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On synchronization in semelparous populations

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Abstract. Synchronization, i.e., convergence towards a dynamical state where the whole population is in one age class, is a characteristic feature of some population models with semelparity. We prove some rigorous results on this, for a simple class of nonlinear one- population models with age structure and semelparity: (i) the survival probabilities are assumed constant, and (ii) only the last age class is reproducing (semelparity), with fecundity decreasing with total population. For this model we prove: (a) The synchronized, or Single Year Class (SYC), dynamical state is always attracting. (b) The coexistence equilibrium is often unstable; we state and prove simple results on this. (c) We describe dynamical states with some, but not all, age classes populated, which we call Multiple Year Class (MYC) patterns, and we prove results extending (a) and (b) into these patterns.

1. Introduction

A species is called semelparous when it reproduces only once in its life. The objective of this paper is to report some rigorous mathematical results on a class of discrete-time nonlinear population models with age structure, having this property. The motivation came from studies of the effect of reproductive delay, which generally tends to imply instability and nonstationary behaviour (Levin and Goodyear 1980, Levin 1981, Bergh and Getz 1988, Silva and Hallam 1993, Wikan and Mjølhus 1996, Wikan 1997 Neubert and Caswell 2000). In some of this work, a rather peculiar phenomenon occurred: (i) the coexistence equilibrium, i.e., the equilibrium with all year classes in balance, tended to be unstable, and (ii) as $t \rightarrow \infty$, a cyclic state was attained where the whole population was in one single age class at each time step (Wikan and Mjølhus 1996). Related theoretical results had, however, been described much earlier by Bulmer (1977). In this paper, we shall term this behaviour Single Year Class (SYC) dynamics (Davydova et al. 2003), (Solberg 1998). Obviously, semelparity is necessary for this kind of behaviour.

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However, SYC behaviour as described above, had been described empirically long time before. In particular, there are several insect species which show SYC behaviour; for a brief literature survey we refer to Bulmer (1977). In those contexts the phenomenon is called synchronization.

Bulmer (1977) studied various classes of dynamical models in order to explain these phenomena of synchronization. Bulmer's class of models termed "competition" is related to the class of models to be studied here, although basically, Bulmer's approach was far wider. Hoppensteadt and Keller (1976) presented a model for the synchronization of the 17-year-cicada (magicicada) which includes both predation and intraspecific competition. A further study of models related to that of Hoppensteadt and Keller has recently been presented by Behncke (2000), while Davydova et al. (2003) discuss the occurrence of convergence towards SYC in biennials within a formulation related to that of Bulmer (1977). Currently, Davydova et al. (2003, *subm.*) are presenting a broad approach to the dynamics of semelparous populations.

The present paper will be devoted to establishing some rigorous mathematical results, for a class of models which is a slight generalization of that considered in Wikan and Mjølhus (1996). Two main results of this paper state that, for the class of models considered, (i) the SYC dynamics is locally attracting, meaning that a small population inserted into an empty year class, will die out (Theorem 1); (ii) the full coexistence equilibrium is "very often" unstable: we prove Theorem 4 saying that a) for an even number of year classes, the full coexistence equilibrium is always unstable, while b) with an odd number of year classes, it is unstable at least just beyond the value of the parameter R (see Sect. 2) at which the equilibrium comes into existence.

However, in addition, we have paid much attention to a range of intermediate dynamical states allowed by the semelparous population model, in which some, but not all age classes are populated. We call this Multiple Year Class (MYC) dynamics. We prove results for these intermediate states which extend those indicated above: (i) Theorem 1 is valid for any sustained dynamical state with empty year classes; (ii) Theorem 2 settles that a unique MYC stationary state exists for any MYC pattern; (iii) Theorem 3 extends the main results of Theorem 4 to all MYC stationary states with more than one populated age class.

The plan of the paper is as follows: In Sect. 2, the simple class of models to be considered in this paper, is formulated. In Sect. 3, the "kinematics" of MYC states is described, and what we have called *the generation map* is derived from the model of Sect. 2. Sect. 4 contains some brief remarks on SYC dynamics, while in Sect. 5, Theorem 1 is stated and proved. In Sect. 6 the existence of stationary MYC states is proved (Theorem 2). Sect. 7 discusses the "internal" stability of the stationary MYC states, based on the linearization of the generation map of Sect. 3, leading to Theorem 3. Sect. 8 discusses the stability theory of the full coexistence equilibrium. The main part of Theorem 4 is merely a special case of Theorem 3, already proved in Sec. 7. In Sect. 8, we also demonstrate, by example of the case of 3 age classes, that SYC and full coexistence dynamics can coexist in cases of 3 age classes. Finally, Sect. 9 contains a summarizing discussion.

2. The model

The class of models to be discussed in this paper, can be formulated as follows: Let the vector $\mathbf{x}_t = (x_{0,t}, \dots, x_{n,t})^T$ represent the population with $x_{j,t}$ representing the population in age class j at time t . Then the dynamics

$$\mathbf{x}_{t+1} = A(X_t)\mathbf{x}_t \quad (1)$$

is assumed, where the Leslie matrix is assumed to have the form

$$A(X) = \begin{bmatrix} 0 & \cdots & F_0 f(X) \\ p_0 & 0 & \\ 0 & p_1 & \\ \vdots & & \\ 0 & p_{n-1} & 0 \end{bmatrix} \quad (2)$$

i.e., with only the last age class productive, and where the fecundity of that age class depends on the total population

$$X = x_0 + \cdots + x_n \quad (3)$$

We shall refer to X as the *population pressure*. We moreover assume that the survival probabilities p_j are constant, with

$$\begin{aligned} 0 < p_j &\leq 1, & j = 0, \dots, n-2 \\ 0 < p_{n-1} &< 1 \end{aligned} \quad (4)$$

The function f , defined on $[0, \infty)$, is assumed to satisfy

$$f(0) = 1 \quad (5a)$$

$$f(X) > 0 \quad (5b)$$

$$f'(X) < 0 \text{ and } f' \text{ continuous} \quad (5c)$$

$$Xf(X) \text{ bounded} \quad (5d)$$

Eq. (5d) ensures that the dynamics remains in a bounded region of \mathbf{x} space, and the form (1),(2) ensures that the components of \mathbf{x} remain non-negative. Eq. (5a) should be regarded as a normalization defining the parameter F_0 , while (5a)– (5d) ensure that the equation

$$Rf(\widehat{X}) = 1 \quad (6)$$

has a unique solution \widehat{X} for any $R > 1$; in particular, (5d) implies that $f(X) \rightarrow 0$ as $X \rightarrow \infty$, while (5c) ensures that it does so monotonically. Eq. (6) arises as a necessary (and also sufficient) condition on the total population \widehat{X} in all cases of equilibrium (in the full coexistence case) or stationary life cycle states (SYC, MYC), where the parameter R , defined as

$$R = F_0 p_0 \cdots p_{n-1} \quad (7)$$

is the net reproductive rate (Caswell 2001) in the limit of small population. This can be readily seen from (1), by assuming $x_{j,t+(n+1)} = x_{j,t}$ for all age classes $j = 0, \dots, n$.

When $R < 1$, the population dies out. The value $R = 1$ is therefore a basic bifurcation value, at which the complicated system of stationary states (coexistence, MYC, SYC) simultaneously come into existence. This bifurcation is highly structurally unstable; for example, at $R = 1$ all eigenvalues of the linearized system obtained by linearizing around the coexistence equilibrium, lie on the unit circle (cf. Sect. 8). On the other hand, there appears no reason to expect any structural instability for any of the unusual behaviour found for this model for $R > 1$.

The condition (4) on the survival probabilities reflects that the state variables x_j are thought of as number densities. The strict inequality for p_{n-1} is then crucial for all the proofs of our theorems; it enters explicitly in the proof of Lemma 1 of Sect. 5, and it enters the proofs of Theorems 2 and 3 through the strict inequalities occurring in (37).

