices of the polygon $\mathscr{P}_{n,k}$ lie in coordinate hyperplanes of codimension 2, in other words, points of $\mathscr{P}_{n,k}$ corresponding to the vertices have two zero components, and the edges of $\mathscr{P}_{n,k}$ lie in hyperplanes of codimension 1, i.e., have one zero component. In particular in the case $k = 3$ the vertices of the equilateral triangle, which $\mathscr{P}_{1,3} = \mathscr{P}_{2,3} = \{N_0 + N_1 + N_2 = \overline{I},\}$ is in this case, lie on coordinate axes and the edges on coordinate planes.

If, on the contrary, $\frac{n}{k}$ is reducible and $\frac{n}{k} = \frac{l}{m}$ with $m < k$, then for a point N on the edge of the polygon, there are $\frac{k}{m}$ different components of N which are equal to zero, and $\frac{2k}{m}$ zero components for a vertex. For example, let $k = 6$ and $n = 2$. The set $\mathscr{P}_{2,6}$ is given expicitly by

$$\mathscr{P}_{2,6} = \{N_0 = N_3, N_1 = N_4, N_2 = N_5, N_0 + N_1 + N_2 = \overline{I}\}.$$

Clearly, e.g., one of the vertices of the polygon lies in the coordinate plane $N_0 = N_3 = N_1 = N_4 = 0$.

If the representer of the circulant C has several roots which are different (and not complex conjugate) roots of unity, we have a result similar to Theorem 6.1. A family of k-periodic points is not (a part of) a line or a plane, but a simplex of dimension equal to the number of such roots, counting complex conjugate roots as different and not counting multiplicity of the roots of the representer. (The last remark follows from the fact that C has always k *different* eigenvectors $\xi_{n,k}$, $n = 0, \ldots, k-1$ because of (5.4); hence the dimension of its null-space (which is also the dimension of the family of k-periodic points of (3.5)) is equal to the number of *different* $\lambda_{n,k}$ which are roots of the representer.

Theorem 6.4. *Let* $\lambda_{n_j,k} = \mathrm{e}^{\mathrm{i}\frac{2\pi n_j}{k}}$, *for* $j = 1, \ldots, q$ *and* $1 \leqslant n_1 < n_2 < \cdots < n_q \leqslant \frac{k}{2}$, *be roots of the representer of a nonnegative singular circulant* C *of order* k *with* $\sum_{i=0}^{k-1} c_i = 1$. *The set* $\mathscr{P}_{\mathbf{n},k}$ *with* $\mathbf{n} = (n_1, \ldots, n_q)^{\mathrm{T}}$ *defined by*

$$\mathscr{P}_{\mathbf{n},k} = \{N :\ N = \overline{I}(\mathbf{1} + \textstyle\sum_{j=1}^{q} \mathrm{Re}(a_j\, \xi_{n_j,k})),\ \text{where } a_j \in \mathbb{C} \text{ are such that } N \text{ is nonnegative}\},$$

(*with* $\xi_{n,k}$ *given by* (5.3)), *is both contained in* $\{N : CN = \mathbf{1}\overline{I}\}$ *and invariant under* S.

The proof of this theorem is completely similar to the proof of Theorem 6.1.

7. Nonlinear circulants

In this section we consider the nonlinear circulant system (4.3) (the key property of a linear or nonlinear *circulant* system is equivariance with respect to the cyclic group). In Section 4 we have observed that (4.3) has a uniform solution $I_0 = \cdots = I_{k-1} = \overline{I}$. And for this solution we have found, in Section 5, conditions on the parameters c_i, under which the recursion (3.5) possesses families of cycles with all year classes present. Now we ask whether (4.3) can have a nonuniform solution or even a family of solutions. We are especially interested in this last possibility because this is exactly what happens in the case of vertical bifurcation.

Theorem 7.1. *If $k-1$ ratios $\frac{h_i}{h_{i+1}}(I)$ are all monotone increasing/decreasing* (*with one strictly increasing/decreasing*), *the system* (4.3) *has only $I_0 = \cdots = I_{k-1} = \overline{I}$ as a solution.*

Proof. Denote the ratios $\frac{h_i}{h_{i+1}}(I)$ by $h_{i\,i+1}$. We divide the second equation in (4.3) by the first, the third by the second etc. and the first by the last. In this way we obtain

$$\begin{aligned}
&h_{01}(I_1)\, h_{12}(I_2) \cdots h_{k-2\,k-1}(I_{k-1}) = h_{01}(I_0)\, h_{12}(I_0) \ldots h_{k-2\,k-1}(I_0),\\
&h_{01}(I_2)\, h_{12}(I_3) \cdots h_{k-2\,k-1}(I_0) = h_{01}(I_1)\, h_{12}(I_1) \ldots h_{k-2\,k-1}(I_1),\\
&\ldots\\
&h_{01}(I_0)\, h_{12}(I_1) \cdots h_{k-2\,k-1}(I_{k-2}) = h_{01}(I_{k-1})\, h_{12}(I_{k-1}) \ldots h_{k-2\,k-1}(I_{k-1}).
\end{aligned}$$

If I_0 is the largest or the smallest of all I_i, the first identity can not be satisfied. The same can be said about I_j and the $j+1$th identity above. Thus none of the values I_i can be the largest or the smallest, hence they are all equal. □

For $k = 2$ we have the following corollary.

Corollary 7.2. *If $\frac{h_0}{h_1}(I)$ is strictly monotone, the system*

$$\begin{aligned}
&h_0(I_0)\, h_1(I_1) = 1,\\
&h_1(I_0)\, h_0(I_1) = 1
\end{aligned} \tag{7.1}$$

has only $I_0 = I_1 = \overline{I}$ as a solution.

For $k = 3$ we can relax the assumption of Theorem 7.1, i.e., we can also deal with the case in which two (necessarily successive) ratios are monotone in opposite directions.

Theorem 7.3. *If two ratios $\frac{h_i}{h_j}(I)$, $i, j = 0, \ldots, 2$, $i \neq j$ are monotone* (*and at least one of them is strictly monotone*), *the system*

$$\begin{aligned} &h_0(I_0)\, h_1(I_1)\, h_2(I_2) = 1, \\ &h_2(I_0)\, h_0(I_1)\, h_1(I_2) = 1, \\ &h_1(I_0)\, h_2(I_1)\, h_0(I_2) = 1 \end{aligned} \tag{7.2}$$

has only $I_0 = I_1 = I_2 = \overline{I}$ *as a solution.*

Proof. If the two successive ratios $h_{i\,i+1}$, $i = 0, 1$ are monotone in the same manner, then the result is a special case of Theorem 7.1. Let now h_{01} be increasing and h_{12} decreasing (or h_{01} decreasing and h_{12} increasing). Then dividing the first equation of (7.2) by the third and the second by the first we have

$$\begin{aligned} &h_{01}(I_0)h_{21}(I_2) = h_{01}(I_2)h_{21}(I_1), \\ &h_{01}(I_1)h_{21}(I_0) = h_{01}(I_0)h_{21}(I_2). \end{aligned}$$

If I_2 lies between I_0 and I_1, the first identity can not be satisfied. The same can be said about I_0 and the second identity. Hence $I_0 = I_1 = I_2$. When h_{20} and h_{01} are monotone in opposite ways the same conclusion can be derived in the same way. □

Notice that for the families (3.12) and (3.13) we have that the ratios of the sensitivity functions are strictly monotone if the corresponding parameters g_i are not equal. Hence we have the following corollary of the results above.

Corollary 7.4. *Consider the Ricker family* (3.12) *or the Beverton–Holt family* (3.13).

(i) *Let* $k = 2$. *If* $g_0 \neq g_1$ *and* $c_0 \neq c_1$ *there can exist no cycle with minimal period* 2 *in the interior of the phase space. If* $g_0 = g_1$ *there exists a one-parameter family of* 2*-cycles in* (*the interior of*) *the phase space.*

(ii) *Let* $k = 3$. *If not all g's are equal and not all c's are equal there can exist no cycle with minimal period* 3 *in the interior of the phase space. If* $g_0 = g_1 = g_2$ *there exists a two-parameter family of* 3*-cycles in* (*the interior of*) *the phase space.*

In other words we have "all or nothing": either there is a whole family of cycles or there is no cycle at all. The first case corresponds to the vertical bifurcation. In each case the second assertion follows directly from Corollary 4.4. The first assertion of (i) has already been reported in a slightly different form in [8].

Notice that the ratio of two functions h_0 and h_1 from the same parameter family (3.11) is not necessarily monotone if $g_0 \neq g_1$. Indeed,

$$\begin{aligned} \operatorname{sign}\left(\frac{\mathrm{d}}{\mathrm{d}I}\frac{h_0(I)}{h_1(I)}\right) &= \operatorname{sign}\left(\frac{h_0'(I)}{h_0(I)} - \frac{h_1'(I)}{h_1(I)}\right) \\ &= \operatorname{sign}\left(\frac{g_0 I\, H'(g_0 I)}{H(g_0 I)} - \frac{g_1 I\, H'(g_1 I)}{H(g_0 I)}\right). \end{aligned}$$

I.e. $\frac{h_0}{h_1}(I)$ is monotone in this case if and only if $\frac{IH'(I)}{H(I)}$ is monotone. This last function is called *elasticity* [3]. Let us give an example of a function with nonmonotone elasticity (which, in addition, satisfies the normalization assumptions (3.4))

$$H(I) = \frac{1}{3}(2 + \cos I)\,\mathrm{e}^{-I}.$$

And indeed, the ratio

$$\frac{h_0}{h_1}(I) = \frac{2 + \cos g_0 I}{2 + \cos g_1 I}\,\mathrm{e}^{(g_1 - g_0)x}$$

is nonmonotone, for example, for $g_0 = 0.4$ and $g_1 = 0.6$.

In Section 10 we consider the case $k = 2$ and a nonmonotone ratio of sensitivity functions. We show that in this case an isolated 2-cycle can exist in the interior of the phase space and that we can have a normal period-doubling bifurcation instead of the vertical one.

Let us now consider general $k > 3$. As we have already said, the system (4.3) has always the uniform solution $I_0 = \cdots = I_{k-1} = \overline{I}$. From the Implicit Function Theorem it follows that there are no other solutions in a neighbourhood of it, if the derivative of the left-hand side of (4.3) at the point $I_0 = \cdots = I_{k-1} = \overline{I}$ is nonsingular. Of particular interest is the case when the derivative is singular. Indeed, new solution branches can appear in the neighbourhood of the uniform solution in this case. The Jacobian of the left-hand side of (4.3) at the point $I_0 = \cdots = I_{k-1} = \overline{I}$ is

$$\begin{pmatrix} h'_0(\overline{I}) & h'_1(\overline{I}) & \cdots & h'_{k-1}(\overline{I}) \\ h'_{k-1}(\overline{I}) & h'_0(\overline{I}) & \cdots & h'_{k-2}(\overline{I}) \\ \cdots & & & \\ h'_1(\overline{I}) & h'_2(\overline{I}) & \cdots & h'_0(\overline{I}) \end{pmatrix}$$

(recall that $\forall j\ h_j(\overline{I}) = 1$). This is again a circulant matrix. Hence the condition for its degeneracy is

$$h'(\overline{I}) \cdot \xi_{n,k} = 0. \tag{7.3}$$

Of course, it is not guaranteed that a system with a zero Jacobian possesses a family of solutions. The question, what further conditions on the functions h_i are required to guarantee this, we leave open.

To train our intuition we first consider a specific example. Let all the functions h_i be of Ricker type (3.12). Then the nonlinear circulant in the left-hand side of (4.3) reduces to a linear circulant and (4.3) can be rewritten as

$$\begin{aligned} &g_0 I_0 + g_1 I_1 + \cdots + g_{k-1} I_{k-1} = \overline{I}, \\ &g_{k-1} I_0 + g_0 I_1 + \cdots + g_{k-2} I_{k-1} = \overline{I}, \\ &\cdots \\ &g_1 I_0 + g_2 I_1 + \cdots + g_0 I_{k-1} = \overline{I} \end{aligned}$$

(noticing that $\sum g_i = 1$) or

$$G\,\mathbf{I} = \mathbf{1}\overline{I}, \tag{7.4}$$

where $\mathbf{I}$ is the vector $(I_0, I_1, \dots, I_{k-1})$. This system has a family of solutions if the circulant G (generated by the vector g) is singular. So all the results of Section 5 are once again relevant.

If G is singular, we can find a family of solutions of the circulant system above in the way of Section 6. By doing that we find a line or a plane but no longer in the phase space with points $\{N_0, \dots, N_{k-1}\}$, but in the space of environmental conditions with points $\{I_0, \dots, I_{k-1}\}$.

The desire is now to reduce somehow the nonlinear circulant to a linear one and use the knowledge we have about linear circulants. The trick is to transform the multiplicative structure into additive structure introducing the functions

$$g_i(I) := \ln h_i(I).$$

Then

$$h_i(I) = \exp g_i(I)$$

and the system (4.3) becomes

$$\begin{aligned} &g_0(I_0) + g_1(I_1) + \cdots + g_{k-1}(I_{k-1}) = 0,\\ &g_{k-1}(I_0) + g_0(I_1) + \cdots + g_{k-2}(I_{k-1}) = 0,\\ &\dots\\ &g_1(I_0) + g_2(I_1) + \cdots + g_0(I_{k-1}) = 0, \end{aligned} \tag{7.5}$$

which we rewrite in a symbolic form (analogous to (7.4)) as

$$G(g, \mathbf{I}) = 0. \tag{7.6}$$

We look for vertical bifurcations, i.e. we ask the question: when does the system (7.6) have a family of solutions? It is, we think, impossible to answer this question fully without specifying the functions $g_i(I)$. But some special (and relatively easy) cases, like the one of Theorem 4.2, can be traced. In particular, we make the following evident statement: a system of k equations with k unknowns can have a family of solutions if (at least) one equation is a *linear combination* of the others. This is neither a sufficient nor a necessary condition, but it helps to find a partial answer to the question above.

