On Nonlinear Age- and Stage-Structured Population Models

Arild Wikan

Department of Business Administration and Social Sciences,
Harstad University College, Havnegata 5, N-9480 Harstad, Norway

Abstract: The scope of this review article is to present and discuss various aspects of discrete nonlinear age- and stage-structured population models. We show that such models cover species which exhibit a wide range of different life histories and that one may use them in order to deduce fairly general ecological principles with respect to stability and dynamical outcomes. From a mathematical point of view, we give several examples of the fact that the nonstationary dynamics generated by such maps is indeed rich as a result of different types of bifurcations of various nature as well as other mechanisms like frequency locking and crises that may occur.

Key words: Model formulation, nonstationary population dynamics, ecological implication

INTRODUCTION

In an influential review article "Simple mathematical models with very complicated dynamics" Sir May (1976) presented an analysis of a first order nonlinear difference equation often referred to as the logistic equation or the quadratic map. Both in May (1976) as well as in Sarkovskii (1964); Li and Yorke (1975); May and Oster (1976); Guckenheimer *et al*. (1977); Feigenbaum (1978) and Singer (1978) it was demonstrated that simple one-dimensional nonlinear maps of biological relevance could exhibit an extraordinary rich dynamical behaviour ranging from stable fixed points, periodic points to chaotic behaviour. An excellent summary of results, in particular results from the quadratic map, may be obtained in Thunberg (2001), see also Jost (2005).

However, from a biological point of view there is a variety of cases where one-dimensional population models are not sufficient modelling tools. A more realistic approach is to apply age-structured models. Such matrix models (often referred to as Leslie matrix models) were independently developed in the 1940's by Bernardelli (1941); Lewis (1942) and Leslie (1945; 1948) but perhaps somewhat strange not widely adopted by ecologists until the 1970's. Originally, the models were linear and various dynamical outcomes may be found in Cull and Vogt (1973; 1974) and Hallam and Levin (1986), Later, density dependent or nonlinear terms were considered too, cf. the classical papers by Guckenheimer *et al*. (1977) and the striped bass fishery model by Levin and Goodyear (1980). As accounted for by Caswell (2001), state variables others than age (for example size) were introduced in

population models by Patten (1976); Boling (1973); see also Metz and Diekmann (1986); Hallam *et al*. (1990) and Gurney *et al*. (1990). Such models are called stage-structured models and have been applied on several different species as well as being analysed from theoretical perspectives. Cushing (1998) and Caswell (2001) the analysis of a wide range of stage-structured matrix models is included.

In this review study focus is mainly on three different topics. First we will discuss the models and the prerequisites they rest upon and together with lots of references show how the models may and have been applied to a large number of cases of ecological relevance. In another direction focus is on possible nonstationary and chaotic dynamics. Avoiding mathematical details and proofs we present several examples involving bifurcations of different type and nature as well as other mechanisms like frequency locking and crisis and show that the dynamics found in these multidimensional maps is much richer than we may find in one-dimensional cases. Finally we discuss ecological implications. In particular we address the question whether it is possible to formulate some general ecological principles with respect to stability and nonstationary behaviour of populations who possess different life histories.

Models: We start by presenting the age-structured model. At time t we split the population x_t into n distinct nonoverlapping age classes $x_t = (x_{1,t},...,x_{n,t})^T$ where the total population x is given by $x = x_1 + \cdots + x_n$. The relation between x at two consecutive time steps may be expressed as a map Eq. 1:

$$x \rightarrow Ax \qquad (1)$$

where, the Leslie matrix A is on the form Eq. 2:

$$A = \begin{pmatrix} f_1 & f_2 & \cdots & f_n \\ p_1 & 0 & \cdots & 0 \\ 0 & & & \\ \vdots & \ddots & & \\ 0 & & p_{n-1} & 0 \end{pmatrix} \qquad (2)$$

Moreover, f_i is the average fecundity (number of daughters born per female) of a member of the ith age class at time t and p_i may be interpreted as the (year to year) survival probability. In maps like (1) there is an implicit assumption that sexual maturity is linked to age or that other properties than age are irrelevant. Another possibility is that if such relevant properties exist they must be highly correlated with age.

The matrix elements may be nonlinear (density dependent) or not. Considering two age classes where members of the oldest age class prey upon members of the youngest class (cannibalism) a natural assumption could be $p = p(x_2)$. In fishery models it is often assumed that older individuals contribute more than younger individuals to density effects, therefore one may suppose (Levin and Goodyear, 1980) $f = f(y)$ where $y = \alpha_1 x_1 + \cdots + \alpha_n x_n$ (a weighted sum of age classes). A third possibility is that f (or p) depends on the total population x. This is a natural choice in this study since one of our main goals is to compare dynamics of species who possess very different life histories.