It is emphasized that the main motivation for the present report is to prove some general results related to findings reported by Wikan and Mjølhus (1996), while biological motivations for the choice of model have been subordinate. However, age-structured models with density dependence in the fecundities, have been frequently studied (e.g., Levin and Goodyear 1980, Levin 1981, Bergh and Getz 1988, Silva and Hallam 1993), in particular in contexts of fish populations (Levin and Goodyear 1980, Tuljapurkar et al. 1994). A rationale for this kind of modelling, is to think of $x_{0,t+1}$ as the density of, e.g., larvae, or fry, establishing themselves from eggs laid by the last generation $x_{n,t}$, assuming that this establishment goes on during a period that is short compared to the primary time step, the latter usually being one year. Then, the simple representation of the population pressure as given by (3), and the influence on the fecundity through the function f , is thought of as a simple representation of the inhibiting influence on this initial establishment from the total population.

It should be admitted that (3) is a rather schematic expression for the population pressure. For example, for the magicicada (Hoppensteadt and Keller 1976, Behncke 2000), it is not reasonable that the parent generation $x_{n,t}$ contribute to the population pressure in the phase of larvae establishment. Also, in many cases it will be reasonable to assume that the newborn generation $x_{0,t+1}$ does contribute.

A more flexible representation of the population pressure is as a weighted sum

$$C = \alpha_0 x_0 + \dots + \alpha_n x_n$$

introducing additional parameters $\alpha_j \geq 0$, $j = 0, \dots, n$. It is mentioned that such cases can be incorporated into the present formulation, provided

$$p_j \frac{\alpha_{j+1}}{\alpha_j} \leq 1$$

$$p_{n-1} \frac{\alpha_n}{\alpha_{n-1}} < 1$$

as can easily be demonstrated by rescaling the age class populations x_j .

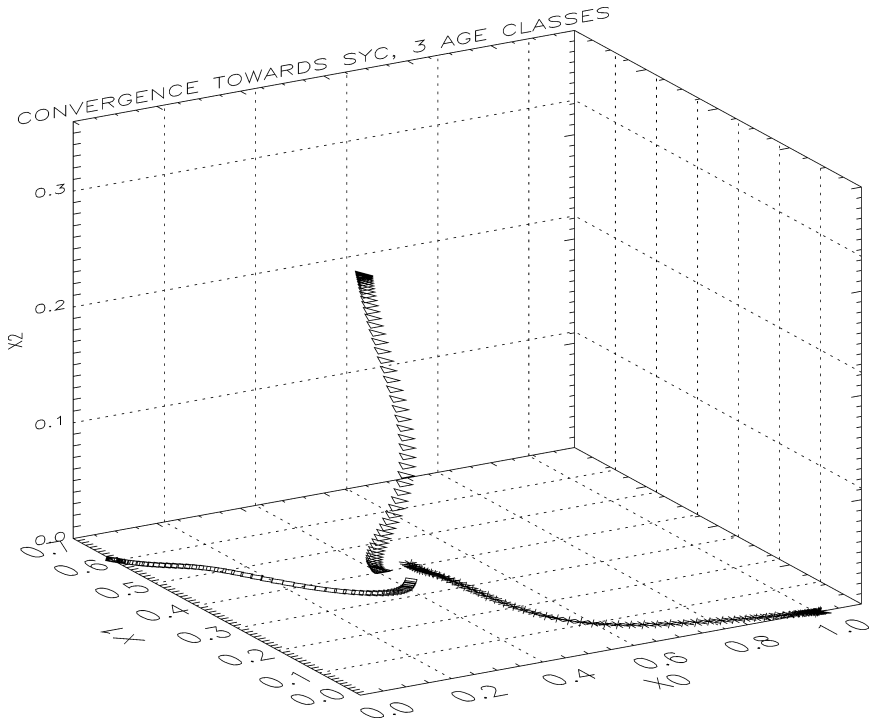


Fig. 1. Example of convergence towards SYNC in a case with 3 age classes. Parameters: $p_0 = p_1 = 0.6$, $F_0 = 4.0$. Initial values: $x_0 = 0.2$, $x_1 = 0.1$, $x_2 = 0.08$ were chosen near the coexistence equilibrium. 3×60 iterations. $f(X) = \exp(-X)$. The points number $3k$ are indicated by asterisk, number $3k + 1$ by diamond, and number $3k + 2$ by square

Examples of functions f satisfying (5), which are wellknown from the literature on population dynamics, are the Ricker family

$$f(X) = \exp(-\alpha X) \quad (8)$$

(Ricker 1954), and the Hassell family

$$f(X) = (1 + \alpha X)^{-\sigma} \quad (9)$$

where $\sigma \geq 1$ is required in order to satisfy (5d). In (8) and (9), the parameter α is unessential, since it can be scaled into the population vector \mathbf{x} .

We have a lot of numerical experience that SYNC behaviour generally results from model (1)–(5); one example is shown in Fig. 1. In Wikan and Mjølhus (1996), a few particular analytical results were noted. Theorems 1–4 in the forthcoming sections contain what we are able to say about this model, related to synchronization.

3. Kinematics of MYC, and the generation map

The semelparous model (1)–(5) allows that some age classes may be empty. If all but one age class is empty, we call the dynamical state SYC dynamics. One may, however, also have that more than one, but not necessarily all, age classes are populated. We shall then use the term Multiple Year Class (MYC) dynamics.

In order to describe the “kinematics” of this, we start with an initial instant of time t_0 , at which the $q + 1$ age classes $n = n_0 > n_1 > \dots > n_q \geq 0$ are populated. This we collect into the *initial age class distribution vector*

$$\mathbf{n}(t_0) = \mathbf{n}^{(0)} = (n_0, n_1, \dots, n_q) = (n_0^{(0)}, n_1^{(0)}, \dots, n_q^{(0)}). \quad (10)$$

This initial age class distribution generates a $q + 1$ MYC *pattern*: a subsequent sequence of $n + 1$ age class distributions connected by

$$\mathbf{n}(t + \tau) = (\mathbf{n}(t) + \tau) \bmod (n + 1) \quad (11)$$

for any integers t and τ . Each of these age class distributions we shall refer to as a *phase* of the given MYC pattern. Note that only for the initial age class distribution do we require ordering of the ages.

Special cases are $q = 0$: SYC, and $q = n$: Full coexistence. Cases with $0 < q < n$ we term *proper* MYC states.

For the dynamics according to our specific model (1)–(5), the *reproducing phases*, in which the maximal component of \mathbf{n} is equal to n , play a decisive role. In defining the initial age class distribution, we added the requirement that it represents a reproducing phase, so that $n_0 = n$. The remaining reproducing phases will then occur at time instants

$$\begin{aligned} t_i &= t_{i-1} + \tau_i \\ \tau_i &= n_{i-1} - n_i, \quad i = 1, \dots, q \end{aligned} \quad (12)$$

At these times of reproduction, the age class distributions are generated by

$$\mathbf{n}^{(i)} = (\mathbf{n}^{(i-1)} + \tau_i) \bmod (n + 1) \quad (13)$$

for $i = 1, \dots, q$. We denote the components

$$\mathbf{n}^{(i)} = (n_0^{(i)}, \dots, n_q^{(i)}), \quad i = 0, \dots, q \quad (14)$$

The population having the age corresponding to each fixed position j in the age class vector, belongs to one and the same *broodline*. Within its life span this is equivalent to “year class”; however, according to model (1)–(5), a broodline is continued by reproduction each time it reaches the maximal age n . For the discussion of MYC dynamics, it has been found convenient to relate the state variables to the broodlines rather than the age classes; furthermore, we shall replace time with an integer parameter s representing *generation*: at the initial instant t_0 , the broodlines $0, 1, \dots, q$ have ages $n_0 = n, n_1, \dots, n_q$, and we adopt that they at this time are all in generation s . At time $t_0 + 1$, broodline 0 has reproduced to enter generation $s + 1$ as *newborns*, while the remaining broodlines are still in generation s . At time $t_i + 1$,

$i = 0, \dots, q$, broodline i has entered generation $s + 1$ as newborns, broodlines $j < i$ are already in generation $s + 1$, while broodlines $j > i$ are in generation s .