We come back for a minute to the linear circulant G. It is singular if

$$g \cdot \xi_{n,k} = 0 \tag{7.7}$$

(see (5.6)). We write the matrix G as

$$G = \begin{pmatrix} g \\ Sg \\ \dots \\ S^{k-1}g \end{pmatrix}$$

and consider a linear combination of the rows

$$(\mathrm{Re}(g\cdot\xi_{n,k}) \quad \mathrm{Re}(Sg\cdot\xi_{n,k}) \quad \cdots \quad \mathrm{Re}(S^{k-1}g\cdot\xi_{n,k}))^{\mathrm{T}}.$$

Because of (7.7) and $S^m g\cdot\xi_{n,k} = g\cdot S^{-m}\xi_{n,k} = \mathrm{e}^{\mathrm{i}\frac{2\pi n}{k}m} g\cdot\xi_{n,k}$, this vector is *zero*. A linear combination of the rows consisting of the imaginary parts of $S^m g\cdot\xi_{n,k}$ is also zero. The linear combination is trivial if k is even and $n=\frac{k}{2}$ since in this case $\mathrm{Im}\,\xi_{n,k}=0$. Therefore the rank of G is (at most) $k-1$ in this last case, or (at most) $k-2$ otherwise.

Arguing in exactly the same way, we notice that if

$$\exists\, 0<n\leqslant\frac{k}{2}:\forall I\geqslant 0 \quad g(I)\cdot\xi_{n,k}=0 \tag{7.8}$$

the nonlinear circulant system (7.5) can have a family of solutions. Indeed, making the same linear combinations as in the case of linear circulants, we can get rid of two (or, in the case $n=\frac{k}{2}$, one) equations. Therefore, we obtain a system of $k-2$ (respectively, $k-1$) equations with k unknowns which possesses, generally speaking, a two- (one-) parameter family of solutions.

Just as in the case of a linear circulant, we can restrict ourselves to the interval $n\in[0,\frac{k}{2}]$ (see Remark after (5.6)) because other values of n give the same conditions on $g(I)$. We exclude $n=0$ because in this case we have $\sum_{j=0}^{k-1} g_j(I)=0$ for any I or, in other words,

$$\prod_{j=0}^{k-1} h_j(I)=1 \quad \forall I,$$

which contradicts the assumption (ii) after (3.7).

For low values of k we can rewrite (7.8) in terms of the original functions as follows (cf. Corollary 7.2 and Theorem 7.3):

$$\begin{array}{ll} k=2 & h_0(I)=h_1(I)\\ k=3 & h_0(I)=h_1(I)=h_2(I)\\ k=4 & \begin{array}{l}h_0(I)=h_2(I)\\ h_1(I)=h_3(I)\end{array} \quad \text{or} \quad h_0(I)h_2(I)=h_1(I)h_3(I).\end{array} \tag{7.9}$$

After these motivating considerations, we now formulate some rigorous results and begin with the case: k is even, $n=\frac{k}{2}$ (cf. Proposition 5.7 and Theorem 6.1.i).

Proposition 7.5. *Let k be even and assume that for all $I\geqslant 0$*

$$\sum_{i=0}^{k/2-1} g_{2i}(I)=\sum_{i=0}^{k/2-1} g_{2i+1}(I)$$

(*or*, *equivalently*, $\prod_{i=0}^{k/2-1} h_{2i}(I)=\prod_{i=0}^{k/2-1} h_{2i+1}(I)$). *The one-parameter set*

$$\begin{cases} I_{2i}=\overline{I}_0\\ I_{2i+1}=\overline{I}_1, \end{cases} \qquad i=0,\ldots,\frac{k}{2}-1$$

with $G_\Sigma(\overline{I}_0) + G_\Sigma(\overline{I}_1) = 0$ *and* $G_\Sigma := \sum_{i=0}^{k-1} g_i$, *is both contained in* $\{\mathbf{I} : G(g, \mathbf{I}) = 0\}$ *and invariant under the shift* S.

Proof. Noticing that $\sum_{i=0}^{k/2-1} g_{2i} = \sum_{i=0}^{k/2-1} g_{2i+1} = \frac{1}{2} G_\Sigma$, the proof is straightforward. □

Thus we have found a family of nonuniform solutions of the nonlinear circulant system (7.5) under a condition on the nonlinearities (which translates into a condition on parameters in case of a parametrized family (3.11)). In the general case (7.8) it is unclear how to obtain a family of nonuniform solutions explicitly. However, in some cases we can simplify the form of the solution and, in particular, notice that the value of the environmental variable I can have periodicity lower than k (cf. Proposition 5.9).

Proposition 7.6. *Let* $m < k$ *be a divisor of* k. *If* $(\overline{I}_0, \overline{I}_1, \ldots, \overline{I}_{m-1})$ *is a solution of the nonlinear circulant of order* m

$$G(g_\Sigma, \mathbf{I}) = 0 \tag{7.10}$$

defined by the m*-dimensional vector*

$$g_\Sigma = \begin{pmatrix} g_0 + g_m + \cdots + g_{k-m} \\ g_1 + g_{m+1} + \cdots + g_{k-m+1} \\ \cdots \\ g_{m-1} + g_{2m-1} + \cdots + g_{k-1} \end{pmatrix}, \tag{7.11}$$

then

$$\begin{cases} I_{mi} = \overline{I}_0 \\ I_{mi+1} = \overline{I}_1 \\ \cdots \\ I_{mi+m-1} = \overline{I}_{m-1} \end{cases} \qquad i = 0, \ldots, \frac{k}{m} - 1 \tag{7.12}$$

is a solution of the nonlinear circulant of order k (7.5).

In addition, if the condition (7.8) *is satisfied for* g *and* $\frac{n}{k} = \frac{l}{m}$ *with* $l \in \mathbb{Z}$, *the condition* (7.8) *on* g *translates into the condition*

$$\exists\, 0 < l \leqslant \frac{m}{2} : \forall I \geqslant 0 \quad g_\Sigma(I) \cdot \xi_{l,m} = 0$$

for g_Σ.

Proof. If we substitute (7.12) into the nonlinear circulant (7.5) we obtain a $\frac{k}{m}$-times repetition of the first m equations and the first m equations form the nonlinear circulant (7.10). This proves the first assertion of the proposition. The second assertion can be obtained similarly to Proposition 5.9. □

Now we want to formulate a more general analogue of Theorem 4.2.

Theorem 7.7. *Let* (7.8) *be satisfied.*

(i) *If k is even and $n = \frac{k}{2}$, the $(k-1)$-dimensional manifold*

$$M_\theta = \{N : N_0 N_2 \ldots N_{k-2} = \theta N_1 N_3 \ldots N_{k-1}, \theta > 0\}$$

is mapped by (3.5) *onto $M_{\theta^{-1}}$.*

(ii) *In all other cases the $(k-2)$-dimensional manifold*

$$M_a = \{N : \ln N \cdot \xi_{n,k} = a\},$$

where a is a complex number, is mapped by (3.5) *onto $M_{a e^{-i\frac{2\pi n}{k}}}$. (Here $\ln N$ denotes the vector with components $\ln N_i$.)*

Proof. We begin with the second assertion. Let N be contained in M_a for a certain a. Then for the image N' of N under (3.5) we have

$$\begin{aligned}\ln N' \cdot \xi_{n,k} &= \sum_{i=0}^{k-1} \lambda_{n,k}^{-i} \ln N_{i-1} h_{i-1}(I)\\ &= \lambda_{n,k}^{-1}\left(\sum \lambda_{n,k}^{-(i-1)} \ln N_{i-1} + \sum \lambda_{n,k}^{-(i-1)} \ln h_{i-1}(I)\right)\\ &= \lambda_{n,k}^{-1}\left(\ln N \cdot \xi_{n,k} + g(I)\cdot \xi_{n,k}\right)\\ &= \lambda_{n,k}^{-1} a.\end{aligned}$$

The first assertion follows by restricting to real a (in order to guarantee $N_i > 0$) and by taking $\theta = e^a$. □

For a particular nonuniform solution $(I_0, \ldots, I_{k-1})$ we can find a corresponding fixed point of the full life cycle map using Eq. (4.4) which is linear with respect to N. Notice also that this fixed point is also a fixed point of an mth iterate of the map (3.5) (where m is a divisor of k), if the value of I has periodicity $m < k$. The fixed point exists and is unique if the matrix in the left-hand side of (4.4)

$$\begin{pmatrix} c_0 & c_1 & \cdots & c_{k-1}\\ c_1 h_0(I_0) & c_2 h_1(I_0) & \cdots & c_0 h_{k-1}(I_0)\\ c_2 h_0(I_0) h_1(I_1) & c_3 h_1(I_0) h_2(I_1) & \cdots & c_1 h_{k-1}(I_0) h_0(I_1)\\ \cdots & & & \\ c_{k-1} h_0(I_0)\cdots h_{k-2}(I_{k-2}) & c_0 h_1(I_0)\cdots h_{k-1}(I_{k-2}) & \cdots & c_{k-2} h_{k-1}(I_0)\cdots h_{k-3}(I_{k-2}) \end{pmatrix} \tag{7.13}$$

is nonsingular. In the case of uniform sensitivity (see the end of Section 4) the determinant of this matrix is zero if and only if the determinant of the corresponding circulant matrix C is singular. We proved that there exists a family of periodic points (Proposition 4.3 and its corollary), i.e. a vertical bifurcation takes place, if C is not singular. We did not manage to construct a family of periodic points in the general case with $k > 3$ and neither we did prove that such a family exists, so below we provide only a conjecture. But first we give a corollary of Theorem 7.7.

Corollary 7.8. *Let* (7.8) *be satisfied.*

(i) *If k is even and $n = \frac{k}{2}$, M_θ is invariant under the second iterate of the map* (3.5). *The restriction of this twice-iterated map to M_θ is a $(k-1)$-dimensional map parametrised by θ. The value of $I = c \cdot N$ performs a two-cycle* (*see Proposition* 7.5).
(ii) *In all other cases, let $\frac{n}{k} = \frac{l}{m}$, where $\frac{l}{m}$ is the irreducible fraction. The manifold M_a is invariant under the m-times iterated map* (3.5). *The restriction of this map to M_a is a $(k-2)$-dimensional map parametrised by a (i.e., by* $\operatorname{Re} a$ *and* $\operatorname{Im} a$*). The value of $I = c \cdot N$ performs an m-cycle* (*see Proposition* 7.6).

Conjecture 7.9. *Under the corresponding conditions of the corollary above and for $k > 3$.*

(i) *Fixed points of the second iterate form a one-parameter family of* 2*-periodic points of* (3.5), *parametrised by θ.*
(ii) *Fixed points of the mth iterate form a two-parameter family of m-periodic points of* (3.5), *parametrised by a.*

8. The characteristic equation corresponding to the internal steady state

If we put $N(t) = \overline{N} + y(t)$ in (3.5), where $\overline{N} = \mathbf{1}\overline{I}$ is the internal steady state, cf. (3.15), and, for small $y(t)$, Taylor expand and ignore higher than first order terms, we obtain the linearized problem:

$$y(t+1) = S\,y(t) + c \cdot y(t)\; L(h'(\overline{I}))\,\overline{N}.$$

This problem has solutions of the form $y(t) = \mu^t x$ provided x is an eigenvector corresponding to eigenvalue μ, i.e.

$$Sx + c \cdot x\; L(h'(\overline{I}))\,\overline{N} = \mu x. \tag{8.1}$$

Note that the relevant matrix is a rank one perturbation of S. As already observed in Section 5, the eigenvalues of S are the kth roots of unity

$$\lambda_{n,k} = \mathrm{e}^{n\frac{2\pi \mathrm{i}}{k}}, \quad n = 0, 1, \ldots, k-1$$

and the corresponding eigenvectors are

$$\xi_{n,k} = \begin{pmatrix} 1 \\ \lambda_{n,k}^{-1} \\ \cdots \\ \lambda_{n,k}^{-k+1} \end{pmatrix}.$$

The matrix $S^{\mathrm{T}} = S^{-1}$ has eigenvectors

$$\eta_{n,k} = \frac{1}{k} \begin{pmatrix} 1 \\ \lambda_{n,k} \\ \cdots \\ \lambda_{n,k}^{k-1} \end{pmatrix} = \frac{1}{k} \bar{\xi}_{n,k},$$

which are normalized such that

$$\eta_{n,k} \cdot \xi_{n',k} = \delta_{nn'}$$

(where the right hand side is the Kronecker δ).

