Journal of Mathematics and Statistics 8 (4): 446-460, 2012
ISSN 1549-3644

doi:10.3844/jmssp.2012.446.460 Published Online 8 (4) 2012 (http://www.thescipub.com/jmss.toc)

TOWARDS SOME GENERAL ECOLOGICAL PRINCIPLES

Arild Wikan

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

Received 2012-12-05, Revised 2012-12-14; Accepted 2013-1-02

ABSTRACT

Discrete deterministic age-structured, stage-structured and difference delay equation population models are analysed and compared with respect to stability and nonstationary behaviour. All three models show that species with iteroparous life histories tend to be more stable than species with semelparous life histories which allow us to conclude that this must be a fairly general ecological principle. Considering iteroparity, the precocious case appears to be more stable than the delayed case. The nonstationary dynamics shows a great deal of resemblance too, but when the number of age classes are even there is a mismatch between the dynamical outcomes of the age- and stage-structured case whenever the survival probabilities are large or moderate. Regarding semelparous species the analysis of the age-structured and the difference delay equation model clearly suggest that precocious semelparous species are more stable than delayed semelparous species and, moreover, that the transfer from stability to instability goes through a Hopf bifurcation. This is in great contrast to the outcome of the stage-structured model. In this case we find that the delayed case is more stable than the precocious and in unstable parameter regions there are orbits of period 2^k, $k > 1$, which we do not find when the life history is precocious.

Keywords: Stage-Structure, Age-Structure, Semelparity, Iteroparity, Stability, Bifurcation

1. INTRODUCTION

In order to reveal the dynamic properties of a species there is a variety of different population models available. Such models may be continuous or discrete, deterministic or stochastic. Considering continuous models we refer to the seminal paper by Gurtin and MacCamy (1974); Webb (1985); Huang (1990) and Cushing (1987) and references therein. Models that incorporate stochasticity may be obtained in Neubert (1997); Dennis *et al*. (1997) and Myers *et al*. (2001). Among the discrete deterministic alternatives, especially three model strategies have proved to be powerful tools, namely (A) Age-structured population models, see for example Leslie (1945); Guckenheimer *et al*. (1977); Levin and Goodyear (1980); Silva and Hallam (1993) and Mjolhus *et al*. (2005), also cf. the review paper by Wikan (2012b), (B) Difference delay equation models (Clark, 1976; Botsford, 1986; 1992; Higgins *et al*., 1997) and (C) Stage-structured models (Cushing, 1987; Neubert and Caswell, 2000; Gourley and Kuang, 2004; Kon *et al*., 2004).

Regarding (A) such models are usually formulated in terms of vectors and matrices. Indeed, at time t we split the population x_t into n distinct nonoverlapping age classes, $x_t = (x_{1,t},\ldots,x_{n,t})^T$ where the total population x is given by $x = x_1 +\ldots+ x_n$. The relation between the population vector x at two consecutive time steps may be expressed as Equation 1:

$$x_{t+1} = A\, x_t \tag{1}$$

where, the transition matrix A (which often is referred to as a Leslie matrix) is on the form Equation 2:

$$A = \begin{pmatrix} f_1 & f_2 & \cdots & & f_n \\ p_1 & 0 & \cdots & & 0 \\ 0 & p_2 & \cdots & & 0 \\ \vdots & & \ddots & & \\ 0 & \cdots & & p_{n-1} & 0 \end{pmatrix} \tag{2}$$

where f_i is the average fecundity of a member of the i^{th} age class at time t. p_i may be interpreted as the (year to

year) survival probability of age class i. In models such 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 dynamics of a variety of ecological populations has been modelled by (1). Linear age-structured models (constant fecundities and constant survivals) have for example been applied to trout (Beland, 1974), rabbits (Darwin and Williams, 1964), beetles (Lefkovitch, 1965) and great tits (Pennycuick, 1969). In case of nonlinear models we refer to Cooke and Leon (1976); Longstaff (1977); Levin and Goodyear (1980); Hastings (1984) and Desharnais and Liu (1987). Other examples may be obtained in Cushing (1987) and Caswell (2001). Theoretical studies which focus on nonstationary and chaotic dynamics may be obtained in Guckenheimer *et al.* (1977); Silva and Hallam (1993); Wikan and Mjolhus (1995; 1996). Wikan (1997); Davydova *et al.* (2003) and Mjolhus *et al.* (2005) the dynamics of semelparous species is revealed. Ergodic results obtained by Cushing (1988; 1989) and Crowe (1994) provide a basic setting for considering stability and bifurcation in matrix models like (1).