As state variables we shall use the population of newborns in each broodline j entering generation s , which we shall denote $w_{j,s}$. In vectorial form, we write $\mathbf{w}_s = (w_{0,s}, \dots, w_{q,s})$. Introducing the survival parameters

$$\begin{aligned}\ell_j &= p_0 \cdots p_{j-1} \\ \ell_0 &= 1\end{aligned}\tag{15}$$

the population of the broodlines at each reproducing phase at time t_i are

$$\begin{aligned}\ell_{n_j^{(i)}} w_{j,s+1} & \quad j < i \\ \ell_{n_j^{(i)}} w_{j,s} & \quad j \geq i\end{aligned}$$

where the integers $n_j^{(i)}$ are generated from $\mathbf{n}^{(0)}$ by (12), (13), (14). The population pressures at these reproducing phases are accordingly

$$X_{i,s} = \ell_{n_0^{(i)}} w_{0,s+1} + \cdots + \ell_{n_{i-1}^{(i)}} w_{i-1,s+1} + \ell_{n_i^{(i)}} w_{i,s} + \cdots + \ell_{n_q^{(i)}} w_{q,s}\tag{16}$$

where we have that $n_i^{(i)} = n$. Then, the model (1)–(5) leads to the iterated map

$$w_{i,s+1} = R w_{i,s} f(X_{i,s})\tag{17}$$

We shall refer to (17) as the *generation map*. One can do explicit forward calculations according to (17) by starting with calculating $w_{0,s+1}, \dots, w_{i-1,s+1}$, and use them when calculating $w_{i,s+1}$, for $i = 1, \dots, q$.

4. SYC dynamics

For the SYC case $q = 0$, we get the one-dimensional map

$$X_{s+1} = R X_s f(X_s)\tag{18}$$

from the generation map (17), where we have $X = \ell_n w_0$. For $R > 1$, the map (18) has a unique fixed point \widehat{X} , where \widehat{X} satisfies (6). This fixed point is stable for

$$\varepsilon < 2\tag{19}$$

where $\varepsilon > 0$ is defined as

$$\varepsilon(\widehat{X}) = -R \widehat{X} f'(\widehat{X})\tag{20}$$

Since f' is assumed continuous, ε depends continuously on R for $R > 1$, and $\varepsilon \rightarrow 0$ when $R \rightarrow 1^+$. Depending on the function f , condition (19) may be satisfied for all values of R , or it may be violated for sufficiently large R . For example, for the Hassell family (9) with $1 \leq \sigma \leq 2$, \widehat{X} is a globally attracting fixed point for (18). In other cases, condition (19) may be violated, and a sequence of period-doubling bifurcations of Feigenbaum type may occur as well as various types of complicated dynamic behaviour (Devaney 1989, Thunberg 2001). For example, this takes place for the Ricker case (8), as well as for the Hassell family (9) provided σ is sufficiently large. For a recent, well updated account of this complexity, we refer to Thunberg (2001).

5. Decay of small inserted broodlines

This section is concerned with the “transverse” stability of a SYC dynamical state, i.e., perturbing it by inserting small populations into the empty broodlines. The partial results of Wikan and Mjølhus (1996) indicate that SYC dynamics is attracting in the sense that when $R > 1$, all but one broodline dies out as $t \rightarrow \infty$. Theorem 1 below expresses this in a local sense: that a small population inserted into an empty broodline will die out. However, a similar result also applies for all cases of proper MYC dynamics. Therefore, we formulate and prove Theorem 1 such that it is valid for all these cases.

For the case of a proper MYC state, it may (and in most cases does) happen that one or more of the broodlines tend to zero as $s \rightarrow \infty$, thus diminishing the number of populated broodlines, but it is also possible that the dynamics sustains in the original MYC pattern.

In the latter case, in order to formulate precise conditions, let $\mathbf{w} = (w_0, \dots, w_q) \in \mathbb{R}_+^{q+1}$ represent the components of the MYC state and $\boldsymbol{\eta} \in \mathbb{R}_+^{n-q}$ the components of inserted population in empty broodlines; then the generation map defined by (17) has the form $(\mathbf{w}_{s+1}, \boldsymbol{\eta}_{s+1}) = \mathbf{F}(\mathbf{w}_s, \boldsymbol{\eta}_s) = (\phi(\mathbf{w}_s, \boldsymbol{\eta}_s), \psi(\mathbf{w}_s, \boldsymbol{\eta}_s))$, where ϕ, ψ are C^1 -smooth functions, and $\psi(\mathbf{w}, \mathbf{0}) = \mathbf{0}$. Let $\phi_0 : \mathbb{R}_+^{q+1} \rightarrow \mathbb{R}_+^{q+1}$ be defined by $\phi_0(\mathbf{w}) = \phi(\mathbf{w}, \mathbf{0})$; then ϕ_0 describes the MYC dynamics. We introduce the following notions:

Definition. A bounded domain $D_1 \subset \mathbb{R}_+^{q+1}$ is said to be separated from extinction if $\mathbf{w} \in \overline{D_1}$ implies that all components of \mathbf{w} are nonzero ($\overline{D_1}$ is the closure of D_1). A MYC state is said to be sustained if there is a bounded domain D_1 separated from extinction which is invariant under ϕ_0 . It is strongly sustained if it is sustained and the bounded domain D_1 can be chosen such that ϕ_0 maps D_1 strictly into itself, i.e.,

$$\text{dist}(\partial D_1, \phi_0(\overline{D_1})) > 0 \quad (21)$$

Then we have:

Theorem 1. Assume that a $q + 1$ MYC state with $0 \leq q < n$ is strongly sustained. Then there are positive K, λ with $0 < \lambda < 1$, and a neighbourhood D_2 of $\boldsymbol{\eta} = \mathbf{0}$ of the form

$$D_2 = \{\boldsymbol{\eta} \in \mathbb{R}_+^{n-q} \mid \|\boldsymbol{\eta}\| < \bar{\delta}\} \quad (22)$$

such that

$$\|\boldsymbol{\eta}_s\| \leq K\lambda^s \|\boldsymbol{\eta}_0\| \quad (23)$$

for all initial points $(\mathbf{w}_0, \boldsymbol{\eta}_0) \in D_1 \times D_2$ and all integers $s \geq 0$. ($\|\cdot\|$ is, e.g., the Euclidean norm.)

In order to prove Theorem 1, we first prove Lemma 1, which expresses the essential mechanism of the model (1)–(5) to give SYC behaviour:

Lemma 1. *In a MYC state, the population pressure in a non-reproductive phase is larger than in the next reproductive phase.*

Proof. Choose an initial reproductive phase of the MYC state, $\mathbf{n} = (n_0, \dots, n_{q-1}, n_q)$, (i.e., assuming $n = n_0 > n_1 > \dots > n_q \geq 0$), occurring at time t_0 , and with no loss of generality, assume that $n - n_1 > 1$, so that there is at least one non-reproductive phase before the next reproductive phase, which occurs at $t_0 + n - n_1$. Consider the population pressure X_m of the non-reproductive phase occurring at time $t_0 + \tau_m$ with $0 < \tau_m < n - n_1$. We can write

$$X_m = Y_m + \beta w_1$$

for some $\beta > 0$, where Y_m contains the contributions from all the broodlines except broodline 1. The population pressure X_1 at time $t_0 + n - n_1$, when broodline 1 reproduces, then satisfies

$$X_1 \leq Y_m + \beta p_{n-1} w_1$$

because broodline 1 has been reduced by at least a fraction p_{n-1} while the others have at least not increased, since there has been no reproduction. This implies

$$X_m \geq X_1 + A$$

with

$$A = \beta(1 - p_{n-1})w_1$$

$A > 0$ since $p_{n-1} < 1$ according to (4). □

Remark. For a sustained MYC state, there is an $\bar{A} > 0$ such that

$$\bar{A} \leq A$$

for all $\mathbf{w} \in \bar{D}_1$, i.e., $\bar{A} = \beta(1 - p_{n-1}) \min_{\mathbf{w} \in \bar{D}_1} w_1$.