Next we observe that

$$L(h'(\overline{I}))\,\mathbf{1} = Sh'(\overline{I})$$

and that, consequently,

$$\eta_{n,k} \cdot L(h'(\overline{I}))\,\overline{N} = \overline{I}\,\eta_{n,k} \cdot Sh'(\overline{I}) = \overline{I}\,\lambda_{n,k}\eta_{n,k} \cdot h'(\overline{I}).$$

Now let the (unknown) vector α represent x with respect to the basis $\{\xi_{n,k}\}$, i.e., put

$$x = \sum_{n=0}^{k-1} \alpha_n \xi_{n,k},$$

then (8.1) amounts to the system of linear equations

$$\lambda_{n,k}\alpha_n + a\,\overline{I}\,\lambda_{n,k}\eta_{n,k} \cdot h'(\overline{I}) = \mu\,\alpha_n \tag{8.2}$$

with

$$a = \sum_{m=0}^{k-1} \alpha_m\, c \cdot \xi_{m,k}.$$

Theorem 8.1. *The eigenvalues μ are the roots of the characteristic equation*

$$\mu^k - 1 - \overline{I} \sum_{m=0}^{k-1} \lambda_{m,k}\,(\eta_{m,k} \cdot h'(\overline{I}))\,(c \cdot \xi_{m,k}) \prod_{\substack{n=0 \\ n \neq m}}^{k-1} (\mu - \lambda_{n,k}) = 0, \tag{8.3}$$

which can also be written as

$$\mu^k - \overline{I} \sum_{l=0}^{k-1} \mu^l\, S^l c \cdot h'(\overline{I}) - 1 = 0. \tag{8.4}$$

Proof. Write (8.2) as

$$(\mu-\lambda_{n,k})\alpha_n = a\,\overline{I}\,\lambda_{n,k}\eta_{n,k}\cdot h'(\overline{I})$$

and multiply both sides with $c\cdot\xi_{n,k}\prod_{\substack{j=0\\ j\neq n}}^{k-1}(\mu-\lambda_{j,k})$. Since $\prod_{j=0}^{k-1}(\mu-\lambda_{j,k})=\mu^k-1$ this yields the identity

$$(\mu^k-1)\alpha_n\, c\cdot\xi_{n,k} = a\,\overline{I}\,\lambda_{n,k}(c\cdot\xi_{n,k})(\eta_{n,k}\cdot h'(\overline{I}))\prod_{\substack{j=0\\ j\neq n}}^{k-1}(\mu-\lambda_{j,k}),$$

which we sum with respect to n to obtain

$$(\mu^k-1)\,a = a\,\overline{I}\sum_{n=0}^{k-1}\lambda_{n,k}(c\cdot\xi_{n,k})(\eta_{n,k}\cdot h'(\overline{I}))\prod_{\substack{j=0\\ j\neq n}}^{k-1}(\mu-\lambda_{j,k}).$$

If μ is such that (8.3) does *not* hold then necessarily $a=0$ and hence, returning to the original form of the equation, we must have that

$$(\mu-\lambda_{n,k})\,\alpha_n = 0 \quad \text{for } n=0,1,\ldots,k-1.$$

If for all n the inequality $\mu\neq\lambda_{n,k}$ holds then $\alpha_n=0$ for all n and x is trivial, so not an eigenvector. If $\mu=\lambda_{j,k}$ for some j then $\alpha_n=0$ for $n\neq j$ and, since we must have that $a=0$, this requires that $c\cdot\xi_{j,k}=0$. But then (8.3) is actually satisfied (since all terms in the sum are zero and $\mu^k-1=\lambda_{j,k}^k-1=0$). We conclude that, in order for μ to be an eigenvalue, (8.3) must hold. As the left-hand side of (8.3) is a polynomial of degree k, it must be the characteristic polynomial.

The rewriting of (8.3) into the form (8.4) involves a few observations. First we note that

$$\prod_{\substack{n=0\\ n\neq m}}^{k-1}(\mu-\lambda_{n,k}) = \frac{\mu^k-1}{\mu-\lambda_{m,k}} = \sum_{j=0}^{k-1}\mu^{k-1-j}\lambda_{m,k}^{j} = \sum_{l=0}^{k-1}\mu^{l}\lambda_{m,k}^{-1-l}.$$

Next we note that

$$(\eta_{m,k}\cdot h'(\overline{I}))(c\cdot\xi_{m,k}) = \frac{1}{k}\sum_{i=0}^{k-1}\sum_{j=0}^{k-1}h_i'(\overline{I})\,c_j\,\lambda_{m,k}^{i-j}.$$

Finally we note that

$$\sum_{m=0}^{k-1}\lambda_{m,k}^{p} = \begin{cases} k & \text{if } p \text{ is a multiple of } k,\\ 0 & \text{otherwise.}\end{cases}$$

(This can be seen as follows. Since $\lambda_{m,k}=\mathrm{e}^{m\frac{2\pi\mathrm{i}}{k}}$ we have that $\lambda_{m,k}^{p}=\lambda_{p,k}^{m}$. So if $\lambda_{p,k}=1$ we do have $\sum_{m=0}^{k-1}\lambda_{m,k}^{p}=k$ while, for $\lambda_{p,k}\neq1$, we have $\sum_{m=0}^{k-1}\lambda_{m,k}^{p}=\sum_{m=0}^{k-1}\lambda_{p,k}^{m}=\frac{1-\lambda_{p,k}^{k}}{1-\lambda_{p,k}}=0$.)

Using the first two observations we write the sum in (8.3) as

$$\frac{\overline{I}}{k}\sum_{m=0}^{k-1}\sum_{i=0}^{k-1}\sum_{j=0}^{k-1}h_i'(\overline{I})c_j\sum_{l=0}^{k-1}\mu^l\lambda_{m,k}^{i-j-l}$$

and, after changing the order of summation, we can use the third observation to obtain

$$\overline{I}\sum_{l=0}^{k-1}\mu^l\sum_{i=0}^{k-1}h_i'(\overline{I})c_{i-l}=\overline{I}\sum_{l=0}^{k-1}\mu^l\,S^lc\cdot h'(\overline{I}). \qquad \square$$

Corollary 8.2. *The linearized problem has eigenvalue* $\lambda_{n,k}$ *if and only if either* $c\cdot\xi_{n,k}=0$ *or* $\eta_{n,k}\cdot h'(\overline{I})=0$.

In connection with this corollary, please observe that $c\cdot\xi_{0,k}=1$ and $\eta_{0,k}\cdot h'(\overline{I})<0$ (recall the assumption (ii) after (3.7)). Since $\lambda_{n,k}$ is on the unit circle, the condition $c\cdot\xi_{n,k}=0$ is a local bifurcation condition. In fact, however, a "vertical" bifurcation occurs as we already know: recall Theorem 6.1 and Lemma 5.4 with the equality (5.6).

Also note that $\eta_{n,k}\cdot h'(\overline{I})=0$ iff $h'(\overline{I})\cdot\xi_{n,k}=0$ and that, unless k is even and $n=\frac{k}{2}$, if $\lambda_{n,k}$ is an eigenvalue so is $\lambda_{k-n,k}$ (indeed, $\bar{\lambda}_{n,k}=\lambda_{k-n,k}$, $\bar{\xi}_{n,k}=\xi_{k-n,k}$, $\bar{\eta}_{n,k}=\eta_{k-n,k}$). This is also a condition for a local bifurcation of the internal steady state, but it does not imply, generally speaking, a vertical bifurcation. For a counterexample see Section 10. However, in some cases (Ricker and Beverton–Holt, see also [8]) it *does* correspond to a vertical bifurcation. Notice also that the identity $h'(\overline{I})\cdot\xi_{n,k}=0$ coincides exactly with the condition (7.3) for zero Jacobian of the nonlinear circulant (4.3).

If $\mu=1$ the characteristic polynomial in the left-hand side of (8.4) becomes

$$\begin{aligned}-\overline{I}\sum_{l=0}^{k-1}S^lc\cdot h'(\overline{I})&=-\overline{I}\sum_{j=0}^{k-1}c_j\sum_{l=0}^{k-1}h_l'(\overline{I})\\&=-\overline{I}\sum_{l=0}^{k-1}h_l'(\overline{I})>0.\end{aligned}$$

This expression is positive because all functions h are non-increasing and at least one h is strictly decreasing. So, we have the following.

Corollary 8.3. $\mu=1$ *is never a root of the characteristic equation* (8.4) (*as to be expected from the uniqueness of the internal steady state*).

Of course, the characteristic equation (8.3)/(8.4) may also have roots on the unit circle away from the kth roots of unity. In Section 11 we shall analyse the details for the relatively simple case $k=3$.

9. The other extreme: SYC and transversal stability

Thus far we have more or less concentrated on (the stability of) steady states in which all year classes are present and on certain degenerate bifurcation phenomena associated with singular circulants. The other extreme is the case in which a single year class (SYC) dominates the world, as it happens in the cicada species mentioned in the introduction. The "full life cycle map" is defined as the kth iterate of the map featuring in (3.5). Our first result is a direct consequence of (4.1).

Lemma 9.1. *The set* $\{N : N_j = 0 \text{ for some } j\}$ *is invariant under the full life cycle map.*

If we consider an orbit of the full life cycle map, we say that as many year classes are *missing* as there are indices j for which $N_j = 0$. The extreme case is when all but one year classes are missing. Note that indeed, as the next corollary shows, it makes sense to talk about missing year classes.

Corollary 9.2. *All coordinate axes are invariant under the full life cycle map.*

The dynamics generated by the restriction of the full life cycle map to an invariant axis is called SYC-dynamics. It is studied extensively in [7], to which we refer for further information (note that the restriction to the various axes are "equivalent", but *not* necessarily by a homeomorphism). Here we focus on another aspect, the *transversal stability*: do perturbations away from the invariant axis damp out or grow? Or, in biological terms, is a missing year class, when introduced in small numbers, doomed to go extinct or will it persist?

Because of the invariance described in Lemma 9.1, there is indeed a well defined eigenvalue/multiplier associated with each of the missing year classes, so the biological terminology and the mathematical formulations are in precise correspondence.

Every fixed point of the full life cycle map corresponds to a k-periodic orbit of the original recursion (3.5). So, in particular, the environmental variable I is k-periodic.

Now consider a SYC fixed point. Let $I_0, I_1, \ldots, I_{k-1}$ denote the values I takes and let the numbering be chosen such that $N_0 > 0$ when I_0 prevails. According to (4.2) we then need to have that

$$\prod_{i=0}^{k-1} h_i(I_i) = 1. \tag{9.1}$$

Next, observe that (4.1) immediately yields an invasibility test: the year class which is j years older than the ruling year class can grow when

$$\prod_{i=0}^{k-1} h_{j+i}(I_i) > 1 \tag{9.2}$$

and is doomed to go extinct when the opposite inequality holds (this is the familiar phenomenon that in population models the stability with respect to missing species can be determined by way of a decoupled eigenvalue problem, whose definition does not involve any differentiation; mathematically, of course, the key point is invariance of coordinate hyperplanes).

Simple as the test may be, to say something systematic about the outcome is considerably more complicated. We have only one result to offer. It gives sufficient conditions for transversal stability, i.e., conditions which guarantee that none of the missing year classes can invade successfully.

The result substantiates a key point (which is relevant for the cicada phenomenon): it is not at all exceptional that a SYC fixed point is an attractor for the recursion (3.5). Or, more precisely, there are large classes of functions h and vectors c for which stable SYC fixed points exist. (A preliminary version of this result was obtained in 1999 by Jennifer Baker.)

A key assumption will be that the function

$$I \mapsto \frac{h_i(I)}{h_{i+1}(I)} \quad \text{is strictly monotone increasing for } i = 0, 1, \ldots, k-2 \tag{9.3}$$

or, equivalently, that for $i = 0, 1, \ldots, k-2$

$$h_i(I^+)h_{i+1}(I^-) > h_i(I^-)h_{i+1}(I^+) \quad \text{for all } I^\pm \text{ with } I^+ > I^-.$$

Note that (9.3) implies that also

$$I \mapsto \frac{h_i(I)}{h_{i+j}(I)} \quad \text{is strictly monotone increasing}$$

for i, j-combinations with $i \geqslant 0$ and $i + j \leqslant k-1$. Hence for such i, j-combinations we as well have that

$$h_i(I^+)h_{i+j}(I^-) > h_i(I^-)h_{i+j}(I^+) \quad \text{for all } I^\pm \text{ with } I^+ > I^-. \tag{9.4}$$

Theorem 9.3. *Let $I_0, I_1, \ldots, I_{k-1}$ be such that*

(i) (9.1) *holds*,

(ii)

$$i \mapsto I_i \quad \textit{is strictly decreasing on } \{0, 1, \ldots, k-1\}. \tag{9.5}$$

Assume that (9.3) *holds. Then for $j = 1, 2, \ldots, k-1$*

$$\prod_{i=0}^{k-1} h_{j+i}(I_i) < 1. \tag{9.6}$$

Proof. Define $m = k - j$ then the left-hand side of (9.6) can also be written as

$$h_0(I_m)h_1(I_{m+1}) \cdots h_{k-1-m}(I_{k-1})h_{k-m}(I_0)h_{k-m+1}(I_1) \cdots h_{k-1}(I_{m-1})$$

This expression can be viewed as a cyclic shift of indices of the arguments I_i of the expression

$$h_0(I_0)h_1(I_1)\cdots h_{k-1}(I_{k-1})$$

which, by (9.1), equals one. Note that such a shift can be realised by repeatedly interchanging two neighbours which, in the starting position, are ordered according to the index. In detail: consider the transformation from $0\ 1\cdots(k-1)$ to $m\ (m+1)\cdots(m-1)\ 0\ 1\cdots(m-1)$; starting from $0\ 1\cdots(m-1)\ m\cdots(k-1)$ first bring $(m-1)$ to the end position by repeatedly interchanging it with its right neighbour; next bring $(m-2)$ to the one-but-last position by the same procedure; et cetera. In each step two neighbours interchange their position with, at the start of the step, the I with the highest index to the right. By (9.5) and (9.4) the value of the expression decreases in each step. It follows that (9.6) holds. □

Remark. The "strict" part in (9.3) and (9.5) is a bit stronger than really needed, as it suffices that there is a strict decrease in at least one of the steps.