Frequently used density functions are members of the Deriso-Schnute family $f_i = F_i(1 - \gamma \beta x)^{1/\gamma}$, $\beta > 0$ (Bergh and Getz,1988; Tuljapurkar *et al.*, 1994) but see Getz (1996) for other examples. Thus, we write the fecundity (or and the survival) as a product of a constant term F_i and a density dependent term $(1 - \gamma \beta x)^{1/\gamma}$. If $\gamma = -1$ we have the well-known compensatory Beverton and Holt relation, if $\gamma \rightarrow 0$ then we arrive at $f_i = F_i \exp(-\beta x)$ (or $p_i = P_i \exp(-\beta x)$) which is called the overcompensatory Ricker relation inspired by the seminal study by Ricker (1954). In this review we shall deal exclusively with the Ricker case.

The dynamics of a large number of ecological populations has been modelled by (1). Linear age-structured models (constant fecundities and constant survivals) have for example been applied on rabbits (Darwin and Williams, 1964), great tits (Pennycuick, 1969) and trout (Beland, 1974). In case of nonlinear models we refer to Cooke and Leon (1976) (birds), Longstaff (1977) (beetles), Levin and Gooodyear (1980) (striped bass), see also Hastings (1984);

Desharnais and Liu (1987); Burkey and Stenseth (1994) and Nisbet and Onyiah (1994). References to lots of other examples may be found in Caswell (2001). Guckenheimer *et al.* (1977); Silva and Hallam (1993) and Wikan and Mjolhus (1995; 1996) have paid attention to the dynamics of (1) in unstable and chaotic parameter regions. Wikan (1997); Davydova *et al.* (2003); Mjolhus *et al.* (2005) and Cushing (2006) focus is on the dynamics of species who reproduce only once at the end of their lifes. Ergodic results may be obtained in Cushing (1988; 1989) and Crowe (1994).

Unlike (1), in stage-structured models we do not divide the population into nonoverlapping age classes. Instead, we split the population into stages, for example one sexual immature stage and one sexual mature stage. The motivation for doing so is that there may be other factors which are more important with respect to maturity than age. As already mentioned, one such factor is body size. Indeed, following Caswell (2001) "size dependent demography is probably the rule rather than the exception". Examples which link body size to sexual maturity may be found among plants (Klinkhamer *et al.*, 1987a; 1987b), crabs (Campbell and Eaglis, 1983; Botsford, 1986; 1992). See also lots of references in Caswell (2001). Among several alternatives we will in this study consider the two-stage model, first proposed by Neubert and Caswell (2000):

$$x \rightarrow Bx \qquad (3)$$

where, the transition matrix B is on the form:

$$B = \begin{pmatrix} \mu_1(1-p) & f \\ \mu_1 p & \mu_2 \end{pmatrix} \qquad (4)$$

The meaning of the entries in (4) is as follows: μ_1 and μ_2 are the fractions of the immature population x_1 and the mature (adult) population x_2 respectively, which survive from time t to t + 1. $x = x_1 + x_2$ is the total population. p is the fraction of the immature population which survives to become adult and f is the fecundity. Just as in (2) the elements of (4) may be nonlinear or not. Neubert and Caswell (2000) consider several submodels. In one submodel it is assumed that $\mu_1 = \mu_1 \exp(-x)$ while the other parameters are constant. In another, $p = p \exp(-x)$ is the only nonlinear term and so on. One some occasions it may be convenient to apply three-stage models. Indeed, in the celebrated collembolan study, Cushing *et al.* (1996); Costantino *et al.* (1997) and Dennis *et al.* (1997) divided the population into three stages, larvae L, pupae P and adult insects A and in fact showed that their LPA model could not only describe but even predict chaotic

behaviour in laboratory insect populations. More on this model, model as well as properties of other stage-structured models may be found in Cushing (1998) and regarding permanence, cf. Kon *et al.* (2004).

Although (1) and (3) rest on different prerequisites both of them cover species with several life histories. Indeed, if $F_i = 0$, $i < n$ and $F_n > 0$ in (2) or $\mu_2 \rightarrow 0$ in (4) the population is semelparous (i.e., reproducing only once). If several $F_i > 0$ or $\mu_2 \rightarrow 1$ the population is iteroparous (repeated reproduction). The subclass $F_1 = 0$, $F_2 > 0$ (two age classes) or $\mu_2 \rightarrow 0$, $p \rightarrow 1$ is often referred to as precocious semelparity which covers species with rapid development followed by only one reproduction, for example biennials and annual plants. Delayed semelparity occurs when n is larger $F_i > 0$, $i < n$, $F_n > 0$ or $\mu_2 \rightarrow 0$ and $0 < p < 1$. Typical examples are periodical cicadas, Behncke (2000) and Davydova *et al.* (2003) and several salmon species that live for many years before they become mature and reproduce only once. We may also divide the iteroparous case into two subclasses. The subclass $F_i > 0$, $i \leq n$ ($F_1 = 0$, $F_i > 0$, $2 \leq i \leq n$) or $\mu_2 \rightarrow 1$, $p \rightarrow 1$ is classified as precocious iteroparity and covers several small mammals species (small rodent species) which start to reproduce at young age and may survive to reproduce for several years. The fourth subclass, delayed iteroparity, is characterized by several nonfertile age classes followed by several age classes who are fertile, for example $F_i = 0$, $i \leq n/2$, $F_i > 0$, $n/2 < i \leq n$ or $0 < \mu_2 < 1$, $0 < p < 1$. In this subclass we find humans and other large mammals.