The next lemma demonstrates the essence of Theorem 1 in terms of linear approximation:

Lemma 2. *Insert a small population η_0 into an empty broodline. Then there are $C > 0$, $\alpha \in (0, 1)$ such that its population η_s after s generations satisfies*

$$\eta_s \leq C\alpha^s \eta_0 \tag{24}$$

in the linear approximation, for all integers $s \geq 0$.

Proof. Choose an initial phase \mathbf{n} , and broodlines m and 1 as in the proof of Lemma 1, and insert a newborn population η_0 at time $t_0 - n_m$, where n_m is the age of broodline m at time t_0 . We label it as generation 0. Then, after s generations we have, in the linear approximation,

$$\eta_s = R^s \prod_{s'=0}^{s-1} f(X_{m,s'}) \eta_0 \tag{25}$$

where $X_{m,s'}$ is the population pressure from the MYC state when the inserted brood-line of generation s' reproduces. At the same time, for the next MYC broodline, we have

$$w_{1,s} = R^s \left(\prod_{s'=0}^{s-1} f(X_{1,s'}) \right) w_{1,0} \quad (26)$$

Since the MYC dynamics is sustained, this gives

$$R^s \prod_{s'=0}^{s-1} f(X_{1,s'}) \leq C \quad (27)$$

(we can, for example, take $C = \max_{\mathbf{w} \in \bar{D}_1} w_1 / \min w_1$). For $\mathbf{w} \in \bar{D}_1$, the population pressure X remains in a compact subset $\bar{D}_0 \subset \mathbb{R}_+$. Then, since f is strictly and continuously decreasing,

$$\alpha = \max_{X \in \bar{D}_0} \frac{f(X + \bar{A})}{f(X)} < 1 \quad (28)$$

Then, we have by (25), (27) and (28):

$$\begin{aligned} \eta_s &= R^s \prod_{s'=0}^{s-1} \frac{f(X_{m,s'})}{f(X_{1,s'})} f(X_{1,s'}) \eta_0 \\ &\leq \alpha^s R^s \prod_{s'=0}^{s-1} f(X_{1,s'}) \eta_0 \\ &\leq C \alpha^s \eta_0 \end{aligned}$$

□

For the further work towards a proof of Theorem 1, we introduce the notation $\mathbf{F}^s = (\phi^s, \psi^s)$ where \mathbf{F}^s is the s times iterate of F . Thus, $\mathbf{w}_s = \phi^s(\mathbf{w}_0, \boldsymbol{\eta}_0)$, $\boldsymbol{\eta}_s = \psi^s(\mathbf{w}_0, \boldsymbol{\eta}_0)$. Furthermore, for differentiation with respect to the second group of arguments at point $\mathbf{w}, \boldsymbol{\eta}$, we introduce the notation $d_{(\mathbf{w}, \boldsymbol{\eta})} \boldsymbol{\psi}$. Then, since the linear approximation is diagonal in $\boldsymbol{\eta}$, Lemma 2 is rephrased as

$$\|d_{(\mathbf{w}, 0)} \boldsymbol{\psi}^s\| \leq C \alpha^s, \quad 0 < \alpha < 1, \quad \mathbf{w} \in D_1 \quad (29)$$

where one can take C and α as the largest of those occurring for each component of $\boldsymbol{\eta}$ in Lemma 2.

Proof of Theorem 1. For $C \leq 1$ the proof is simple: First, by the mean value theorem, there is a neighbourhood D_2 of the form (22) such that $\boldsymbol{\eta}_1 = \boldsymbol{\psi}(\mathbf{w}_0, \boldsymbol{\eta}_0)$ satisfies

$$\|\boldsymbol{\eta}_1\| \leq \lambda \|\boldsymbol{\eta}_0\| \quad (30)$$

with $\alpha \leq \lambda < 1$, $\mathbf{w}_0 \in D_1$, $\boldsymbol{\eta}_0 \in D_2$. By possibly diminishing D_2 , due to the condition of strongly sustained MYC dynamics, D_2 can be chosen small enough that $\phi(D_1 \times D_2) \subset D_1$, and consequently, by (30), we have $F(D_1 \times D_2) \subset D_1 \times D_2$. Then, (23) with $K = 1$ follows by iteration, for $(\mathbf{w}_0, \boldsymbol{\eta}_0) \in D_1 \times D_2$. To handle $C > 1$, which allows that $\|\boldsymbol{\eta}\|$ may increase at some steps, we proceed as follows: Choose an integer m such that $m > -\log C / \log \alpha$; i.e., the integer $m > 1$ is such that $m = -\log C / \log \alpha + r$ with $r > 0$. Then, $\mu = C\alpha^m$ satisfies $\mu = \alpha^r < 1$. The condition of strongly sustained MYC dynamics implies that we can pick a neighbourhood \tilde{D}_2 of the form (22) such that $\phi^m(D_1, \tilde{D}_2) \subset D_1$. Put $\boldsymbol{\chi} = \psi^m$. By (29) and the definition of μ , we have, for $\mathbf{w} \in D_1$:

$$\|d_{(\mathbf{w},0)}\boldsymbol{\chi}\| \leq \mu$$

By the mean value theorem, after shrinking \tilde{D}_2 if necessary, we have

$$\|\boldsymbol{\chi}(\mathbf{w}_0, \boldsymbol{\eta}_0)\| \leq \rho \|\boldsymbol{\eta}_0\|$$

for some $\rho, \mu < \rho < 1$ for $(\mathbf{w}_0, \boldsymbol{\eta}_0) \in (D_1 \times \tilde{D}_2)$. This in turn implies that $\mathbf{F}^m(D_1 \times \tilde{D}_2) \subset (D_1 \times \tilde{D}_2)$. By iteration, we then get

$$\|\boldsymbol{\chi}^k(\mathbf{w}, \boldsymbol{\eta})\| \leq \rho^k \|\boldsymbol{\eta}_0\| \quad (31)$$

Next, pick a neighbourhood $D_2 \subset \tilde{D}_2$ of the form (22) such that $\psi^\ell(D_1, D_2) \subset \tilde{D}_2$ and $\phi^\ell(D_1, D_2) \subset D_1$ for all integers ℓ satisfying $0 \leq \ell < m$, $\mathbf{w} \in D_1$, $\boldsymbol{\eta} \in D_2$. We can write a uniform Lipschitz condition

$$\|\psi^\ell(\mathbf{w}_0, \boldsymbol{\eta}_0)\| \leq K_0 \|\boldsymbol{\eta}_0\|$$

for all $\mathbf{w}_0 \in D_1$, $\boldsymbol{\eta}_0 \in D_2$ and all integers ℓ , $0 \leq \ell < m$. By the decomposition $s = \ell + km$, with ℓ a nonnegative integer less than m , one has

$$\|\boldsymbol{\eta}_s\| \leq K_0 \rho^k \|\boldsymbol{\eta}_0\|$$

which, by $\lambda = \sqrt[m]{\rho}$, $K_0 = \lambda^\ell K$, translates to (23). \square

Remark 1. For the SYC case $q = 0$, the condition of strongly sustained state is satisfied once $R > 1$, because then the origin is repelling and $Xf(X)$ bounded.

Remark 2. Lemma 2 overlaps with results noticed already by Bulmer (1977): Lemma 2 specialized to the case of SYC equilibrium is a special case of eq. (8) of Bulmer (1977).