The condition (9.5) is not directly in terms of the ingredients of the model. Our next objective is to give a sufficient condition, in terms of c, for (9.5) to hold. In order to facilitate the application, we do so in terms of the unscaled c. In this connection it is important to recall that h_i^u is, for $i = 0, 1, \ldots, k-2$, a survival probability, so that it takes values less than (or equal to) one.

Lemma 9.4. *Let $\overline{N}^{ss}$ be a SYC fixed point ("ss" denotes the doubly scaled variable N, see Section* 3). *Define*

$$I_i = c_i^s\overline{N}_i^{ss} = c_i^u\overline{N}_i^u.$$

Assume that

$$i \mapsto c_i^u \quad \textit{is strictly monotone decreasing on } \{0, 1, \ldots, k-1\}. \tag{9.7}$$

Then (9.5) *is satisfied*.

Proof

$$I_{i+1} = c_{i+1}^u\overline{N}_{i+1}^u = c_{i+1}^u h_i^u(I_i)\overline{N}_i^u \leqslant c_{i+1}^u\overline{N}_i^u < c_i^u\overline{N}_i^u = I_i,$$

where the first inequality derives from the interpretation of h_i^u as a survival probability and the second from assumption (9.7). □

Remark. Note that the condition (9.3) on h is invariant under our scaling, as the scaled version of the quotient differs only by the constant $\frac{h_{i+1}^u(\bar{I})}{h_i^u(\bar{I})}$ from the unscaled version.

In the Ricker case (3.12) the assumption (9.3) amounts to the strict monotonicity of

$$i \mapsto g_i.$$

The interpretation of this condition is that the sensitivity is an increasing function of age, while (9.7) means that the impact is a decreasing function of age. So in case of (3.12) one can say that this combination of age dependence of sensitivity and impact guarantees that a SYC fixed point is transversally stable (this is the result originally proved by J. Baker).

One can also formulate a variant of Theorem 9.3 in which both assumptions (9.3) and (9.5) are reversed (meaning that "decreasing" is changed into "increasing" and vice versa). The corresponding variant of Lemma 9.4 is more problematic, as the bound on h_i^u works in the wrong direction. So one has to replace (9.7) by the condition that $i \mapsto c_i^u$ increases sufficiently strongly, where "sufficiently" incorporates quantitative details.

Finally, note that one can also formulate transversal *instability* results in the spirit of Theorem 9.3. We refrain from doing so.

10. Biennials ($k = 2$)

For $k = 2$ the condition $c_0 = c_1 = \frac{1}{2}$ in Theorem 4.1 defines a codimension one surface in parameter space (recall that $c_0 + c_1 = 1$) and hence it can serve as a full-fledged stability boundary. In the case of Ricker nonlinearities (cf. (3.1)) the same can be said about $g_0 = g_1 = \frac{1}{2}$ in connection with Corollary 7.4. The main conclusion of [8] is that for $k = 2$ and Ricker nonlinearities there is, for $R_0 > 1$ but not too large, a strict dichotomy: either the coexistence steady state is stable or the period two SYC state is stable. The transition between these two generic situations is by way of vertical period-doubling bifurcations as they occur when either $c_0 = c_1 = \frac{1}{2}$ or $g_0 = g_1 = \frac{1}{2}$. As a result of the present analysis of the more general model we now understand the underlying reasons for this degenerate bifurcation phenomenon. The fact that I is a one-dimensional quantity is crucial for the phenomenon of Theorems 4.1 and 6.1. And, finally, the phenomena described in Theorem 4.2 and Proposition 4.5 occur because we deal with functions h_i given by (3.11) such that the ratio $\frac{h_0}{h_1}$ switches from strictly decreasing for $g_0 > g_1$ to strictly increasing for $g_0 < g_1$ by way of being constant for $g_0 = g_1$ (recall also Corollary 7.2).

To illustrate the last point, we shall briefly look at the corresponding period-doubling bifurcation when $\frac{h_0}{h_1}$ can *not* be constant (for all parameter values). We shall now focus on a particular example, but analyse it in a way that exposes the general pattern for a nonmonotone quotient $\frac{h_0}{h_1}$. Consider h_i defined by (recall the normalisation (3.9a))

$$h_0(I, \overline{I}) = e^{\overline{I}-I},$$
$$h_1(I, \overline{I}) = \frac{1+2\overline{I}}{1+2I},$$

where we write $\overline{I}$ as another argument of h_i. Then

$$\frac{h_0}{h_1}(I,\overline{I}) = \frac{f(I)}{f(\overline{I})},$$

where by definition

$$f(I) = (1+2I)\mathrm{e}^{-I}.$$

From $f'(I) = (1-2I)\mathrm{e}^{-I}$ we deduce that f is strictly increasing on $[0, \frac{1}{2})$ and strictly decreasing on $(\frac{1}{2}, \infty)$. For $1 \leqslant y < 2\mathrm{e}^{-\frac{1}{2}} \approx 1.213$ the function f assumes the value y twice, once in $I_0(y) \in [0, \frac{1}{2})$ and once in $I_1(y) \in (\frac{1}{2}, \tilde{I})$, where $\tilde{I}$ is the positive solution of $f(I) = 1$. Thus we find a family, parametrised by y, of solutions to the equation

$$\frac{h_0}{h_1}(I_0,\overline{I}) = \frac{h_0}{h_1}(I_1,\overline{I}). \tag{10.1}$$

In order to satisfy (7.1) we should, in addition to (10.1), also satisfy

$$h_0(I_0,\overline{I})\, h_1(I_1,\overline{I}) = 1. \tag{10.2}$$

The idea now is to consider (10.2) as an equation for $\overline{I}$. In our particular example, (10.2) can be rewritten as

$$(1+2\overline{I})\mathrm{e}^{\overline{I}} = (1+2I_1(y))\mathrm{e}^{I_0(y)} \quad (= (1+2I_0(y))\mathrm{e}^{I_1(y)}),$$

which has a unique solution $\overline{I}(y)$. So by considering (7.1) as two equations in three unknowns $(I_0, I_1, \overline{I})$, we were able to find a one-parameter family of non-trivial solutions. (By inserting $\overline{I}(y)$ into the defining equation (3.8), one can find one of the parameters in the original unscaled h_i^u in terms of y and, provided the relationship is invertible, parametrise the branch of non-trivial (I_0, I_1) solutions of (7.1) by this parameter.)

For $y = 2\mathrm{e}^{-\frac{1}{2}}$ we have $I_0 = I_1 = \frac{1}{2}$ and, also, $\overline{I}(y) = \frac{1}{2}$. So the non-trivial branch "originates" as a symmetry breaking bifurcation from the trivial branch $(I_0, I_1) = (\overline{I}, \overline{I})$ (note that $h_0'(\overline{I}) = -1$ and $h_1'(\overline{I}) = \frac{-2}{1+2\overline{I}}$, which is indeed equal to -1, hence to $h_0'(\overline{I})$, for $\overline{I} = \frac{1}{2}$). To see that the branch also connects to the SYC boundary states, we need to investigate the equations

$$\begin{aligned} c_0N_0 + c_1N_1 &= I_0, \\ c_0N_1h_1(I_0) + c_1N_0h_0(I_0) &= I_1, \end{aligned} \tag{10.3}$$

which have the solution

$$\begin{pmatrix} N_0 \\ N_1 \end{pmatrix} = \frac{1}{c_0^2h_1(I_0) - c_1^2h_0(I_0)} \begin{pmatrix} c_0h_1(I_0)I_0 - c_1I_1 \\ c_0I_1 - c_1h_0(I_0)I_0 \end{pmatrix}. \tag{10.4}$$

First note that for $I_0 = I_1 = \overline{I} = \frac{1}{2}$ we do indeed recover the steady state (3.15): $N_0 = N_1 = \overline{I}$. Secondly, note that the branch ceases to be biologically relevant when we "hit the wall", i.e., when one of the two components becomes zero. The limiting point then is a SYC fixed point, so a period two point at the boundary.

In (10.4) any of the two components can become zero, but this reflects the choice of the phase rather than an intrinsic phenomenon. Indeed, the point defined by (10.4) forms, together with its image

$$\begin{pmatrix} h_1(I_0)N_1, \\ h_0(I_0)N_0 \end{pmatrix},$$

a period two orbit. If instead of (10.3) we solve the equations

$$\begin{aligned} &c_0\tilde{N}_0 + c_1\tilde{N}_1 = I_1, \\ &c_0\tilde{N}_1 h_1(I_1) + c_1\tilde{N}_0 h_0(I_1) = I_0 \end{aligned}$$

we find, as one can easily verify using (7.1), the solution

$$\begin{pmatrix} \tilde{N}_0 \\ \tilde{N}_1 \end{pmatrix} = \begin{pmatrix} h_1(I_0)N_1 \\ h_0(I_0)N_0 \end{pmatrix}.$$

So if we choose to represent the branch of period two orbits by the solution of (7.1), rather than by that of (10.3), it is the other axis that is hit.

If a SYC fixed point is characterized by

$$h_0(I_0)h_1(I_1) = 1$$

the transversal (in)stability is determined by (cf. (9.2))

$$\operatorname{sign}(h_0(I_1)h_1(I_0) - 1).$$

Along the branch of interior period two points (7.1) holds, so when the branch hits the wall, there is a stability switch for the SYC fixed point. So, just as in [8], there is a branch of period two orbits "originating" in the uniform steady state and "dying" in the (boundary) SYC fixed points and related to stability changes of, respectively, the uniform steady state and the SYC fixed points. But whereas in [8] the branch is vertical, i.e., exists for a particular parameter combination, here it is of a standard type, involving changes in a parameter as well (most easily expressed in terms of changes in $\overline{I}$ but these, in turn, can be regarded as being caused by changes in some other, suitable, parameter). In [7] a detailed analysis of SYC dynamics in case of $k = 2$ and Ricker nonlinearities is presented. We conclude that the case $k = 2$ can be analysed in quite some detail and refer once again to [8] for biological interpretations of the results.

11. Triennials ($k = 3$)

Let us start it up by presenting some preliminary results concerning stability conditions of a steady state for a three-dimensional discrete time dynamical system. For completeness we derive these in detail.

Lemma 11.1. *Consider, for given real numbers a_i, the equation*

$$\mu^3 + a_0\mu^2 + a_1\mu + a_2 = 0. \tag{11.1}$$

Then

(i) $\mu = 1$ *is a root iff* $1 + a_0 + a_1 + a_2 = 0$;
(ii) $\mu = -1$ *is a root iff* $1 - a_0 + a_1 - a_2 = 0$;
(iii) $\mu = \mathrm{e}^{\pm\mathrm{i}\phi}$, *with* $0 < \phi < \pi$, *are complex-conjugate roots iff*

$$-2 < a_2 - a_0 < 2$$
$$1 - a_2^2 = a_1 - a_0 a_2$$

and then $\cos\phi = \frac{1}{2}(a_2 - a_0)$.

Lemma 11.2. *The relations*

$$1 - a_0 + a_1 - a_2 = 0$$

and

$$1 - a_2^2 = a_1 - a_0 a_2$$

are both satisfied iff either

$$a_2 = 1, \quad a_0 = a_1$$

or

$$a_0 = 2 + a_2, \quad a_1 = 1 + 2a_2$$

(*or both*). *In the first case* (11.1) *has both a simple root at* -1 *and a pair of complex roots* $\mathrm{e}^{\pm\mathrm{i}\phi}$ *iff* $-1 < a_0 < 3$ *and then* $\cos\phi = \frac{1}{2}(1 - a_0)$ (*hence there is a triple root at* -1 *for* $a_0 = 3$ *and a double root at* $+1$ *for* $a_0 = -1$). *In the second case* (11.1) *has a double root at* -1 (*which is actually a triple root if both conditions are satisfied, i.e. for* $a_2 = 1,\ a_0 = a_1 = 3$).

Proof. Writing $1 - a_2^2 = (1 - a_2)(1 + a_2)$ and $a_1 - a_0 a_2 = a_0 - (1 - a_2) - a_0 a_2 = (a_0 - 1)(1 - a_2)$ we see that for $a_2 \neq 1$, we can divide out a factor $1 - a_2$ to obtain $1 + a_2 = a_0 - 1$. Elementary considerations then yield the desired conclusions. □

Lemma 11.3. *All roots of* (11.1) *lie strictly inside the unit circle iff*

$$\begin{array}{ll} 1 + a_0 + a_1 + a_2 > 0 & \text{(a)} \\ 1 - a_0 + a_1 - a_2 > 0 & \text{(b)} \\ |a_2| < 1 & \text{(c)} \\ 1 - a_2^2 > a_1 - a_0 a_2 & \text{(d)} \end{array} \qquad (11.2)$$

Proofs of the first and the third lemma are given in the Appendix. We remark that the stability conditions (11.2) can be found in many books such as [13,15,17,18,20]. Usually condition (d) is written as

$$|1 - a_2^2| > |a_1 - a_0 a_2|.$$

Given (a)–(c), this is equivalent to the more informative version presented in [15] and here, which also fits much better to Lemma 11.1.iii.