Finally, we will also like to mention some other model strategies. Difference delay equation models are models on the form $x_{t+1} = g(x_t, x_{t-T})$ where *x* is the size of the population and T the time from birth to maturity. Such models may be regarded as aggregated versions of (1) where detailed information of the dynamics within age classes is neglected, cf. the Baleen model by Clark (1976). In case of other species we refer to Botsford (1986; 1992); Tuljapurkar *et al.* (1994) and Higgins *et al.* (1997). One may also incorporate spatial structure in matrix models, see for example Gyllenberg *et al.* (1993). In wildlife protection studies one often divides the habitat of a species in a reserve and a harvest zone. Regarding fish populations several interesting properties of such a strategy is discussed in Hastings and Botsford (1999). There are also discrete time growth dispersal models, i.e., models where growth is modelled in discrete time while dispersal is modelled in continuous time. Kot and Schaffer (1986); Neubert *et al.* (1995) and Lutscher and Lewis (2004) provide excellent examples.

Analysis and examples: Under the assumption that all density dependent terms are on Ricker form and

functions of the total population both (1) and (3) possess a unique nontrivial fixed point. In (1) we express the fixed point as $(x_1^*,\ldots,x_n^*)$ where $x^* = x_1^* + \cdots + x_n^*$ is the total equilibrium population. In (3) we denote the fixed point as (x_1^*, x_2^*). Stability analysis is performed by linearizing about the fixed point which in turn gives birth to an *n*th degree eigenvalue equation. Provided all eigenvalues λ are located in the inside of the unit circle in the complex plane the fixed point is stable. If we increase a parameter (in this study we will restrict the analysis to an increase of the fecundity) such that an eigenvalue leaves the unit circle the fixed point becomes unstable. The parameter value at which this takes place may be termed the threshold. As is well-known, the location where an eigenvalue leaves the unit circle has crucial impact on the nonstationary dynamics at parameter values just beyond threshold. Just as in one-dimensional maps an eigenvalue may leave through $\lambda = 1$ or $\lambda = -1$. If $\lambda = 1$, the general case is that the fixed point will undergo a saddle node bifurcation at threshold. The other possibilities are the pitchfork and the transcritical bifurcations. $\lambda = -1$ results in a flip (period doubling) bifurcation. The third possibility is that a pair of modulus 1 complex valued eigenvalues leave the unit circle at threshold. Then the fixed point will go through a Hopf (Neimark Sacker) bifurcation. A detailed description of all bifurcations referred to above may be obtained in Devaney (2003) or Guckenheimer and Holmes (1983). We shall now provide several examples where focus is on the nonstationary dynamics.

Example 1 (Precocious iteroparity): Assuming constant fecundities (indicated by capital letters F_i) $F_1 = 0$, $F_2 = \ldots = F_n > 0$ and density dependent survivals $p_i = P_i \exp(-\alpha x)$, $\alpha > 0$, $0 < P_i \leq 1$ we may express (1) as:

$$(x_1,\ldots,x_n) \rightarrow (F_2 x_2 + \cdots + F_n x_n, p_1 x_1, p_2 x_2,\ldots,p_{n-1}x_{n-1}) \qquad (5)$$