Difference delay equation models (B) 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. In this study we will focus on the model Equation 3:

$$x_{t+1} = px_t + fx_{t-T} \tag{3}$$

which expresses that the size of the population at time t + 1 equals the part of the adult population which survives from the previous year plus the part which augments the adult population from births T years earlier. Just like (1), (3) has also been applied on several concrete species, see for example the Baleen whale model by Clark (1976). In case of other species we refer to Botsford (1986; 1992); Tuljapurkar *et al.* (1994) and Higgins *et al.* (1997). In many respects we may classify (3) as an aggregated version of (1) where detailed information of the dynamics within age classes is neglected. The model prerequisites birth pulse fertilities triggered at a specific age.

In stage-structured models (C) 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 such models is that there may be other factors which are more important with respect to maturity than age. For many species body size is more vital than age. Indeed, following Caswell (2001), size-dependent demography is probably the rule rather than the exception. Examples of species that must reach a certain size before they are able to reproduce may be found among plants (Werner, 1975; Klinkhamer *et al.*, 1987a; 1987b), crabs (Campbell and Eaglis, 1983), fish (Alm, 1959), see also Caswell (2001) and several references therein. Temperature is also an important factor that may trigger reproduction, especially in insect populations, cf. Wagner *et al.* (1984) and Bellows (1986). In this study we shall focus on the two-stage model Equation 4:

$$\begin{aligned} x_{1,t+1} &= \mu_1(1-p)x_{1,t} + fx_{2,t} \\ x_{2,t+1} &= \mu_1 p x_{1,t} + \mu_2 x_{2,t} \end{aligned} \tag{4}$$

where, μ_1 and μ_2 are the fractions of the immature population x_1 and the mature population x_2 respectively which survive from time t to t + 1. $x = x_1 + x_2$ is the total population. Moreover, p is the fraction of the immature population which survives to become adult and f is the fecundity. We may also express (4) on matrix form as Equation 5:

$$x_{t+1} = A\,x_t \tag{5}$$

where, $x = (x_1, x_2)^T$ and:

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

Model (4) (or (5)) is identical to the general stage-structured model presented by Neubert and Caswell (2000), see also the cod model by Wikan and Eide (2004). Another approach may be obtained in insect models where the population is divided into three stages, larvae, puppae and grown up insects, see the celebrated study by Cushing *et al.* (1996); Costantino *et al.* (1997) and Dennis *et al.* (1997).

The purpose of this paper is to compare and discuss stability properties and dynamical outcomes of models (1), (3) and (4) and in doing so we shall assume that density dependence is included in the recruitment terms and not in the survivals. Hence, in (1) we let $f_i = F\exp(-x)$, i = 1,…,n and $p_i = P$ where the use of capital letters indicates density independent terms. In the difference delay equation model (3) we use the same approach and in the stage-structured model (4), $f = F\exp(-x)$ and μ_1, μ_2 and p are regarded as constants. Thus we consider.