For $k = 3$ the characteristic equation (8.4) is of the form (11.1) with

$$a_0 = -\overline{I}\, S^2 c \cdot h'(\overline{I}),$$
$$a_1 = -\overline{I}\, S^2 c \cdot h'(\overline{I}),$$
$$a_2 = -\overline{I} c \cdot h'(\overline{I}) - 1,$$

so that (since $c + Sc + S^2c = (c_0 + c_1 + c_2)\mathbf{1} = \mathbf{1}$)

$$a_0 + a_1 + a_2 = -\overline{I}(h_0'(\overline{I}) + h_1'(\overline{I}) + h_2'(\overline{I})) - 1.$$

This motivates us to consider

$$\begin{pmatrix} a_0 \\ a_1 \\ a_2 \end{pmatrix} = \theta \begin{pmatrix} \alpha_0 \\ \alpha_1 \\ \alpha_2 \end{pmatrix} - \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}$$

with

$$\theta = -\overline{I}(h_0'(\overline{I}) + h_1'(\overline{I}) + h_2'(\overline{I})), \tag{11.3}$$

$\alpha_i \geqslant 0$ and $\alpha_0 + \alpha_1 + \alpha_2 = 1$ (so, in a sense, θ gives the magnitude of the vector a and α the direction, as far as these depend on the original model parameters). We shall make pictures of stability regions in the (α_2, α_0)-plane for various values of θ. Due to the above conditions on α we consider only a triangle in this plane defined by $\alpha_0 \geqslant 0, \alpha_2 \geqslant 0, \alpha_0 + \alpha_2 \leqslant 1$.

The first stability condition (11.2 a) is always satisfied (easy to check, but see also Corollary 8.3).

The second condition (11.2 b) can be written as

$$\alpha_0 < \frac{1}{\theta} + \frac{1}{2} - \alpha_2. \tag{11.4}$$

For $\theta < 2$ this inequality is always satisfied, but for $\theta > 2$ it is only satisfied in a θ-dependent part of the (α_2, α_0) parameter-triangle (corresponding to the shaded area in Fig. 3). At the boundary, where (11.4) turns into an equality, a period doubling bifurcation can take place.

The third condition (11.2 c) amounts to $\alpha_2 < \frac{2}{\theta}$ which is a constraint only if $\theta > 2$.

The fourth condition (11.2 d) can be written as

$$\alpha_0 > \alpha_2 + \frac{1}{\theta}\left(\frac{1}{\alpha_2} - 3\right). \tag{11.5}$$

Define, for $\alpha_2 > 0$,

$$\varphi(\alpha_2) := \alpha_2 + \frac{1}{\theta}\left(\frac{1}{\alpha_2} - 3\right).$$

From $\varphi'(\alpha_2) = 1 - \frac{1}{\theta}\frac{1}{\alpha_2^2}$ we deduce that φ has a unique minimum for $\alpha_2 = \frac{1}{\sqrt{\theta}}$, given by

$$\varphi\left(\frac{1}{\sqrt{\theta}}\right) = \frac{1}{\sqrt{\theta}}\left(2 - \frac{3}{\sqrt{\theta}}\right).$$

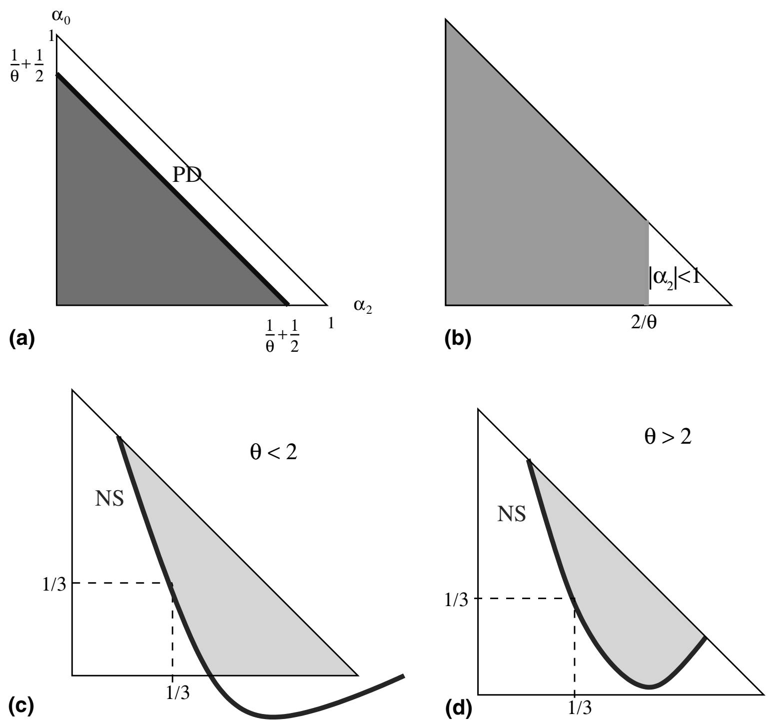

Fig. 3. In this figure one can see parameter regions (as shaded) where the stability conditions (11.2) are satisfied: (**a**) condition (b) or (11.4); (**b**) condition (c); (**c**) condition (d) or (11.5) for $\theta < 2$; (**d**) condition (d) or (11.5) for $\theta > 2$.

The graph of φ intersects the line $\alpha_2 \mapsto 1 - \alpha_2$ at

$$\alpha_2^{\pm} = \frac{1}{4}\left(\frac{3}{\theta} + 1\right) \pm \sqrt{\left(\frac{3}{4\theta} + \frac{1}{4}\right)^2 - \frac{1}{2\theta}}.$$

Note that there are, for all θ, two intersections (this follows most easily by checking that the minimum of φ computed above is less than $1 - \frac{1}{\sqrt{\theta}}$ for all $\theta > 0$). For $\theta = 2$ these occur at $\alpha_2^+ = 1$ and $\alpha_2^- = \frac{1}{4}$.

In view of the second (and the third) condition we are also interested in intersections of the graph of φ with the line $\alpha_2 \mapsto \frac{1}{\theta} + \frac{1}{2} - \alpha_2$. Since

$$\varphi(\alpha_2) - \frac{1}{\theta} - \frac{1}{2} + \alpha_2 = \left(\alpha_2 - \frac{2}{\theta}\right)\left(2 - \frac{1}{2\alpha_2}\right)$$

these occur for $\alpha_2 = \frac{1}{4}$ and for $\alpha_2 = \frac{2}{\theta}$. According to Lemma 11.3, there is a double root at -1 for $\alpha_2 = \frac{1}{4}$, while for $\alpha_2 = \frac{2}{\theta}$ and $0 < \theta < 8$ there is a simple root at -1 and a pair of roots $\mathrm{e}^{\pm\mathrm{i}\phi}$ with $\cos\phi = 1 - \frac{\theta}{4}$.

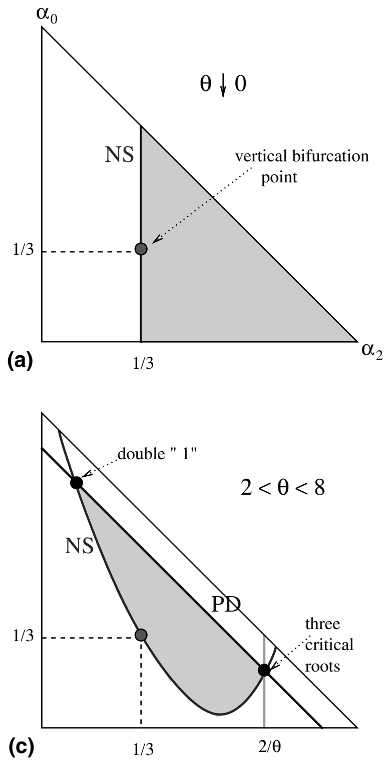

Fig. 4. Stability diagrams of the internal steady state in the case $k = 3$ for different values of θ (given by (11.3)). The relevant parameter region is the triangle defined by $\alpha_0 \geqslant 0,\ \alpha_2 \geqslant 0,\ \alpha_0 + \alpha_2 \leqslant 1$. For $0 < \theta \leqslant 2$ the gray area corresponding to the stability of the steady state is bounded by the NS-curve on which a pair of complex-conjugate roots lies on the unit circle. For $2 < \theta < 8$ the stability region is bounded also by the PD-curve where -1 is a root of the characteristic equation. For $\theta \geqslant 8$ the stability domain is empty because the area between the PD and NS curve lie to the right of the line $\alpha_2 = \frac{2}{\theta}$.

Based on this information we now draw stability diagrams in the (α_2, α_0)-triangle for various values of θ (Fig. 4). The PD-curve corresponds to $\mu = -1$ being a root of the characteristic equation where a period doubling bifurcation may occur. The NS-curve corresponds to a pair of complex-conjugate roots lying on the unit circle; on this curve a so-called Neimark–Sacker bifurcation may occur when an invariant circle emerges from the internal equilibrium (a Hopf bifurcation for maps).

The complex 3rd-roots of unity are characterised by $\cos\phi = -\frac{1}{2}$. With $\cos\phi = \frac{1}{2}(a_2 - a_0) = \frac{1}{2}\theta(\alpha_2 - \alpha_0) - \frac{1}{2}$ this amounts to $\alpha_2 = \alpha_0$. So a vertical bifurcation can occur where the 45°-line intersects the NS-curve. This happens for $\alpha_0 = \alpha_2 = \frac{1}{3}$ (but in order for this point to lie on the stability boundary, it should be below the PD-curve; this amounts to $\theta < 6$).

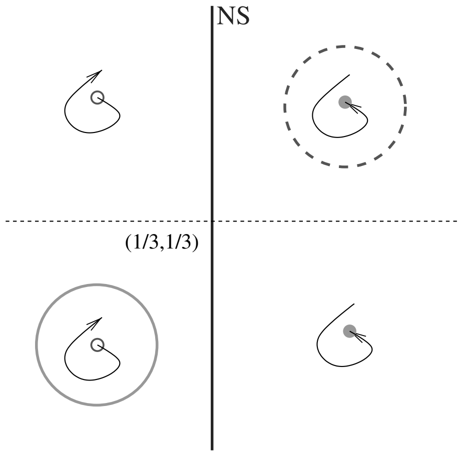

Fig. 5. Two directions of the Neimark–Sacker bifurcation. On one part of the curve the internal equilibrium loses stability and a stable invariant circle appears around it, while on the other part the equilibrium becomes unstable because an unstable invariant circle, surrounding it, lands on the equilibrium.

Presumably the direction of bifurcation of the invariant circle changes along the NS-curve in the point $\left(\frac{1}{3}, \frac{1}{3}\right)$. This means that on one part of the curve the internal equilibrium loses stability and a stable invariant circle appears around it, while on the other part the equilibrium becomes unstable because an unstable invariant circle, surrounding it, lands on the equilibrium (Fig. 5). (Of course, there should be (at least) a bifurcation curve intersecting the NS-curve in the point $\left(\frac{1}{3}, \frac{1}{3}\right)$ and corresponding to a non-local bifurcation in which the (stable and unstable) invariant circles (dis)appear. But we come to that later in this section).

The main conclusion of our analysis is that for $k = 3$ the stability boundary of the internal steady state (in some parameter space) consists of a PD part and a NS part, and that the set of vertical bifurcation points forms a lower dimensional subset of the NS part.

We realise that a "translation" of the stability conditions in terms of α and θ into conditions in terms of parameters like c and g may still involve a considerable investment of energy (if possible at all). Yet we notice that, with the results as presented here available, one can always check whether the steady state is stable for particular values of the original parameters just by calculating the corresponding values of α and θ.

Let us now consider the particular case of Beverton–Holt dependence (3.13) which demonstrates that the bifurcations shown in Fig. 4 do not always take place. Using (3.13) we have

$$-\overline{I}\, h_i'(\overline{I}) = \frac{g_i \overline{I}}{1 + g_i \overline{I}} < 1$$

and hence

$$-0 \leqslant a_i < 1, \quad i = 0, 1,$$
$$-1 \leqslant a_2 < 0.$$

In particular, we have the following consequence of it.

Proposition 11.4. *For $k = 3$ and the Beverton–Holt nonlinearity* (3.13), $\mu = -1$ *is never a root of the characteristic equation* (8.4).

Proof. We substitute $\mu = -1$ in the left-hand side of (8.4) and obtain $-1 + a_0 - a_1 + a_2 < 0$ because $a_0 - 1 < 0$, $-a_1 \leqslant 0$ and $a_2 < 0$. □

Corollary 11.5. *In the case $k = 3$ and the Beverton–Holt nonlinearity a period doubling bifurcation of the internal steady state is impossible.*

(If we calculate θ we notice that $\theta < 3$, i.e. it can be larger than 2 and we can in principle expect the period-doubling (Fig. 4). But

$$\alpha_0 + \alpha_2 = \frac{a_0}{\theta} + \frac{a_2 + 1}{\theta} < \frac{1}{\theta} + \frac{1}{\theta} < \frac{1}{\theta} + \frac{1}{2}$$

and hence the condition (11.4) is always satisfied.)