Now, using the fact that *F* is large at instability an asymptotic argument (Wikan and Mjolhus, 1995; Wikan, 1998) shows that the solution of the *n*th order eigenvalue equation (at instability) is very close to the solution of the eigenvalue equation when n = 2. This has the immediate consequence that the dynamics of the n age class model (5) is maintained already in the two age class case. Hence, in (5), it suffices to consider n = 2. Then $x^* = \alpha^{-1} \ln(FP_1)$ and whenever F is small we find from the Jury criteria (Murray, 2003) that the fixed point (x_1^*, x_2^*) is stable. By increasing F we also increase x^* and when $F = F_H$ where F_H is defined through $F_H^{-1} \exp[2(1 + F_H)/ F_H] = P_1$ the fixed point undergoes a supercritical Hopf bifurcation.
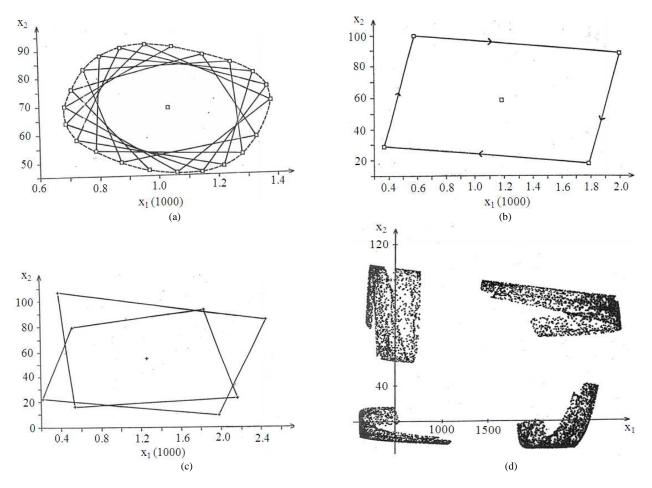
Fig. 1: (a) A quasistationary (almost 4 periodic) orbit (solid line) restricted to an invariant curve (dashed line). Parameter values $\alpha = 0.02$, $P = 0.6$ and $F = 15$. Only the 20 last iterations are shown; (b) An exact 4 -periodic orbit generated by map (5). Parameter values as in Fig. 1a but $F = 20$; (c) An exact 8-periodic orbit. $F = 22$; (d) Map (5) in the chaotic regime. $F = 27$. The attractor has been divided into 4 disjoint subsets which are visited once every fourth iteration

Thus, if $F > F_H$ and $|F-F_H|$ is small the dynamics is restricted to an attracting invariant curve which surrounds the unstable fixed point as displayed in Fig. 1a. On such a curve (5) is topological equivalent to a circle map which means that (5) does nothing but move or rotate points around the curve. Associated with a circle map there is also a rotation number σ which in this context (see Guckenheimer and Holmes (1983) can be expressed as $\sigma = c + (bd/a)(F_H-F)$ where $c = \arg \lambda$. If σ is irrational an orbit of a point is often referred to as a quasistationary orbit. If $\sigma = 1/n$ rational, the dynamic outcome is an orbit of period n. Also, note that whenever σ is rational for a given parameter value $F = F_r$ it follows from the implicit function theorem that there exists an open interval about F_r where the periodicity is maintained. This phenomenon is known as frequency locking of periodic orbits.

Now, returning to our example, λ is close to the imaginary axis at bifurcation threshold (i.e., $c = \arg \lambda \approx \pi/2$. Consequently, close to the bifurcation $\sigma \approx \frac{1}{4}$ which is clearly seen in Fig. 1a and if we continue to increase F an exact 4-period orbit (frequency locking) is established. This is shown in Fig. 1b. When F becomes even larger we find that the fourth iterate of (5) undergoes a flip bifurcation which results in an 8-period orbit which is illustrated in Fig. 1c. Through further enlargement of F new flip bifurcations occur which result in orbits of period 16, 32 and 64 respectively. From a mathematical point of view the dynamics in this part of parameter space is similar to what one finds in one-dimensional maps, see the review papers by May (1976) and Thunberg (2001). Eventually the dynamics becomes chaotic as displayed in Fig. 1d. Note that the attractor is divided in 4 disjoint subsets and that each of the subsets

are visited once every fourth iteration so there is a kind of 4-periodicity preserved even in the chaotic regime. In Fig. 2 we show a "4-period" chaotic attractor generated by (5) in case of n = 3. A detailed analysis of (5) may be obtained in Wikan and Mjolhus (1995).

Example 2 (Delayed semelparity): A slightly different situation occurs in the 3-age class map:

$$(x_1, x_2, x_3) \rightarrow (Fx_3, px_1, px_2) \qquad (6)$$

where, $p = P \exp(-x)$. In case of small and "moderate" F values the dynamics of (6) is similar to what we found from (5). Whenever F is small, (x_1^*, x_2^*, x_3^*) is stable and when we increase F to a level F_H a supercritical Hopf bifurcation occurs. Moreover, $\sigma \approx \frac{1}{4}$ at threshold and here too we experience the existence of a fecundity interval beyond F_H where the dynamics is exact 4-periodic.

However, if we continue to increase F the result is not a flip bifurcation which creates an exact 8-period orbit. Instead we find that the fourth iterate of (6) undergoes a supercritical Hopf bifurcation at a threshold $F = F_{H2}$. Therefore, beyond F_{H2} and in case if $|F - F_{H2}|$ small the dynamics is restricted to 4 disjoint invariant attracting curves which are visited once every fourth iteration. This is displayed in Fig. 3a. As we continue to increase F the curves become twisted which signal that we are on the onset to chaos. In Fig. 3b we show the chaotic attractor in case of F = 55.