6. Stationary MYC states

A stationary $q + 1$ MYC state is one for which $w_{j,s} = w_{j,s+1} \stackrel{\text{def}}{=} w_j$, $j = 0, \dots, q$, all s . By (17), one has eq. (6) with $X_i \mapsto \widehat{X}$, where X_i is given by (16) with $w_{j,s} = w_j$, $j = 0, \dots, q$. Since (6) has a unique solution, it follows that $X_i = \widehat{X}$, $i = 0, \dots, q$. We choose to normalize according to

$$w_i = \widehat{w}_i \widehat{X} \quad (32)$$

Then, $\widehat{\mathbf{w}} = (\widehat{w}_0, \dots, \widehat{w}_q)$ satisfies

$$\mathbf{L} \widehat{\mathbf{w}} = \mathbf{b} \quad (33)$$

where the matrix \mathbf{L} and the vector \mathbf{b} are given by

$$\mathbf{L} = \begin{bmatrix} \ell_{n_0}^{(0)} & \ell_{n_1}^{(0)} & \cdots & \ell_{n_q}^{(0)} \\ \ell_{n_0}^{(1)} & \ell_{n_1}^{(1)} & \ell_{n_1}^{(2)} & \cdots & \ell_{n_q}^{(1)} \\ \vdots & & & & \\ \ell_{n_0}^{(q)} & \ell_{n_1}^{(q)} & \cdots & & \ell_{n_q}^{(q)} \end{bmatrix} \quad \mathbf{b} = \begin{bmatrix} 1 \\ \vdots \\ \vdots \\ 1 \end{bmatrix} \quad (34)$$

Here, the integers $n_i^{(j)}$ are generated from $\mathbf{n}^{(0)}$ by (12), (13). We shall refer to the matrix \mathbf{L} as the *MYC matrix* for the given MYC pattern and the chosen initial age class distribution. It can also be expressed as

$$\mathbf{L} = \begin{bmatrix} \ell_n & \ell_{n_1} & \ell_{n_2} & \cdots & \ell_{n_q} \\ \ell_{n-n_1-1} & \ell_n & \ell_{n_2+(n-n_1)} & \cdots & \ell_{n_q+(n-n_1)} \\ \ell_{n-n_2-1} & \ell_{n_1-n_2-1} & \ell_n & \cdots & \ell_{n_q+(n-n_2)} \\ \cdots & & & & \\ \ell_{n-n_q-1} & \ell_{n_1-n_q-1} & \cdots & & \ell_n \end{bmatrix} \quad (35)$$

In order to be a meaningful stationary $q + 1$ MYC state, the solution must satisfy

$$\widehat{w}_j > 0, \quad j = 0, \dots, q \quad (36)$$

Since ℓ_m is non-increasing with integer m , and $\ell_n < \ell_m$ for any $m < n$, by (4), there is an ordering structure in the MYC matrix \mathbf{L} in a circulating, or “toroidal”, sense:

$$\begin{aligned} \ell_{n_j^{(i)}} &\geq \ell_{n_j^{(i+1)_c}}, \quad i = (j+1)_c, (j+2)_c, \dots, (j+q-1)_c \\ \ell_{n_j^{(j-1)_c}} &> \ell_{n_j^{(j)}} \end{aligned} \quad (37)$$

and

$$\begin{aligned} \ell_{n_j^{(i)}} &\leq \ell_{n_{(j+1)_c}^{(i)}}, \quad j = (i+1)_c, (i+2)_c, \dots, (i+q-1)_c \\ \ell_{n_i^{(i)}} &< \ell_{n_{(i+1)_c}^{(i)}} \end{aligned} \quad (38)$$

Here and later in this section, $(i + \ell)_c$ means cyclic addition:

$$(i + \ell)_c \stackrel{\text{def}}{=} (i + \ell) \bmod (q + 1)$$

We also remind that the diagonal elements $\ell_{n_i^{(i)}} = \ell_n$, $i = 0, \dots, q$, and that the strict inequalities occurring in (37), (38), are consequences of the strict inequality regarding p_{n-1} in (4).

Theorem 2. *For any $q + 1$ MYC pattern, a unique stationary MYC state exists.*

Proof. We have to prove that the linear system (33), (34) has a unique solution satisfying (36). The basic property implying this, is inequalities (37). We first introduce some notation: Let $K \subset \mathbb{R}^{q+1}$ denote the set $K = \{(\widehat{w}_0, \dots, \widehat{w}_q) \mid \widehat{w}_j \geq 0, j = 0, \dots, q\}$, let

$$\pi_j(\widehat{\mathbf{w}}) = \ell_{n_0^{(j)}} \widehat{w}_0 + \dots + \ell_{n_q^{(j)}} \widehat{w}_q$$

introduce the coordinate planes $P_j \subset K$:

$$P_j = \{\widehat{\mathbf{w}} \in K \mid \widehat{w}_j = 0\}, \quad j = 0, \dots, q$$

and finally introduce the hyperplane segments $\Pi_j \subset K$ as

$$\Pi_j = \{\widehat{\mathbf{w}} \in K \mid \pi_j(\widehat{\mathbf{w}}) = 1\}$$

Each Π_j is a bounded set because the coefficients $\ell_{n_i^{(j)}}$ are all positive. Using the introduced notation (33) can also be expressed as

$$\pi_j(\widehat{\mathbf{w}}) = 1, \quad j = 0, \dots, q \quad (39)$$

The proof proceeds by induction on q : It is true for $q = 0$; we assume that it is true for all $q' + 1$ MYC patterns with $q' = 0, 1, \dots, q - 1$. We shall prove that it is valid for $q' = q$.

Our induction hypothesis implies that the q MYC pattern obtained from the given $q + 1$ pattern by making broodline 0 empty, has a unique MYC stationary state, i.e.,

$$\pi_j(\widehat{\mathbf{w}}) = 1 \text{ on } P_0, \quad j = 1, \dots, q \quad (40)$$

has unique solution $\widetilde{w}_1, \dots, \widetilde{w}_q, \widetilde{w}_j > 0, j = 1, \dots, q$. By the implicit function theorem, there is a straight line segment Γ defined by $\pi_1(\widehat{\mathbf{w}}) = 1, \dots, \pi_q(\widehat{\mathbf{w}}) = 1, \widehat{\mathbf{w}} \in K$, starting at $Q_0 = (0, \widetilde{w}_1, \dots, \widetilde{w}_q)$ and ending at a point $Q_1 \in P_\nu$ for some $\nu \neq 0$; the latter follows since all Π_j are bounded sets, implying that Γ is bounded.

Lemma. *a) $\pi_i(\widehat{\mathbf{w}}) - \pi_{(i+1)_c}(\widehat{\mathbf{w}}) > 0$ on P_i if $w_{i+1} > 0$. b) If all inequalities of (37) are strict, then $\pi_i(\widehat{\mathbf{w}}) - \pi_{(i+1)_c}(\widehat{\mathbf{w}}) > 0$ on P_i for all $\widehat{\mathbf{w}} \neq 0, \widehat{\mathbf{w}} \in K$.*

Proof. The lemma follows easily by subtracting, putting $\widehat{w}_i = 0$ and using inequalities (37). \square

Proof of Theorem 2 continued. It follows from a) of the Lemma that $\pi_0(Q_0) > 1$, since $\pi_1(Q_0) = 1, \widetilde{w}_1 > 0$, and $\pi_0(\widehat{\mathbf{w}}) - \pi_1(\widehat{\mathbf{w}}) > 0$ on P_0 . We first complete the proof for the case that all inequalities (37) are strict. Then it follows from b) of the Lemma that $Q_1 \in P_q$, because $\pi_j(Q_1) = 1, j = 1, \dots, q$, while $\pi_\nu(Q_1) - \pi_{(\nu+1)_c}(Q_1) > 0$, which is impossible unless $\nu = q$. Now, since $\pi_q(Q_1) - \pi_0(Q_1) > 0$ and $\pi_q(Q_1) = 1$, it follows that $\pi_0(Q_1) < 1$. Therefore, $\pi_0(\widehat{\mathbf{w}})$ changes from > 1 to < 1 when proceeding along Γ from Q_0 to Q_1 . Consequently, there is an interior point \overline{Q} on Γ at which $\pi_0(\overline{Q}) = 1$. At this point all equations (39)

as well as (36) are satisfied, and the proof is completed for the case of strict inequalities. For limiting cases where equality is permitted in (37), we embed the system (33) in a one-parameter family $\mathbf{L}(\varepsilon)$ depending continuously on ε for $0 \leq \varepsilon \leq \varepsilon_0$, where $\mathbf{L}(0)$ is the given system, while the strict inequalities are satisfied for $\varepsilon > 0$. This can be achieved by, e.g., putting $p_{j,\varepsilon} = (1 - \varepsilon)p_j$. Taking the limit as $\varepsilon \rightarrow 0$, the point Q_1 remains in P_q , since P_q is a closed set. Moreover, $w_0(Q_1) > 0$. It follows that $\pi_0(Q_1) < 1$ by a) of the Lemma. Then Theorem 2 follows also in the limiting cases. \square