We perform further analysis of the case $k = 3$ for a very specific situation: $h_1(I) = h_2(I) = 1$, i.e., we assume that only the survival probability of the youngest year class is density dependent. This is not an unusual assumption in age-structured population modelling (see e.g., [19] and references therein).

The recursion (3.5) is now given by

$$N_0(t+1) = N_2(t),$$
$$N_1(t+1) = N_0(t)h_0(I(t)),$$
$$N_2(t+1) = N_1(t)$$

with

$$I = c_0N_0 + c_1N_1 + c_2N_2.$$

The quantity $\theta = -\overline{I}h_0'(\overline{I})$ and

$$a_0 = \theta c_1,$$
$$a_1 = \theta c_2,$$
$$a_2 = \theta c_0 - 1.$$

The stability conditions (11.2 b–d) can be rewritten (noticing that $c_0 + c_1 + c_2 = 1$) in the original parameters as respectively

$$\begin{aligned} &c_1 < \tfrac{1}{2} + \tfrac{1}{\theta} - c_0, \\ &c_0 < \tfrac{2}{\theta}, \\ &c_1 > c_0 + \tfrac{1}{c_0\theta} - \tfrac{3}{\theta}. \end{aligned} \tag{11.6}$$

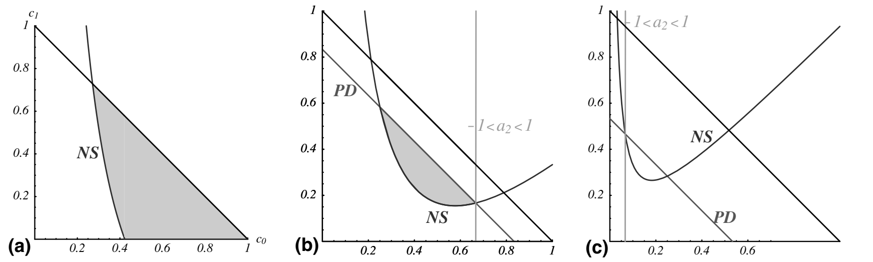

Fig. 6. Stability regions of the internal steady state in the original parameter plane (c_0, c_1) for the case $h_1(I) = h_2(I) = 1$: (a) $\theta < 2$, (b) $2 < \theta < 8$, (c) $\theta > 8$.

Regions of stability in the parameter plane (c_0, c_1) are shown in Fig. 6 for different values of θ. We notice that only a triangle $c_0 \geqslant 0$, $c_1 \geqslant 0$, $c_0 + c_1 \leqslant 1$ is relevant. Of course, we see precise correspondence with Fig. 4: for $\theta < 2$ only the NS-curve bounds the region of stability, while for $2 < \theta < 8$ the PD curve appears and finally for $\theta > 8$ the internal steady state is always unstable. For the Beverton–Holt nonlinearity we have in this case $\theta = -\overline{I}h_0'(\overline{I}) = \frac{g_0\overline{I}}{1+g_0\overline{I}} < 1$.

Now we look at SYC-equilibria and consider their transversal stability. For $k = 3$ a SYC fixed point is determined by the system

$$\begin{aligned} &h_0(I_0)\, h_1(I_1)\, h_2(I_2) = 1,\\ &I_0 = c_0\, N_0,\\ &I_1 = c_1\, N_0\, h_0(I_0),\\ &I_2 = c_2\, N_0\, h_0(I_0)\, h_1(I_1). \end{aligned}$$

Since in our case $h_1(I) = h_2(I) = 1$ for any I, the first identity becomes $h_0(I_0) = 1$ and consequently

$$\begin{aligned} &I_0 = \overline{I},\\ &I_1 = \frac{c_1}{c_0}\overline{I},\\ &I_2 = \frac{c_2}{c_0}\overline{I}. \end{aligned}$$

According to (9.2) a one year older year class can invade if

$$h_1(I_0)h_2(I_1)h_0(I_2) = h_0\left(\frac{c_2}{c_0}\overline{I}\right) > 1$$

and a two years older year class invades if

$$h_2(I_0)h_0(I_1)h_1(I_2) = h_0\left(\frac{c_1}{c_0}\overline{I}\right) > 1.$$

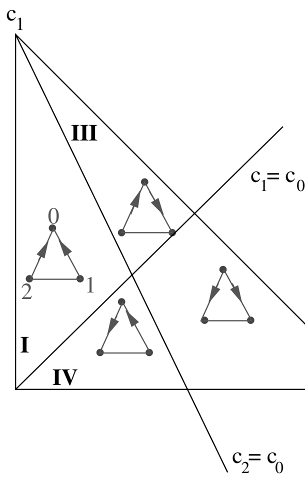

Fig. 7. Bifurcation diagram for a SYC point. The vertices 0, 1 and 2 of the small triangles represent points on the axes N_0, N_1 and N_2 corresponding to the SYC 3-cycle. An arrow pointing from 0 to 1 shows that the one year older year class can invade, an opposite arrow means that it can not invade. Similarly, for arrows between 0 and 2.

Since $h_0(I) > 1$ for $I < \overline{I}$, these inequalities simplify to

$$c_2 < c_0,$$
$$c_1 < c_0.$$

In Fig. 7 we show schematically whether a missing year can or can not invade in different regions of the (c_0, c_1)-triangle.

Now we turn our attention to MYC-equilibria in which one year class of the three is missing. Let at time t two age classes N_0 and N_1 be present. Then after three years we shall have again these age classes. According to (4.1) their densities are at equilibrium if

$$h_0(I_0)h_1(I_1)h_2(I_2) = h_0(I_0) = 1,$$
$$h_0(I_2)h_1(I_0)h_2(I_1) = h_0(I_2) = 1$$

and hence $I_0 = I_2 = \overline{I}$. On the other hand (see (4.4))

$$I_0 = c_0N_0 + c_1N_1,$$
$$I_1 = c_1N_0h_0(I_0) + c_2N_1h_1(I_0),$$
$$I_2 = c_2N_0h_0(I_0)h_1(I_1) + c_0N_1h_1(I_0)h_2(I_1),$$

which simplifies to

$$\begin{aligned} &c_0N_0 + c_1N_1 = \overline{I},\\ &c_2N_0 + c_0N_1 = \overline{I},\\ &I_1 = c_1N_0 + c_2N_1. \end{aligned} \tag{11.7}$$

From the first two identities we have

$$\begin{aligned} N_0 &= \overline{I}\,\tfrac{c_1-c_0}{c_2c_1-c_0^2}, \\ N_1 &= \overline{I}\,\tfrac{c_2-c_0}{c_2c_1-c_0^2}. \end{aligned} \tag{11.8}$$

Biologically relevant values of N_i are positive. There are two parameter regions where this is indeed the case: either

$$\begin{aligned} c_1 &> c_0, \\ c_2 &> c_0 \end{aligned} \tag{11.9}$$

or

$$\begin{aligned} c_1 &< c_0, \\ c_2 &< c_0. \end{aligned} \tag{11.10}$$

If we compare these sets with the parameter sets in Fig. 7 we see an interesting correspondence: in the first region (11.9) the SYC-cycle is stable: neither of the missing year classes can invade, while in the second region (11.10) both can invade. Therefore *MYC equilibria with two year classes present exist (in the positive cone) only if the SYC equilibria are either stable or unstable in both directions* (see Fig. 8).

We conjecture even more: in regions III and IV there can exist a *heteroclinic cycle for the third iterate of the map* (3.5). The existence of the heteroclinic cycle means

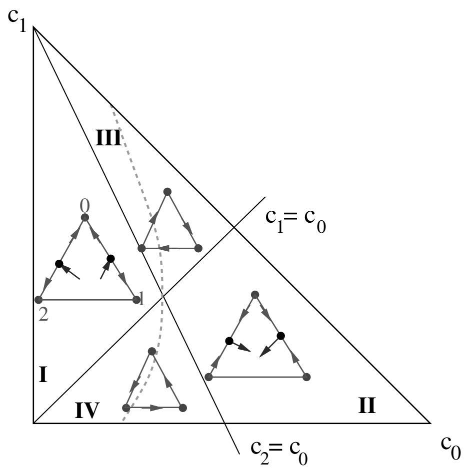

Fig. 8. Combined bifurcation diagram for SYC-points and MYC-points. The MYC-points exist only in the regions I and II. In the region I the MYC-points are transversally stable (as indicated by arrows inside the triangles), and in the region II they are transversally unstable. We conjecture that a heteroclinic cycle exists in regions III and IV. The dashed curve is its stability boundary: to the left of it the heteroclinic cycle is stable, to the right it is unstable.

that the unstable manifold of a SYC fixed point has another SYC fixed point as its ω–limit set so that, by cyclic symmetry a cycle of connecting manifolds is formed.

We reformulate this in biological terms (see Fig. 10). Notice that if we look three years ahead, "age class" coincides with "year class". Let us have a population consisting of a single year class 0. If we introduce a one year older year class 1, it invades and takes over. Eventually we have a population consisting of the single year class 1. If however a one year older year class 2 can invade, it takes over again and the population will consist of the single year class 2. Here the year class 0 can invade. If the latter does invade, we approach the original situation with the year class 0 dominating the population.

Although it may not be easy to prove the existence of the heteroclinic cycle, numerous simulations confirm the conjecture. (In a special case, about which we learned by reading [4], the proof is actually very easy. If $c_2 = 0$ the full life cycle map restricted to a boundary plane is partly decoupled: one of the recursions is independent of the other. So one can analyse the global asymptotic behaviour rather easily.)

The heteroclinic cycle can be stable or unstable. The condition for its stability is that the product of the eigenvalues λ_1 and λ_2 corresponding to the stable and the unstable manifolds is less than one [14]. These eigenvalues are $\lambda_1 = h_0(I_2)h_1(I_0)$ $h_2(I_1)$ and $\lambda_2 = h_0(I_1)h_1(I_2)h_2(I_0)$. In our case

$$\lambda_1\lambda_2 = h_0\left(\frac{c_2}{c_0}\overline{I}\right) h_0\left(\frac{c_1}{c_0}\overline{I}\right).$$

This product is less than one in the region I, because there both eigenvalues are less than one; and it is larger than one in the region II, because there both eigenvalues are larger than one. Since the eigenvalues are continuous functions of c's, the product is equal to 1 in the point $(c_0, c_1) = \left(\frac{1}{3}, \frac{1}{3}\right)$. Moreover, the condition

$$h_0\left(\frac{c_2}{c_0}\overline{I}\right) h_0\left(\frac{c_1}{c_0}\overline{I}\right) = 1 \tag{11.11}$$

can hold only in the regions III and IV because if, for example, $c_1 > c_0$ we need $c_2 < c_0$ to satisfy this identity (since $h_0(I) > 1$ for $I < \overline{I}$ and $h_0(I) < 1$ for $I > \overline{I}$). Eq. (11.11) can be rewritten as

$$\frac{c_2}{c_0} = \frac{1}{I}h_0^{-1}\left(\frac{1}{h_0(\frac{c_1}{c_0}\overline{I})}\right).$$

The right-hand side is a function (on an appropriate domain) because $h_0(I)$ is strictly decreasing and hence can be inverted. Since there is one-to-one correspondence between the interior of the (c_0, c_1) triangle and the interior of the positive cone of the plane $\left(\frac{c_1}{c_0}, \frac{c_2}{c_0}\right)$, (11.11) is a curve in (c_0, c_1) lying in the regions III and IV and intersecting the point $\left(\frac{1}{3}, \frac{1}{3}\right)$ (the dashed line in Fig. 8).

We notice also a useful property of this curve, viz. that it is vertical in the point $\left(\frac{1}{3}, \frac{1}{3}\right)$. If we differentiate the identity (11.11) with respect to c_1 considering c_0 as a function of c_1 $\left(\text{in a neighbourhood of } \left(\frac{1}{3}, \frac{1}{3}\right)\right)$ and take into account that $c_0 + c_1 + c_2 = 1$, we find that $\frac{dc_0}{dc_1}\left(\frac{1}{3}\right) = 0$.

Let us now consider the transversal stability of the MYC-point (11.8). It is transversally stable (i.e., the missing year class can not invade) if

$$h_0(I_1)\,h_1(I_2)\,h_2(I_0) < 1$$

or in our case, if

$$h_0(I_1) < 1 = h_0(\overline{I}).$$

Since h_0 is strictly decreasing, this is the case if

$$I_1 > \overline{I}.$$

From (11.7) $I_1 = c_1N_0 + c_2N_1$ and, if we substitute N_0 and N_1 from (11.8), we obtain

$$I_1 = \frac{c_1^2 - c_1c_0 + c_2^2 - c_2c_0}{c_2c_1 - c_0^2}\overline{I}$$

and $I_1 > \overline{I}$ if

$$\frac{c_1^2 - c_1c_0 + c_2^2 - c_2c_0}{c_2c_1 - c_0^2} > 1.$$

In the region I $c_2c_1 - c_0^2 > 0$, hence the above identity is equivalent to

$$c_1^2 + c_2^2 + c_0^2 - c_1c_0 - c_2c_0 - c_1c_2 > 0.$$

This we can rewrite as

$$(c_0 + c_1 + c_2)^2 - 3(c_1c_0 + c_2c_0 + c_1c_2) > 0,$$

which, since $c_0 + c_1 + c_2 = 1$, is equivalent to

$$c_1c_0 + c_2c_0 + c_1c_2 < \frac{1}{3}.$$

The left-hand side attains its maximum $\frac{1}{3}$ in the point $c_0 = c_1 = c_2 = \frac{1}{3}$. So, in all other points in region I this inequality is satisfied, i.e., the MYC-point is transversally stable in the region I.