Example 3 (Precocious iteroparity): Next, consider:

$$(x_1, \ldots, x_n) \rightarrow (fx_1 + \cdots + fx_n, Px_1, Px_2, \ldots, Px_{n-1}) \qquad (7)$$

where, $f = F \exp(-x)$ and constant year-to-year survival probabilities P, $0 < P \leq 1$. The unique nontrivial fixed point is:

$$(x_1^*, x_2^*, \ldots, x_n^*) = \left(\frac{1}{K} x^*, \frac{P}{K} x^*, \ldots, \frac{P^{n-1}}{K} x^* \right) \qquad (8)$$

$K = \sum_{i=0}^{n-1} P^i$ and $x^* = \ln(FK)$ and the eigenvalue equation may be cast in the form:

$$\lambda^n - \frac{(1-x^*)}{K} \sum_{i=0}^{n-1} P^i \lambda^{n-1-i} = 0 \qquad (9)$$

Here, we concentrate on the case n = 2. Then from (9) and the Jury criteria we find that (x_1^*, x_2^*) is stable in case of F small and will undergo supercritical bifurcations at the thresholds:

$$F = \{ F_F = (1/(1+P)) \exp[2/(1-P)] \qquad 0 < P < 1/2 \qquad (10a)$$

$$F = \{ F_H = (1/(1+P)) \exp[(1+2P)/P] \qquad 1/2 < P < 1 \qquad (10b)$$

where, the subscripts F and H refer to a flip and a Hopf bifurcation respectively. From a mathematical point of view the most interesting interval is $\frac{1}{2} < P < 1$ and in the bifurcation diagram, Fig. 4, we have summarized the result when P = 0.9. For small values of F there is one stable attractor, namely the fixed point (x_1^*, x_2^*). When F is increased to 10.036 the third iterate of (7) undergoes a saddle node bifurcation which gives birth to a stable 3-cycle but also an unstable 3-cycle (not visible in the diagram). Thus, if 10.036 < F < 12.20 there are two stable attractors and the ultimate fate of an orbit depends on the initial condition. At the threshold F = 11.81 (cf. (10b)) the fixed point undergoes a supercritical Hopf bifurcation and an attracting invariant curve is established. Due to the fact that λ is close to third root of unity at bifurcation there is an almost 3-period orbit restricted to the curve. Hence, in the interval 11.81 < F < 12.20 a 3-cycle of large amplitude coexists with an almost 3-cyclic attractor of small amplitude. At F = 12.20 the invariant curve is hit by the unstable 3-cycle created at the earlier value 10.036. This makes the invariant curve disappear, hence when F > 12.20 there is only one attractor, the 3-cycle. At even higher F values successive flip bifurcations take place generating orbits of period $3 \cdot 2^k$, k = 1,2,... Eventually the dynamics becomes chaotic. For details and further analysis of (7), cf. Wikan and Mjolhus (1996).
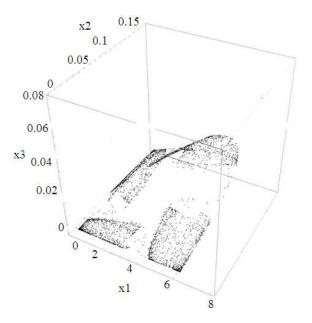

Fig. 2: A chaotic attractor generated by (5) in case of 3 age classes
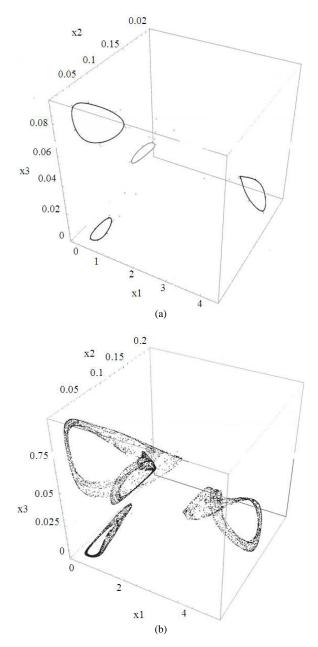
(a)

(b)

Fig. 3: (a) Map (6) after the secondary Hopf bifurcation (P,F) = (0.6, 48); (b) Map (6) in the chaotic regime (P,F) = (0.6, 55)