We proceed to give explicit solutions to (33) in some special cases:

(i) *Full coexistence case, $q = n$.* In this case, the MYC matrix is a circulant matrix (Meyer 2000, Muir 1960):

$$\mathbf{L} = \begin{bmatrix} \ell_n & \ell_{n-1} & \cdots & \ell_0 \\ \ell_0 & \ell_n & \cdots & \ell_1 \\ \cdots & & & \\ \ell_{n-1} & \ell_{n-2} & \cdots & \ell_0 & \ell_n \end{bmatrix}$$

In this case it is easily verified that the solution to (33) is $\widehat{w}_0 = \cdots = \widehat{w}_n = 1/K$, where

$$K = \sum_{j=0}^n \ell_j \quad (41)$$

The stationary age distribution becomes

$$\widehat{x}_j = \frac{\ell_j}{K} \widehat{X}, \quad j = 0, \dots, n \quad (42)$$

In this case, $\widehat{\mathbf{x}} = (\widehat{x}_0, \dots, \widehat{x}_n)$ is an equilibrium state for the original map (1)–(5).

(ii) *Symmetric proper MYC.* We define a symmetric MYC pattern as follows: Assume that $q + 1$ divides $n + 1$, and define $d > 1$ as their quotient: $n + 1 = d(q + 1)$. Then an MYC initial reproducing age class distribution $\mathbf{n} = (n_0, n_1, \dots, n_q)$ is defined by $n_0 = n, \dots, n_j = n_{j-1} - d, \dots, n_q = d - 1$. In fact, this is the only initial reproducing age class distribution in this case. By defining $\widetilde{\ell}_{q-j} = \ell_{n_j}$, $j = 0, \dots, q$, this case becomes similar to the full coexistence case: By defining $P_j = \prod_{v=jd}^{(j+1)d-1} p_v$, we have $\widetilde{\ell}_j = \prod_{i=0}^j P_i$, $j = 0, \dots, q$. The stationary solution becomes $\widehat{w}_0 = \cdots = \widehat{w}_q = 1/\widetilde{K}$ with $\widetilde{K} = \sum_{j=0}^q \widetilde{\ell}_j$. The populations of the populated age classes in the reproducing phases become

$$\widehat{x}_{(j+1)d-1} = \frac{\ell_{(j+1)d-1}}{\widetilde{K}} \widehat{X}, \quad j = 0, \dots, q$$

(iii) *The homogeneous case.* By this we mean that $p_j = p$, $j = 0, \dots, n - 1$, where $0 < p < 1$, which gives $\ell_m = p^m$ for all integers m , $0 \leq m \leq n$. For this case, we have the stationary $q + 1$ MYC solution

$$\begin{aligned}
\widehat{w}_0 &= \left(p^{-(n-n_1-1)} - p \right) / D, & \widehat{w}_1 &= \left(p^{-(n_1-n_2-1)} - p \right) / D, \\
\cdots, & \widehat{w}_q = \left(p^{-n_q} - p \right) / D \\
D &= 1 - p^{n+1}
\end{aligned} \tag{43}$$

which can be verified a posteriori.

7. Stability of the stationary MYC states

While Sect. 5 was concerned with the “transverse” stability of a given sustained MYC pattern, this section treats its internal stability, i.e., the effect of perturbations within the given MYC pattern. In the previous section, we proved that a unique MYC stationary state exists for any MYC pattern. In this section it is proved that these stationary states are often unstable when $q + 1 > 1$. This includes the case of full coexistence, for which many partial results were reported in Wikan and Mjølhus (1996). A numerical example with $q + 1 = 3$ is shown in Fig. 1. We shall prove the following general result:

Theorem 3. *a) Any stationary MYC state with $q + 1$ even, is internally unstable. b) When $q + 1$ is odd and $q > 0$, it is internally unstable for sufficiently small ε .*

We remind that ε is defined in (20), and that small ε occur when $R \rightarrow 1$ from above, because \widehat{X} bifurcates from 0 at $R = 1$. In order to prove theorem 3, we linearize the generation map (17) around the stationary MYC state defined by (32), (33):

$$\mathbf{w}_s = \widehat{X}\widehat{\mathbf{w}} + \boldsymbol{\eta}_s$$

and seek a solution on the form

$$\boldsymbol{\eta}_s = \widehat{\boldsymbol{\eta}}\lambda^s$$

which leads to

$$[(\lambda - 1)\mathbf{I} + \varepsilon\mathbf{W}(\lambda\mathbf{L}^- + \mathbf{L}^+)]\widehat{\boldsymbol{\eta}} = 0 \tag{44}$$

where \mathbf{I} is the $(q + 1) \times (q + 1)$ unit matrix, \mathbf{W} is the diagonal matrix $\mathbf{W} = \text{diag}(\widehat{w}_0, \dots, \widehat{w}_q)$, \mathbf{L}^- (\mathbf{L}^+) has the elements of \mathbf{L} below the diagonal (above and on the diagonal) and 0 elsewhere. Accordingly, the characteristic equation becomes

$$P(\lambda) \stackrel{\text{def}}{=} \det [(\lambda - 1)\mathbf{I} + \varepsilon\mathbf{W}(\lambda\mathbf{L}^- + \mathbf{L}^+)] = 0 \tag{45}$$

Lemma 1. *a) The stationary MYC state is unstable if $\det \mathbf{L} < 0$. b) It is unstable for sufficiently small $\varepsilon > 0$ if*

$$P_1(\lambda_1) = \det(\lambda_1\mathbf{I} + \mathbf{W}\mathbf{L}) \tag{46}$$

has a root with $\text{Re}(\lambda_1) > 0$.

Proof. a) We have $P(1) = \varepsilon^{q+1} \det \mathbf{W} \det \mathbf{L}$. The two first factors are positive. If $\det \mathbf{L} < 0$, we have $P(1) < 0$. As $\lambda \rightarrow +\infty$, the product of the diagonal terms dominates, so $P(\lambda) \rightarrow +\infty$ as $\lambda \rightarrow +\infty$. Therefore, P has a root $\lambda > 1$, which implies that there is a growing solution to the linearized generation map. b) Expanding $\lambda = 1 + \varepsilon\lambda_1 + \dots$, the leading order requires $P_1(\lambda_1) = 0$. Since $|\lambda| = 1 + \varepsilon\text{Re}(\lambda_1) + \mathcal{O}(\varepsilon^2)$, it follows that if P_1 has a root with positive real part, then P has a root with $|\lambda| > 1$ for sufficiently small ε , which implies a growing solution to the linearized generation map. \square

Lemma 2. $\det \mathbf{L} < 0$ for $q + 1$ even.

Proof. It follows from Theorem 2 that $\det \mathbf{L} \neq 0$. The given MYC matrix can be obtained by a deformation from the one obtained by $p_j \mapsto \varepsilon p_j$, $j = 0, 1, \dots, n-1$, with $0 < \varepsilon \leq 1$. It remains a MYC matrix for all values of ε in this range, and so $\det \mathbf{L}(\varepsilon)$ does not change sign. For ε sufficiently small, $\det \mathbf{L}$ is dominated by the largest element in each column of \mathbf{L} , which is the one below the diagonal (cyclic). This product has negative sign. \square

Lemma 3. P_1 has the root $\lambda_1 = -1$.