In the region II $c_2c_1 - c_0^2 < 0$ and the above inequality must be reverted. Therefore, it can never be satisfied. Hence the MYC-point is transversally unstable in the region II. We indicate this in Fig. 8 by arrows inside the small triangles.

Now we combine the bifurcation diagram for the internal steady state in Fig. 6 with the bifurcation diagram in Fig. 8. For simplicity we restrict ourselves to $\theta < 2$ (as is indeed the case for the Beverton–Holt nonlinearity). The combined bifurcation diagram is represented in Fig. 9. A lot of things which are shown on the diagram we

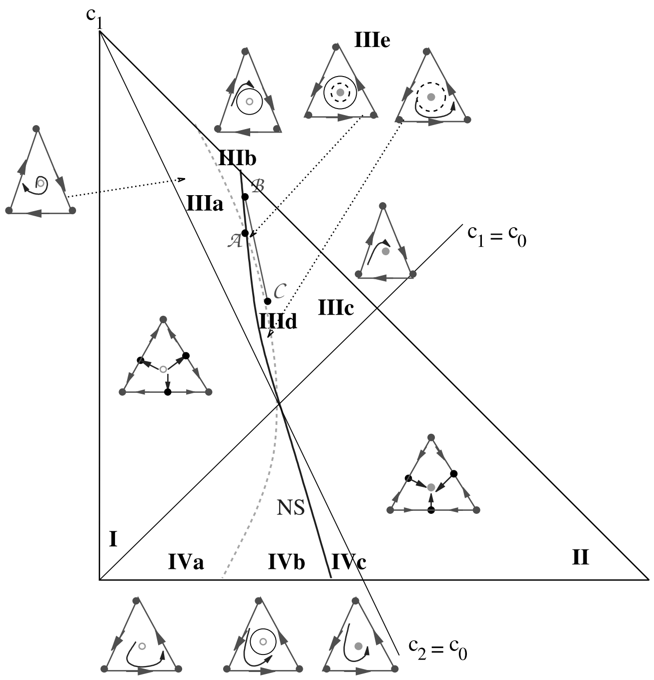

Fig. 9. A combination of the bifurcation diagrams presented earlier in Figs. 6a and 8.

did not prove (as, for example, the existence of the heteroclinic cycle), but numerical simulations corroborate it.

Notice that for $\theta < 9$ the Neimark–Sacker curve $c_1 = c_0 + \frac{1}{c_0\theta} - \frac{3}{\theta}$ (cf. the second inequality in (11.6)) is increasing in the point $\left(\frac{1}{3}, \frac{1}{3}\right)$. Recalling that the curve corresponding to stability change of the heteroclinic cycle is vertical in this point, the mutual position of these curves near this point is such as shown in Fig. 9.

Do these two curves intersect at other points? Numerical investigations show that they indeed intersect (the point $\mathscr{A}$ in Fig. 9). Generically, in a neighbourhood of such a point there should be a region with two invariant circles. "Generically" means that the Neimark–Sacker bifurcation is not degenerate in this point, more precisely that the first Lyapunov value is not zero. (The first Lyapunov value is proportional to the coefficient of the cubic term in the normal form of the bifurcation. It determines the nonlinear (in)stability of the fixed point along the Neimark–Sacker curve.) Using the package CONTENT [16] we can look for points on the NS-curve where the Lyapunov value is zero. We find a point $\mathscr{B}$ and this point does not coincide with $\mathscr{A}$. The parameter region with two invariant circles (the region IIIe in Fig. 9) is extremely small, but we have managed to find it (one can check it: choose, for example, $\overline{I} = 1.5$, $c_0 = 0.32486$, $c_1 = 0.45539$). It is bounded by a curve $\mathscr{B}\mathscr{C}$ corresponding to "collision" of the stable and unstable invariant circles. The point $\mathscr{C}$

is an analogue of the point $\mathscr{B}$ but for the bifurcation corresponding to stability of the heteroclinic cycle, so that a coefficient of the cubic term in the normal form of this bifurcation is zero in the point $\mathscr{C}$.

Let us explain the behaviour of the system corresponding to different regions in the diagram in Fig. 9. We will make a tour around the point $\left(\frac{1}{3}, \frac{1}{3}\right)$ moving successively from region to region.

- In region I the attractor of the system is the SYC 3-cycle. The MYC-points exist and are transversally stable, but seem to be unstable with respect to the dynamics within the coordinate planes (this we have not proven).
- In region IIIa the MYC-points leave the positive cone and we observe a stable heteroclinic cycle. We can leave this region by intersecting either the dashed line or the NS-curve.
- The dashed line corresponds to a change of stability of this cycle, i.e., in region IIIb the heteroclinic cycle is unstable and numerical observations show that there appears a stable invariant circle in the interior of the positive cone.
- If we leave IIIa by intersecting the NS-curve and entering the region IIId, the heteroclinic cycle remains stable but the internal equilibrium becomes also stable and an unstable invariant circle appears around it. Thus we have bistability in this region.
- From both the regions IIIb and IIId we can immediately enter IIIc. There are no more invariant circles in it. The internal equilibrium is stable and the heteroclinic cycle is unstable.
- From IIIb and IIId we can also enter the region IIIe of two invariant circles: the larger one is stable and the smaller one is unstable. Intersecting a curve where these circles come together, we enter IIIc again.
- In region II the MYC-points enter the positive cone again, but they are unstable and the only attractor is again the internal steady state.
- In region IVc the MYC-points disappear again. The difference with the region IIIc is that the unstable heteroclinic cycle rotates in the opposite direction.
- By intersecting the NS-curve we enter the region IVb where the internal equilibrium becomes unstable and a stable invariant circle appears around it. This region is an analogue of the region IIIb but with the opposite rotation direction.
- The invariant circle grows if we move to the left in the region IVb and finally disappears on the dashed line. In the region IVa the heteroclinic cycle inherits the stability.
- But on the diagonal the cycle breaks down by the MYC-points entering the positive cone and we are back in region I.

In this bifurcation diagram we clearly see two directions of the Neimark–Sacker bifurcations around the point $\left(\frac{1}{3}, \frac{1}{3}\right)$ shown schematically in Fig. 5.

One can notice that the phase diagrams which we draw (the small triangles in Fig. 9) are flat and, moreover, the dynamics of the third iterate of the map (3.5)

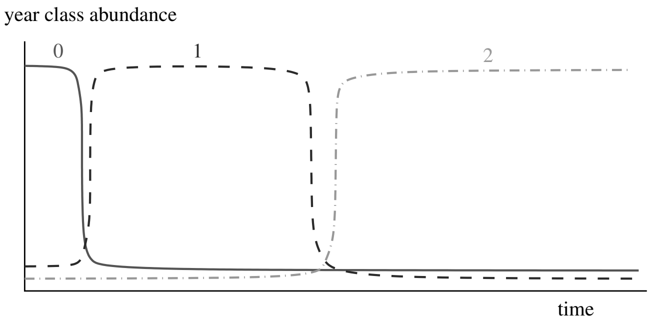

Fig. 10. Heteroclinic dynamics with switches of year classe dominance. This visualises the attracting heteroclinic cycle of the third iterate of the map (3.5).

look like those of a planar vector field (if we consider a time-shift map along the flow). There is a good reason for that. While it may not be easy to prove, we conjecture that in the Beverton–Holt case, or in a general case with $\theta < 2$, there exists an attracting two-dimensional invariant manifold in the phase space. The system loses this property for larger θ. We know already that a period-doubling bifurcation of the internal steady state is possible. The instability occurs in the direction transversal to the invariant manifold and the latter does not exist any longer. The SYC-points and the MYC-points can also become *internally unstable* (as opposed to transversal (in)stability) by means of a period-doubling or a saddle-node bifurcation.

The heteroclinic cycle corresponds to a very interesting type of behaviour (let us call it heteroclinic dynamics/behaviour). During some period of time (many years) one observes a year class which is much more abundant than the other two (but they are not extinct). Then, at some year, the number of one of the less-abundant year classes grows fast and, in the next year, it dominates the population, while the former dominant declines. In other words, a switch between year classes occurs (see Fig. 10). And such switches can happen again and again.

We notice that the bifurcation diagram in Fig. 9 is constructed for the special case $h_1(I) = h_2(I) \equiv 1$. Amazingly enough, the bifurcation diagram remains qualitatively the same if we have density dependence of the Beverton–Holt type for all age classes. We have found this numerically. More precisely, we mean that no extra parameter regions occur. But the regions with two cycles can disappear for some parameter combinations. We think that this is also true for other types of nonlinearity for $\theta < 2$ (probably, we need that the ratios of the functions h_i are monotone). The positions of the parameter regions inside the (c_0, c_1)-triangle do change depending on the sensitivity of the age classes to competition. In particular, due to the cyclic symmetry of Lemma 3.1, we will have exactly the same bifurcation diagram in (c_1, c_2)- or (c_2, c_0)-triangles, if, respectively, only the age class N_1 is sensitive to competition or the age class N_2 [19].

On the basis of the bifurcation diagram in Fig. 9, and taking into account the cyclic symmetry, we can make the following biological conclusions:

- If the sensitive age class (the only age class which suffers from competition) has the largest (expected) impact on the environment, all age classes coexist in a steady equilibrium (region II in the diagram).
- If the sensitive age class has the smallest impact, single year class behaviour occurs (region I).
- If the sensitive age class has an intermediate impact (less than one of the other age classes, but larger than the second), all age classes can coexist either in a steady equilibrium or while oscillating (quasiperiodic behaviour) (regions IIIb, IIIc, IVb and IVc).
- If the sensitive age class has a small, but not the smallest, impact, heteroclinic dynamics is possible with switches of year class dominance (Fig. 10) (regions IIIa and IVa).
- Bistability is possible for some impact combinations (the region IIId). Depending on initial conditions the population either stabilizes in a coexistence steady state or tends to a heteroclinic cycle.

We do not describe the tiny region IIIe in the biological conclusions, because any kind of stochasticity (say, environmental or demographic) will drive the system out of this region. However, we emphasize the importance of its existence. It is crucial for understanding of the continuous change in the phase portraits and non-existence of a (second) degenerate Neimark–Sacker point (like one corresponding to the vertical bifurcation). In other words it demonstrates a structural stability aspect of the system. More precisely, we mean that slight modifications of the functions h can not lead to appearance of parametric regions with new behaviour. Another useful aspects of the existence of this region is described in Section 12.

12. Discussion

Of course, the analysis of the recursion (3.5) is far from complete. To see that the dynamics can be very complicated it is enough to look at it for $k = 1$ and $k = 2$. In the first case the description of the dynamics is typically given by a bifurcation diagram with period-doubling cascades. In the latter case the occurence of a strange attractor (either on the boundary or in the interior of the phase space) is a rather common situation.

However, we believe that we have shed some light on those problems which are the most interesting from a biological point of view. In particular, the “coexistence versus exclusion” problem. We think that the most important phenomenon governing the dynamics of the system is the occurence of the vertical bifurcations. They serve as a switch between coexistence and exclusion. Let us give some comments on that.

We know that manifolds filled with cycles exist only for some particular parameter combinations corresponding to vertical bifurcations. Moreover, if k is even and the vertical bifurcation corresponds to the eigenvalue -1 (Corollary 8.2), it has a codimension 1, because we have only one condition on parameter values (see e.g., Table 1). The vertical bifurcation is a degenerate case of period-doubling bifurcation. An example is the vertical bifurcations happening for $c_0 = c_1$ if $k = 2$. Codimension 1 means also that it happens for points in a m-dimensional parameter space lying on $m - 1$-dimensional curves or (hyper)-surfaces. We ask ourselves how the dynamics change if the values of the parameters vary so that we intersect such a surface transversally. In other words, what happens in a neighbourhood of a vertical bifurcation. We restrict ourselves to a case of a singular circulant.

Let a condition for a singular circulant be satisfied and let the corresponding manifold $\mathscr{L}_k$ (see Theorem 6.1) be normally hyperbolic and attracting. Then, under small changes in the parameters, the manifold persists and we restrict our attention only to the dynamics on the manifold. Under the condition for the vertical bifurcation the internal steady state has an eigenvalue -1, corresponding to neutral stability within the invariant manifold. We change c slightly in such a way that the eigenvalue moves inside the unit circle. In this case the internal steady state becomes stable. Indeed, it belongs to a stable manifold and is stable within the manifold. All orbits starting near the steady state eventually approach it. We conjecture that *all orbits* in a neighbourhood of the invariant manifold converge to the internal steady state. The intuition behind it, is that if some orbits diverge, there should be a boundary of the basin of attraction of the steady state. This boundary is an invariant set in the interior of the manifold and, most likely, this set is a 2-cycle. If we exclude situations like those described in Section 10, in which there is an isolated 2-cycle in the interior of the phase space, we come to a contradiction. However, to prove the result rigourously probably requires a detailed perturbation analysis of the vertical bifurcation. Now we change c so that the eigenvalue of the steady state moves outside the unit circle. If again there are no cycles in the interior, all orbits diverge from the steady state and go to the boundary of the phase space. So half of the year classes go extinct and become missing.