As we have seen bifurcations can be of both supercritical and subcritical nature. If a fixed point undergoes a supercritical bifurcation when the parameter μ is increased to a value μ_0 there is established an attracting orbit (stable 2-cycle in the flip case, a quasiperiodic orbit restricted to an invariant attracting curve in the Hopf case) above μ_0. In the

subcritical case such attractors do not exist. Now, if we shall prove that a Hopf bifurcation which occurs in a two-dimensional map is super- or subcritical we first write the map on complex form and provided $\lambda^3 \neq 1$, $\lambda^4 \neq 1$ (that means we are outside the strong resonance cases) we may through a series of near identity transformations (normal form calculations) express it as (Govaerts and Ghaziani, 2006):

$$z \to ze^{i\theta_0}(1+\mu+d\,|\,z\,|^2)+O(|\,z\,|^4) \qquad (11)$$

and the sign of a = Re(d) will determine the nature of bifurcation (a < 0 implies supercritical, a > 0 subcritical). a is a complicated formulae which first was established by Wan (1978). Wikan (1998) it is proved that the fixed point of a map like the one considered in Example 1 where the density dependent survivals belong to the Deriso-Schnute family undergoes a supercritical Hopf bifurcation at instability. The nature of flip bifurcations in two-dimensional maps can be studied by first performing a center manifold restriction and then express the map as:

$$w \to -(1+\mu)w+aw^3+O(w^4) \qquad (12)$$

where, w is real. Details and stability formulaes may be found in Guckenheimer and Holmes (1983). Finally, it should also be mentioned that there exist several numerical packages designed for studying bifurcation phenomena, see for example Ueta *et al*. (1999); Kuznetsov (2004) and Kuznetsov and Meijer (2005). In particular, confer Govaerts and Ghaziani (2006) where they use the MATLAB package CL_MatCont on bifurcation problems in a stage-structured cannibalism model. Our experience is that supercritical bifurcations dominate in age and stage-structured models like (1) and (3).

Next, let us briefly focus on possible routes to chaos. Referring to Example 1 we have the route: Stable fixed point $\to$ Invariant curve, quasiperiodic orbit (Hopf) $\to$ Periodic orbit (frequency locking) $\to$ Periodic orbits where the periods are doubled (successive flip bifurcations) $\to$ chaos. Hence, once a periodic orbit is established the route to chaos is similar to what one finds in one-dimensional maps as summarized in Thunberg (2001). Another possibility is that once a periodic orbit is established there may be a secondary Hopf bifurcation and chaotic behaviour may evolve when the disjoint subsets start to get twisted, cf. Example 2 and Fig. 3b. A third scenario is that one from the periodic orbit may return to quasiperiodicity again as the bifurcation parameter increases. It is also possible to go directly from quasiperiodicity (invariant curve) to chaos. This may happen as the invariant curve starts to break up. An example may be found in Wikan (2012) by use of the Neubert and Caswell map (3)

(density dependent μ_1 values). We may also face the situation that the invariant curve becomes kinked so that it is not topologically equivalent to a circle anymore (see Wikan (1998) by use of small positive γ values in the Deriso-Schnute model). A comprehensive study of crises (collisions of attractors and unstable periodic orbits) in Leslie matrix models may be obtained in Ugarcovici and Weiss (2004) (see also Example 3). Crises as well as subcritical bifurcations may lead to large and discontinuous population changes.

Example 4 (Precocious and delayed semelparity): First we consider the precocious case where both fecundity and survival probability is density dependent, i.e.:

$$(x_1, x_2) \rightarrow (fx_2, px_1) \qquad (13)$$

where, $f = F \exp(-\alpha x)$ and $p = P \exp(-\beta x)$. The model possesses a unique nontrivial fixed point (x_1^*, x_2^*) and it is stable provided:

$$(\beta - \alpha)[1 - P\exp(-\beta x^*)]x_1^* > 0 \qquad (14a)$$

$$2 - (\beta x_1^* + \alpha x_2^*) > 0 \qquad (14b)$$

(Wikan, 2012). Now, if $\beta > \alpha$ it is obvious that (x_1^*, x_2^*) is stable in case of small equilibrium populations x^*. Regarding the nonstationary dynamics, $\beta \gg \alpha$ gives the same qualitative picture as accounted for in Example 1, 3-periodic dynamics is also a possibility. If $\beta > \alpha$ and $\beta - \alpha$ small we detect quasistationary orbits. Next, assume $\beta \leq \alpha$. Then the left hand side of (14a) is always negative (or equal to zero if $\beta = \alpha$). Consequently, the nontrivial fixed point is always unstable. Since (14a) is associated with the possibility that (x_1^*, x_2^*) shall undergo a flip bifurcation at instability threshold it is natural to seek for a stable 2-cycle in case of x^* small. Indeed, such a stable 2-cycle exists and the points in the cycle are on the form $(\hat{x}_1, \hat{x}_2) = (A, 0)$ or $(0, B)$ which implies that only one age class is populated at each time. (If $\alpha = 1$ and $\beta = 0$ then $A = P^{-1} \ln(FP)$ and $B = \ln(FP)$). Dynamics in which only one age class is populated at each time has been referred to as SYC (Single Year Class) dynamics, cf. Mjolhus *et al.* (2005). It has also been termed synchronization, see Bulmer (1977). As far as we know Bulmer (1977) appears to be the first to have noticed SYC dynamics in theoretical models, see also Wikan and Mjolhus (1996); Behncke (2000); Mjolhus *et al.* (2005) and Cushing (2006). Precise results of conditions which lead to SYC dynamics and conditions where age classes can coexist may also be obtained in a slightly different