Proof. Eq. (33) can be written as

$$\mathbf{LWb} = \mathbf{b}$$

which implies that \mathbf{LW} has 1 as an eigenvalue and \mathbf{b} as the corresponding eigenvector. Multiplying with \mathbf{W} from the left, it follows that 1 is an eigenvalue of \mathbf{WL} (with \mathbf{Wb} as eigenvector). It follows that -1 is a root of P_1 . \square

Proof of theorem 3. Theorem 3 a) follows immediately from a) of Lemma 1 and Lemma 2. To prove b), we notice that the trace of \mathbf{WL} is

$$\text{tr } \mathbf{WL} = \ell_n(\widehat{w}_0 + \dots + \widehat{w}_q)$$

We have $\text{tr } \mathbf{WL} < 1$ since

$$\ell_n(\widehat{w}_0 + \dots + \widehat{w}_q) < \sum_{j=0}^q \ell_{n_j} \widehat{w}_j = 1$$

since $\ell_n < \ell_{n_j}$ for $j = 1, \dots, q$, and the last equality is the first component of (33). Denoting the eigenvalues of \mathbf{WL} by $-\lambda_1^{(0)}, \dots, -\lambda_1^{(q)}$, i.e., $\lambda_1^{(0)}, \dots, \lambda_1^{(q)}$ are the roots of P_1 , and put $\lambda_1^{(0)} = -1$ by Lemma 2, one therefore has

$$\sum_{j=1}^q \lambda_1^{(j)} > 0$$

This implies that P_1 must have a root with positive real part. Then b) of Theorem 3 follows by lemma 1b. \square

8. Further results on the full coexistence case

In this section, we discuss some further results for the case of full coexistence. The full coexistence equilibrium was obtained in Sect. 6, giving the formulas (42), (41). Linearizing the original map (1)–(5) around this equilibrium and seeking a solution varying as μ^t , gives the characteristic equation

$$\mu^{n+1} + \frac{\varepsilon}{K} q_n(\mu) - 1 = 0 \tag{47a}$$

$$q_n(\mu) = \sum_{j=0}^n \ell_j \mu^{n-j} \tag{47b}$$

Theorem 4. *a) For an even number of age classes, the full coexistence equilibrium (34) is always unstable;*
b) for an odd number of age classes, it is unstable for ε sufficiently small;
c) for an odd number of age classes, it is also unstable for sufficiently large ε .

Proof. a) and b) are special cases of Theorem 3. The feature c) has only been proved for the present case (and the symmetric MYC, see below). c) follows by a simple application of the intermediate value theorem, and it follows from the fact that $q_n(-1) > 0$ when $n + 1$ is odd. When $n + 1$ is odd, since $q_n(-1) > 0$, the lefthand side of (47a) will be positive at $\mu = -1$ when

$$\varepsilon > 2K/q_n(-1) \tag{48}$$

Since μ^{n+1} dominates, and $\rightarrow -\infty$ as $\mu \rightarrow -\infty$, it follows that a root $\tilde{\mu}$ of (47a) with $\tilde{\mu} < -1$ exists when (48) is satisfied. \square

Remark 1. It depends on the actual form of the function f whether (48) can actually be achieved. Using (6) to eliminate R , we get

$$\varepsilon = - \frac{\widehat{X} f'(\widehat{X})}{f(\widehat{X})}$$

For example, for the Hassell family (9) we have

$$\varepsilon = \sigma \frac{\widehat{X}}{1 + \widehat{X}}$$

and so, $\varepsilon < \sigma$. For the Ricker family (8), we have

$$\varepsilon = \ln R$$

so that all values can be achieved, though possibly at extreme values of R .

Remark 2. Theorem 4c is also valid for the symmetric stationary MYC state, with “number of age classes” $n + 1$ replaced by “number of populated age classes” $q + 1$.

Remark 3. It is easy to prove Theorem 4a directly from (47): When $n + 1$ is even, it is readily seen that $q_n(-1) < 0$. Consequently, the lefthand side of (47a) is negative

at $\mu = -1$. As $\mu \rightarrow -\infty$, the lefthand side of (47a) goes to $+\infty$. Therefore, (47a) has a root $\bar{\mu} < -1$ when $n + 1$ is even (Solberg 1998). We also know proofs of Theorem 4b based on (47), but they are not simpler than the one given for Theorem 3. The homogeneous case, as well as some low-dimensional cases, were obtained in Wikan and Mjølhus (1996).

We now proceed to demonstrate, by example, that in the case of an odd number of age classes, sustained non-stationary full coexistence dynamics can actually coexist with SYC, which is attracting by theorem 1. For the case of 3 age classes, the Jury criteria (Murray 1993) applied to (47) gives that the full coexistence equilibrium is stable whenever

$$\varepsilon_H < \varepsilon < \varepsilon_F \quad (49)$$

where

$$\varepsilon_H = K \frac{1 - 2p_0p_1 + p_0}{p_0p_1(1 - p_0p_1)} \quad (50a)$$

$$\varepsilon_F = K \frac{2}{1 - p_0 + p_0p_1} \quad (50b)$$

Since,

$$\varepsilon_F - \varepsilon_H = K \frac{(1 - p_0)[(3p_1 - 1)p_0 - 1]}{p_0p_1(1 - p_0 + p_0p_1)(1 - p_0p_1)} \quad (51)$$

and in view of (4), in order to have $\varepsilon_F > \varepsilon_H$, one must have

$$\begin{aligned} 1 &> p_1 > (1 + p_0)/(3p_0) \\ 1 &> p_0 > \frac{1}{2} \end{aligned} \quad (52)$$

When ε passes ε_H from above, two complex conjugate roots of (47) leave the unit disk, so that one has a Hopf bifurcation. Our numerical experience indicates that for $0 < \varepsilon < \varepsilon_H$, the SYC dynamics is globally attracting (except possibly for a set of zero measure, e.g., the stable manifold of the coexistence equilibrium). For $\varepsilon_H < \varepsilon < \varepsilon_F$, the stable full coexistence equilibrium coexists with the SYC dynamics, and our numerical experience indicates that the Hopf bifurcation at ε_H is subcritical. When ε passes through ε_F from below, one root of (47) leaves the unit disk through -1 , so that there is a flip bifurcation, which in the numerical examples we have considered, appeared supercritical (we have observed 16 crossings of ε_F , all using the Ricker law for f). Then for ε just above ε_F , a two-periodic coexistence attractor coexists with the (in this regime highly nonstationary) SYC dynamics. As ε was further increased, the next bifurcation was in all cases a supercritical Hopf bifurcation, so that each of the two points of the unstable 2-orbit was surrounded by a closed curve invariant under the 2-iterated map. These two closed curves then formed a local attractor, where the dynamics consisted in alternating between them.

Increasing ε further, various bifurcations occurred, showing various kinds of attractors, including chaotic-looking ones. However, in all cases, when following the attractor numerically by increasing ε in small steps and using the end state of the previous run as the initial state of the next, the attractor was eventually lost