Summarizing what we have said above, the vertical bifurcation is a boundary between stability of the internal steady state and the stability of a boundary cycle, i.e. the boundary between coexistence and exclusion. This result is proven rigorously for $k = 2$ in [8].

What we described above concerns the case when the coexistence equilibrium has an eigenvalue -1. Let it have a couple of non-real eigenvalues which are roots of unity. In this case there are two conditions (corresponding to the real and the imaginary parts of the eigenvalues) on parameter values guaranteeing the vertical bifurcation and, therefore, the vertical bifurcation is of codimension 2. It is a degenerate case of a Neimark–Sacker bifurcation, as, for example, in the case $k = 3$, $c_0 = c_1 = c_2$. In the neighbourhood of the vertical bifurcation there is a change of direction of the Neimark–Sacker bifurcation as shown in Fig. 5. Therefore we have two ways from coexistence to exclusion: catastrophic or sharp loss of stability (above the dashed line in Fig. 5) and non-catastrophic or mild loss of stability (under the dashed line). Concluding, we do not necessarily have a *switch* from coexistence to exclusion, a soft transition via growing fluctuations is possible, but whenever we have a vertical bifurcation of codimension 2 there is always a branch of Neimark–Sacker bifurcation (which is of codimension 1) corresponding to sharp loss of stability of the coexistence equilibrium. Do we necessarily end up with a situation of exclusion if this happens? Our experience says *No*: if we move from region IIIe in the diagram 9 to region IIIb, we have a sharp loss of stability, but the new attractor is the outer invariant circle with all year classes present. (This is indeed the usefulness of noting that the tiny region IIIe exists: the sharp loss of stability does not necessarily imply competitive exclusion, even though in most cases it does.)

The problem remains how many year classes go missing if we switch from coexistence to exclusion. In a neighbourhood of a vertical bifurcation the dynamics is restricted to an invariant manifold which is "almost" the line segment $\mathscr{L}_k$ or the polygon $\mathscr{P}_{n,k}$. The first situation is only possible if k is even. In this case, if the internal steady state loses stability via the vertical bifurcation, we switch to a boundary 2-cycle with exactly half of the year classes missing, more precisely all even or all odd year classes are missing. In the case of the polygon $\mathscr{P}_{n,k}$ the edges correspond to the situation of $\frac{k}{m}$ year classes missing and the vertices to $\frac{2k}{m}$ year classes missing, where m is the least common multiple of n and k (see the end of Section 6). Our conjecture, supported by numerical simulations, is that the attractor is exactly the m-cycle consisting of the vertices of the polygon.

In the present analysis we have not exploited the "competitiveness" of the full life cycle map (see [24] and the references in there). We are optimistic that, in fact, this property can be exploited to deduce that there exists an invariant $(k-1)$-dimensional manifold which contains all ω-limit sets. Moreover, the intersection of this manifold with invariant coordinate (hyper)planes yields further invariant subsets of lower dimension. Thus for $k = 3$ a proof of both the existence of the heteroclinic cycle and the (internal) instability of the MYC points in region I of Fig. 9 should come within (easy) reach.

We think that the full life cycle map is competitive when the functions h_i are of Beverton–Holt type (by which we mean, in particular, that $N_i \mapsto N_i h_i(c \cdot N)$ is monotone increasing, for any given combination of $N_j, j = 0, \ldots, i-1, i+1, \ldots, k-1$, while h_i itself is monotone decreasing). When the functions $N_i \mapsto N_i h_i(c \cdot N)$ have a humped graph, as they do in the Ricker case, the situation is more complicated in general. Yet for some parameter region the attractor may be confined to a region of the phase space in which the nonlinearities are Beverton–Holt like. So we expect that the theory of competitive maps will also yield information about global aspects of the dynamics for the Ricker type maps under additional parameter constraints. We intend to investigate these matters in the near future.

Appendix

A. Proofs of lemmas from Section 11

First we formulate an extra lemma which is useful for the proofs.

Lemma A.1. *Let* μ_1, μ_2 *and* μ_3 *be the three roots of Eq.* (11.1). *Then the products* $\mu_1\mu_2$, $\mu_1\mu_3$ *and* $\mu_2\mu_3$ *are roots of the equation.*

$$p^3 - a_1 p^2 + a_0 a_2 p - a_2^2 = 0. \tag{A.1}$$

Proof. We have the identity

$$(\mu_2\mu_3)^3 - (\mu_2\mu_3 + \mu_1\mu_2 + \mu_1\mu_3)(\mu_2\mu_3)^2 + \mu_1\mu_2\mu_3(\mu_1 + \mu_2 + \mu_3)(\mu_2\mu_3) - (\mu_1\mu_2\mu_3)^2 = 0.$$

It can, using $a_0 = -(\mu_1 + \mu_2 + \mu_3)$, $a_1 = \mu_2\mu_3 + \mu_1\mu_2 + \mu_1\mu_3$ and $a_2 = -\mu_1\mu_2\mu_3$, be rewritten as (A.1) with $p = \mu_2\mu_3$. □

Proof of Lemma 11.1. The assertions (i) and (ii) can be verified by substitution. For the case (iii) let Eq. (11.1) have a pair of complex-conjugate roots $\mu = \mathrm{e}^{\pm \mathrm{i}\phi}$, $0 < \phi < \pi$.Then we have two identities

$$\begin{aligned} &\mathrm{e}^{3\mathrm{i}\phi} + a_0 \mathrm{e}^{2\mathrm{i}\phi} + a_1 \mathrm{e}^{\mathrm{i}\phi} + a_2 = 0, \\ &\mathrm{e}^{-3\mathrm{i}\phi} + a_0 \mathrm{e}^{-2\mathrm{i}\phi} + a_1 \mathrm{e}^{-\mathrm{i}\phi} + a_2 = 0. \end{aligned} \tag{A.2}$$

Multiplying the second identity by $\mathrm{e}^{2\mathrm{i}\phi}$ and substracting the first identity, we obtain

$$(a_0 - a_2)(\mathrm{e}^{2\mathrm{i}\phi} - 1) = \mathrm{e}^{-\mathrm{i}\phi}(1 - \mathrm{e}^{4\mathrm{i}\phi}).$$

Dividing out $(\mathrm{e}^{2\mathrm{i}\phi} - 1)$ (which is not zero because the roots are not real) we achieve

$$a_0 - a_2 = -2\cos\phi. \tag{A.3}$$

Hence $|a_0 - a_2| < 2$. By Lemma A.1 the product of the roots satisfies (A.1) and, since the product is 1,

$$1 - a_1 + a_0 a_2 - a_2^2 = 0.$$

Conversely, suppose this relation holds. Then, by substitution, $\mu = -a_2$ is a root of Eq. (11.1) and the equation can be rewritten as

$$(\mu + a_2)(\mu^2 + (a_0 - a_2)\mu + 1) = 0.$$

If, in addition, $-2 < a_2 - a_0 < 2$, then the second polynomial factor at the left-hand side has complex roots $\mu = \mathrm{e}^{\pm \mathrm{i}\phi}$ with $\phi \in (0, \pi)$ defined by $\cos\phi = \frac{1}{2}(a_2 - a_0)$. □

Proof of Lemma 11.3. *Necessity.* First assume that all roots lie strictly inside the unit circle. Define

$$f(\mu) = \mu^3 + a_0\mu^2 + a_1\mu + a_2.$$

For real μ one finds $f(+\infty) = +\infty$ and $f(-\infty) = -\infty$ so, since f can not change sign outside the interval $(-1, 1)$, we must have $f(1) > 0$ and $f(-1) < 0$, which are exactly the conditions (a) and (b) of (11.2). If we denote the three roots of (11.1) by μ_1,μ_2 and μ_3, then $a_2 = \mu_1\mu_2\mu_3$ and accordingly (c) holds.

For products of pairs of roots we have Eq. (A.1). Applying the same arguments to this equation as we applied above to f, we find two conditions

$$1 - a_1 + a_0a_2 - a_2^2 > 0$$

and

$$1 + a_1 + a_0a_2 + a_2^2 > 0.$$

The latter is satisfied whenever (a)–(c) are, and the former is (d).

Sufficiency. Assume that (a)–(d) hold. By (a) and (b) the function f has a real root in $(-1, 1)$. We consider first the case that the other two roots are complex (with non-zero imaginary part). Then, of the three possible products of two roots, two are complex and only one is real, which is the square of the modulus of the complex-conjugate roots. Hence (A.1) has a unique real root which lies in (0, 1) if (d) is satisfied. Namely, define for $m = r^2 \geqslant 0$

$$g(m) = m^3 - a_1m^2 + a_0a_2m - a_2^2.$$

Since $g(0) = -a_2^2 < 0$, this function has a root $0 < m < 1$ if $g(1) > 0$, i.e. exactly if (d) is satisfied. Hence the complex-conjugate roots are inside the unit circle.

We now consider the case that all three roots of (11.1) are real. By (a)–(b) the number of roots in $(-1, 1)$ is odd. If all three are in $(-1, 1)$ we are done. So assume that $|\mu_1| < 1$ but $|\mu_2| > 1$ and $|\mu_3| > 1$. Applying exactly the same arguments to the function g we find that $|\mu_1\mu_2| < 1$, $|\mu_2\mu_3| > 1$ and $|\mu_1\mu_3| > 1$ (when the numbering corresponds to the absolute value). But if $|\mu_2| > 1$ and $|\mu_1\mu_3| > 1$ then also $|\mu_1\mu_2\mu_3| > 1$ which is in contradiction with (c). We conclude that also in the case of three real roots they all must lie in the unit circle. □

References

[1] H. Behncke, Periodical cicadas, J. Math. Biol. 40 (2000) 413–431.
[2] M.G. Bulmer, Periodical insects, The Amer. Natural. 111 (1977) 1099–1117.
[3] H. Caswell, Matrix Population Models, second ed., Sinauer Associates, Inc. Publishers, Sunderland, MA, 2001.
[4] J.M. Cushing, Cycle chains and the LPA model, J. Differ. Eqs. Appl. 9 (7) (2003) 655–670.
[5] J.M. Cushing, J. Li, Intra-specific competition and density dependent juvenile growth, Bull. Math. Biol. 54 (1992) 503–519.
[6] P.J. Davis, Circulant Matrices, Wiley, New York, 1979.
[7] N.V. Davydova, Old and young. Can they coexist? Ph.D. thesis of Utrecht University, Netherlands, 2004. Available from: <http://laurel.library.uu.nl/cgi-bin/mus212/dialogserver?DB=da>.

[8] N.V. Davydova, O. Diekmann, S.A. van Gils, Year class coexistence or competitive exclusion for strict biennials? J. Math. Biol. 46 (2003) 95–131.
[9] O. Diekmann, S.A. van Gils, Difference equations with delay, Jpn. J. Indust. Appl. Math. 17 (2000) 73–84.
[10] O. Diekmann, S.A. van Gils, Invariance and symmetry in a year-class model, Trends Math.: Bifurcations, Symmetry and Patterns (2003) 141–150.
[11] O. Diekmann, M. Gyllenberg, H. Huang, M. Kirkilionis, J.A.J. Metz, H.R. Thieme, On the formulation and analysis of general deterministic structured population models. II. Nonlinear theory, J. Math. Biol. 43 (2001) 157–189.
[12] O. Diekmann, M. Gyllenberg, J.A.J. Metz, Steady state analysis of structured population models, TPB 63 (2003) 309–338.
[13] L. Edelstein-Keshet, Mathematical Models in Biology, Random House, New York, 1988.
[14] J. Hofbauer, K. Sigmund, Evolutionary Games and Population Dynamics, Cambridge University Press, Cambridge, 1998.
[15] E.I. Jury, Theory and Application of the z-Transform Method, Wiley, 1964.
[16] Yu.A. Kuznetsov, V.V. Levitin, CONTENT: a multiplatform environment for analyzing dynamical systems, Dynamical Systems Laboratory, CWI, Amsterdam, 1997. Available from: <ftp://ftp.cwi.nl/pub/CONTENT>.
[17] E.R. Lewis, Network Models in Population Biology, Springer-Verlag, Berlin, Heidelberg, New York, 1977.
[18] R.M. May, Stability and Complexity in Model Ecosystems, Princeton University Press, Princeton and Oxford, 2001.
[19] E. Mjølhus, A. Wikan, T. Solberg, On synchronization in semelparous populations, J. Math. Biol., in press (doi:10.1007/S00285-004-0275-5).
[20] J.D. Murray, Mathematical Biology, Springer-Verlag, 1989.
[21] R.M. Nisbet, L.C. Onyiah, Population dynamics consequences of competition within and between age classes, J. Math. Biol. 32 (1994) 329–344.
[22] E. Seneta, Non-Negative Matrices: An Introduction to Theory and Applications, Allen and Unwin, London, 1973.
[23] T.S. Solberg, Rare phenomena in an age-structured population model, Master Thesis, University of Tromsø, 1998.
[24] Y. Wang, J. Jiang, The general properties of discrete-time competitive dynamical systems, J. Differ. Eqs. 176 (2001) 470–493.
[25] A. Wikan, E. Mjølhus, Overcompensatory recruitment and generation delay in discrete age-structured population models, J. Math. Biol. 35 (1996) 195–239.