model analysed by Davydova *et al.* (2003). Turning to delayed semelparity we consider:

$$(x_1, \ldots, x_n) \rightarrow (fx_n, Px_1, \ldots, Px_{n-1}) \qquad (15)$$

where, $f = F \exp(-x)$, see Mjolhus *et al.* (2005). The only dynamics we find in case of $x^* = \ln(FP^{n-1})$ small is an attracting n-cycle of SYC form:

$$(P^{1-n}x^*, 0, \ldots, 0), \ldots, (0, \ldots, 0, P^{i-n}x^*, 0, \ldots, 0) \ldots (0, \ldots, 0, x^*) \qquad (16)$$

Assuming n even, as x^* becomes larger successive flip bifurcations create stable SYC cycles of period $2^k n$. Also in the chaotic regime we only find SYC dynamics. When n is odd much of the same picture emerges. The only difference is that in case of intermediate values of x^* there may exist small parameter windows where the fixed point is stable, cf. Mjolhus *et al.* (2005).

However, note that SYC dynamics is not a very likely outcome in stage-structured models, see the discussion in Kon (2005). Indeed, Neubert and Caswell (2000) present by use of (3) an interesting analysis of the precocious semelparous case $\sigma_2 = 0.1$, $p = 0.9$. They found a stable nontrivial equilibrium in case of F small and when F was increased (they considered F values as large as 10^7) the dynamics alternated between stable orbits of low period and chaotic regions in the sense that prior to a chaotic region the period of an orbit was q and after the region the period was found to be $q + 1$. This phenomenon is known as period adding cycles and may also be found in the age-structured model by Guckenheimer *et al.* (1977). (We urge the reader to extend the bifurcation diagram in Fig. 4 and see if the same happens there too).
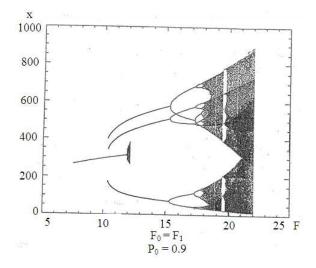

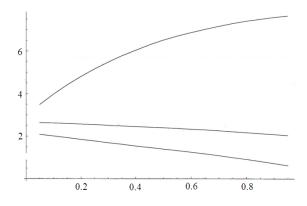Fig. 4: Bifurcation diagram generated by (7). n = 2 and P = 0.9

Fig. 5: The equilibrium population x* (map (3)) at instability threshold. Upper curve corresponds to $\mu_2 = 0.9$, middle curve $\mu_2 = 0.5$ and bottom curve $\mu_2 = 0.1$. The stable region is below the curves

Ecological implications: We start by considering density dependent survivals. The asymptotic argument referred to in the beginning of Example 1 shows that precocious iteroparous species possess qualitatively the same dynamics independent of number of age classes both with respect to the size of the stability region and nonstationary behaviour. Additionally, we may also argue that precocious iteroparous species on the whole show much of the same dynamics as precocious semelparous species. Moreover, see Example 2, by performing a rigorous analysis of (6) we may conclude that species with delayed semelparous as well as delayed iteroparous life histories exhibit poorer stability properties than species who possess precocious (iteroparous or semelparous) life histories. However, as is shown by Neubert and Caswell (2000), the analysis of the stage-structured model (3) ($\mu_1 = \mu_1 \exp(-x)$ and all other parameters constant) does only support parts of the findings reported above. Indeed, they conclude that there are no qualitative differences between populations with precocious or delayed life histories with respect to stability. On the other hand, regarding the nonstationary dynamics, pronounced 4-periodic behaviour has been detected by use of (3) in species which possess precocious semelparous life histories and there are also several examples of 4-periodicity in the delayed semelparous case. Therefore, beyond instability threshold there is an excellent agreement between the outcomes of (1) and (3). Hence, these observations seem to imply that it is a fairly general ecological principle that density dependent growth (μ_1) in the stage-structured model which in the age-structured model corresponds to density dependent year-to-year survival leads to periodic behaviour of low period. In nature one may find several examples of species who possess cyclic behaviour of low period (Stenseth *et al*.,

1977; Stenseth and Antonsen, 1988; Burkey and Stenseth, 1994). Especially among lemmings, cf. Stenseth and Ims (1993) this is the case. Lemming cycles are not very well understood. Thereforeriod (Stenseth *et al*., 1977; Stenseth and Antonsen, 1988; Burkey and Stenseth, 1994). Especially among lemmings, cf. Stenseth and Ims (1993) this is the case. Lemming cycles are not very well understood. Therefore, an interesting and challenging task could be to apply some of the density dependent survival models presented here on small rodent populations.