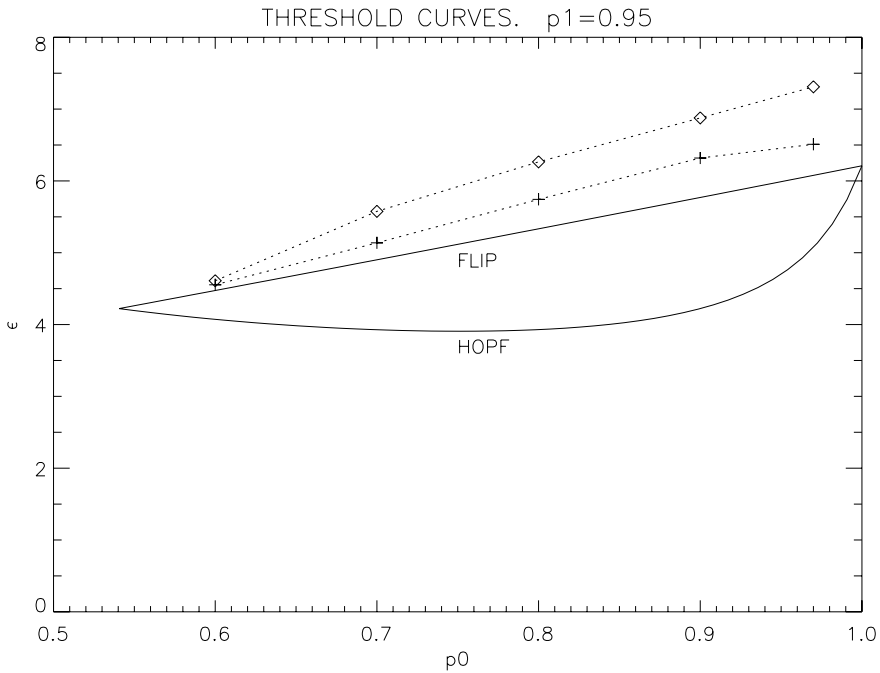


Fig. 2. Parameter window for coexistence dynamics in case of 3 age classes, $f(X) = \exp(-X)$. Between the Hopf curve and the flip curve, a locally stable coexistence equilibrium exists. Above the flip curve, a locally stable 2-period emerged. The + signs indicate thresholds for a supercritical Hopf bifurcation. The diamonds mark where the attractor was lost

and the dynamics went to SYC. In Fig. 2, we show an example of a parameter plane for these bifurcations.

We remind of Remark 1 after Theorem 4, implying that it depends on the function f whether the values of ε where these bifurcations take place, actually can occur. It should also be emphasized that for a large range of values of the parameters p_0, p_1 , namely those breaking (the righthand sides of) conditions (52), these bifurcations do not occur, and SYC appears as the globally attracting alternative.

For the proper MYC states discussed in previous sections, we have not made any investigations of possible coexistence with SYC. However, at least in the symmetric MYC state with $q + 1 = 3$, one will have the same stable coexistence stationary state as above. This shows that parameter windows can exist for which sustained proper MYC dynamics coexists with the SYC dynamics. However, from our numerical experience, we do not expect such cases to be prominent features of the model (1)–(5).

9. Concluding remarks

In this paper we have described a rather peculiar kind of dynamical behaviour in certain age structured discrete time nonlinear population models with extreme

reproductive delay: semelparity. We have termed this dynamical behaviour Single Year Class (SYC) dynamics (Solberg 1998, Davydova et al. 2003). In some contexts, the phenomenon is also called synchronization. Our main results on SYC dynamics for this class of models are summarized in Theorems 1 and 4, which say that the SYC state is always attracting (Theorem 1) and that the full coexistence equilibrium is often unstable (Theorem 4). In addition, we have included throughout a discussion of Multiple Year Class dynamics (MYC), which generalizes the results referred to above: Theorem 1 includes what we have termed strongly sustained MYC states; moreover, it was proven that stationary MYC states always exist (Theorem 2), but that they are often internally unstable (Theorem 3), in a pattern similar to the full coexistence case. Finally, we have by example with 3 age classes demonstrated that stable coexistence equilibrium, or sustained coexistence nonstationary dynamics, can coexist with SYC dynamics in a case with an odd number of age classes.

Even if the class of models (1)–(5) is rather extreme, the results described by Theorems 1 and 4 have a kind of robustness, since the attractors described are of hyperbolic type (e.g., Katok and Hasselblatt, 1995), at least in the finite periodic cases. This implies that if the model is slightly changed, attractors situated near those of our system will occur in the perturbed system. For example, if model (1)–(5) is perturbed with sufficiently small fecundities in age classes near the reproductive one, the resulting $t \rightarrow \infty$ dynamics would be very small populations in all but one age class, etc.

The surprising behaviour observed in these models, in particular the basic feature behind Theorem 1, can be quite easily explained verbally. The crucial point is that in the population pressure (3) entering the recruitment function f , the juveniles have the same weight as the veterans. The equilibrium condition (6) concerns the SYC population when it is in a reproductive phase. In the other phases, the population pressure is larger. Therefore, small perturbing populations inserted into empty age classes will experience a higher population pressure in their reproductive phase than the main population, and will therefore have a sub-critical recruitment. The proof of Theorem 1 extends this to nonstationary behaviour and MYC. The mechanism thus described is precisely expressed in Lemma 1 of Sect. 5.

Bulmer (1977) appears to be the first to have noticed the SYC phenomenon in theoretical models related to those discussed in this paper. Bulmer (1977) interprets it, within his more general formulation, as a result of the property that “... competition is more severe between than within age classes ...” (p. 1102). Indeed, a similarity between the SYC phenomenon and classical models of competition, was also noticed by Solberg (1998). Even so, we find Bulmer’s interpretation, when applied to the present case, to be somewhat formal; in view of eqs. (1)–(5) we prefer the one given above.

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References

- Behncke, H.: Periodical cicadas. *J. Math. Biol.* **40**, 413–431 (2000)
- Bergh, M.O., Getz, W.M.: Stability of discrete age-structured and aggregated delay-difference population models. *J. Math. Biol.* **26**, 551–581 (1988)
- Bulmer, M.G.: Periodical insects. *Am. Naturalist* **111**, 1099–1117 (1977)
- Caswell, H.: Matrix population models. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, 2001
- Davydova, N.V., Diekmann, O., van Gils, S.A.: Year class coexistence or competitive exclusion for strict biennials? *J. Math. Biol.* **46**, 95–131 (2003)
- Davydova, N.V., Diekmann, O., van Gils, S.A.: On circulant populations. I. The algebra of semelparity. *Subm. to J. Math. Biol.*, 2003
- Devaney, R.L.: An introduction to Chaotic Dynamical Systems. Addison–Wesley, 1989
- Hassell, M.P.: Density dependence in single-species populations. *J. Animal Ecology* **44**, 283–296 (1974)
- Hoppensteadt, F.C., Keller, J.B.: Synchronization of periodical cicada emergences. *Science* **194**, 335–337 (1976)
- Katok, A., Hasselblatt, B.: Introduction to the modern theory of dynamical systems. Cambridge University Press, 1995
- Levin, S.A.: Age-structure and stability in multiple-age spawning populations. In: Renewable Resource Managements, T.L. Vincent, J.M. Skowronski (eds.), Springer Verlag, Heidelberg, 1981
- Levin, S.A., Goodyear, P.H.: Analysis of an age-structured fishery model. *J. Math. Biol.* **9**, 245–274 (1980)
- Meyer, C.: Matrix Analysis and Applied Linear Algebra. SIAM, 2000
- Muir, T.: A treatise on the theory of determinants. Dover, New York, 1960
- Murray, J.D.: Mathematical Biology. 2. ed. Springer-Verlag, 1993
- Neubert, M.G., Caswell, H.: Density dependent vital rates and their population and dynamic consequences. *J. Math. Biol.* **41**, 103–121 (2000)
- Ricker, W.E.: Stock and recruitment. *J. Fisheries Res. Board Canada* **11**, 559–623 (1954)
- Silva, J.A., Hallam, T.G.: Effects of delay, truncation and density dependence in reproduction schedules on stability of nonlinear Leslie matrix models. *J. Math. Biol.* **31**, 367–395 (1993)
- Solberg, T.: Rare Phenomena in an Age-Structured Population Model. Master thesis, University of Tromsø, Norway, 1998
- Thunberg, H.: Periodicity versus Chaos in One-Dimensional Dynamics. *SIAM Rev.* **43**, 3–30 (2001)
- Tuljapurkar, S., Boe, C., Wachter, K.W.: Nonlinear Feedback Dynamics in Fisheries: Analysis of the Deriso–Schnute Model. *Can. J. Fish. Aquat. Sci.* **51**, 1462–1472 (1994)
- Wikan, A.: Dynamic consequences of reproductive delay in Leslie matrix models with nonlinear survival probabilities. *Math. Biosci.* **146**, 37–62 (1997)
- Wikan, A., Mjølhus, E.: Overcompensatory recruitment and generation delay in discrete age-structured population models. *J. Math. Biol.* **35**, 195–239 (1996)