Next, consider precocious iteroparous species under the assumption of density dependent fecundity terms. From Example 3 we found that (x_1^*, x_2^*) is stable in case of x^* small. Regarding the nonstationary dynamics there were two scenaria, if $0 < P < \frac{1}{2}$ an increase of x^* (or F) leads to the period doubling route to chaos. If $\frac{1}{2} < P \leq 1$ the result is given through Fig. 4. Now, following Wikan and Mjolhus (1996) or Wikan (2012) assuming an odd number of age classes n it is possible to show that the value of x^* at instability threshold is an increasing function of both n and P. In particular, if $P = 1$ then $x^* = n + 1$ at threshold. Nonstationary dynamics is introduced when $\lambda = -1$. Hence, for all $0 < P < 1$ the dynamics beyond instability threshold is in many respects similar to what we found in the $0 < P < \frac{1}{2}$ case when n = 2. When n is even and small, x^* is not an increasing function of P at instability but as n becomes larger ($n \geq 8$) the dynamics becomes similar to what we find when n is odd. These findings clearly suggest that in case of large or moderate P values an increase of n acts stabilizing. See also Levin and Goodyear (1980); Vincent and Skowronski (1981) and Bergh and Getz (1988). Delayed iteroparous species may be studied through the map (Wikan, 2012):

$$(x_1, \ldots, x_n) \rightarrow (f_i x_i + \cdots + f_n x_n, Px_1, Px_2, \ldots, Px_{n-1}) \qquad (17)$$

where, $i = (n + 1)/2$ in case of $n \geq 3$, n odd and $i = n/2 + 1$ in case of $n \geq 4$ and n even. $f_i = F_i \exp(-x)$. By comparing the size of the stable parameter region found from (17) with the precocious situation (7) we find that it is always smaller in the delayed case.

Neubert and Caswell (2000) support the findings above by use of (3) ($f = F \exp(-x)$ and all other parameters constant). In Fig. 5 we show $x^* = x^*(p)$ in the cases $\mu_2 = 0.9$ (upper curve), $\mu_2 = 0.5$ (middle curve) and $\mu_2 = 0.1$ (bottom curve). The stable region is below the curves. Hence, the combined findings from the age-structured models and the stage-structured model (large μ_2) makes it natural to propose that it is a fairly general principle that species with precocious iteroparous life histories are more stable than species

with delayed iteroparous life histories. Moreover, on the whole, iteroparous species have better stability properties than semelparous species. Still assuming density dependent fecundities our analysis of the semelparous maps (13) and (15) shows that the nontrivial fixed point is unstable ($\beta \leq \alpha$) both in the delayed and precocious case. Instead, the dynamics is on SYC form. From a biologically point of view it is not obvious how such dynamics should be interpreted. Bulmer (1977) interprets its presence as "competition is more severe between than within age classes". Mjolhus *et al.* (2005) argue along the following line: Considering (15) recruitment acts as a birth pulse and juveniles have the same weight as older individuals. Moreover, at equilibrium $FP^{n-1} \exp(-x) = 1$, i.e., the relation concerns the SYC population when it is in a reproductive phase. In other phases $x = x_0 + [pic] + x_n$ is larger. Therefore, small populations inserted into empty age classes will experience a larger value of x in their reproductive phase than the main population which again will lead to a subcritical recruitment. Wikan (2012) where (13) is analysed, we conclude that it is the strength of density dependence which will decide if the two age classes will coexist or not. Coexistence occurs whenever the strength of density dependence in the survival is stronger ($\beta > \alpha$) than the density dependence in the fecundity. SYC dynamics is the outcome when $\beta \leq \alpha$. Davydova *et al.* (2003) who perform a thorough analysis of biennials arrive at a similar conclusion. Also, confer Ebenman (1987; 1988) and Roos *et al.* (1990) and the papers on cicada cycles by Hoppensteadt and Keller (1976); Heliovaara *et al.* (1994); Yoshimura (1997); Behncke (2000) and Webb (2001).

CONCLUSION

As we have seen, nonlinear age- and stage-structured population models serve as excellent tools in order to study the dynamical outcomes of ecological populations who possess different life histories ranging from biennials to species who may live for many years. Depending on parameter values and location on density dependent elements the dynamics may vary from stable fixed point to chaotic behaviour of stunning complexity. Hence, the models at hand which are easily understandable also for readers outside the biological and ecological communities provide excellent examples of nonlinear phenomena. Although the models rest on different prerequisites we find on several occasions that they qualitatively generate much of the same dynamics. This enables us to suggest important general principles with respect to stability and nonstationary behaviour of ecological populations.

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