Age structure Equation 6:

$$x_{t+1} = A\,x_t \text{ where}$$
$$A = \begin{pmatrix} F\exp(-x) & \cdots & & F\exp(-x) \\ P & 0 & \cdots & 0 \\ 0 & \ddots & & \vdots \\ \vdots & & \ddots & \\ 0 & \cdots & P & 0 \end{pmatrix} \quad (6)$$

Difference delay Equation 7:

$$x_{t+1} = Px_t + Fe^{-x_{t-T}}x_{t-T} \quad (7)$$

Stage structure Equation 8:

$$\begin{aligned} x_{1,t+1} &= \mu_1(1-p)x_{1,t} + Fe^{-x_t}x_{2,t} \\ x_{2,t+1} &= \mu_1 p x_{1,r} + \mu_2 x_{2,t} \end{aligned} \quad (8)$$

1.1. Analysis

We start with the age-structured model (6). Assuming all age classes fertile (species with such properties are often referred to as iteroparous species) the nontrivial fixed point of (6) may be expressed as Equation 9:

$$(x_1^*, x_2^*, \ldots, x_n^*) = \left(\frac{1}{K}x^*, \frac{P}{K}x^*, \ldots, \frac{P^{n-1}}{K}x^*\right) \quad (9)$$

where, $K = \sum_{i=0}^{n-1} P^i$ and $x^* = \text{In}(Fk)$.

The eigenvalue equation may be cast in the form Equation 10:

$$\lambda^n - \frac{(1-x^*)}{K}\sum_{i=0}^{n-1} P^i \lambda^{n-1-i} = 0 \quad (10)$$

and provided that all eigenvalues of (10) are located within the unit circle, (9) is a stable fixed point. Now, using the same method as in Wikan and Mjolhus (1996), $x^* < 2$ is sufficient in order to guarantee a stable equilibrium (9). Indeed, we may write (10) as $g(\lambda) + h(\lambda) = 0$ where $g(\lambda) = \lambda^n$ and the first observation is that $g(\lambda) = 0$ has n roots located inside the unit circle. On the boundary Equation 11:

$$\begin{aligned} |h(\lambda)| &\le \left|\frac{(1-x^*)}{K}\lambda^{n-1}\right| \\ &+ \cdots + \left|\frac{(1-x^*)}{K}P^{n-1}\right| \le |1-x^*| < 1 \end{aligned} \quad (11)$$

whenever $x^* < 2$. Consequently, on the boundary $|h(\lambda)| < 1 = |g(\lambda)|$ and from Rouche's theorem we conclude that $g(\lambda) + h(\lambda) = 0$ has n roots inside the unit circle which means that (9) is stable.

Regarding the nonstationary dynamics it depends on the values of both n and P as we now shall demonstrate. Keeping P fixed, an increase of F leads to an increase of the total equilibrium population (cf. (9)) and when n = 2 it follows from (9), (10) and the Jury criteria (Murray, 2003) that the value of x^* at instability threshold is Equation 12:

$$\begin{aligned} x^* &= x_F = 2/(1-P) \quad 0 < P < 1/2 \\ x^* &= x_H = (1+2P)/P \quad 1/2 < P \le 1 \end{aligned} \quad (12)$$

where, the indices F and H refer to a flip or Hopf bifurcation at threshold respectively. Note that $P \to 0$ implies $x^* \to 2$ (see (12)). Hence we may interpret our previous result $x^* = 2$ as the stability threshold when the survivals approach zero. For other values of P, x^* at instability becomes larger and according to (12) $x^*_{\max} = x^*(P = 1/2) = 4$ at threshold.

Assuming $0 < P < 1/2$ it was proved in Wikan and Mjolhus (1996) that the flip bifurcation at threshold $x^* = x_F$ (12) is of supercritical nature. Hence, in case of $x^* > x_F$, $|x^* - x_F|$ small there are stable orbits of period 2. If we continue to increase x^* (or F) we observe periodic orbits of 2^k, k = 2,3,… (the flip bifurcation sequence) and eventually the dynamics becomes chaotic. The Hopf bifurcation at $x^* = x_H$ (12) in the 1/2 <p< 1 interval is also supercritical. Thus, whenever $x^* > x_H$, $|x^* - x_H|$ small we find nonperiodic orbits restricted to an invariant curve. Moreover, these orbits coexist with a stable large amplitude 3-cycle which is born through a saddle node bifurcation at a critical value $x_S < x_H$ so the ultimate fate of an orbit depends on the initial condition. For higher values of x^* the invariant curve disappears (as it is hit by the branches of the unstable 3-cycle created at $x^* = x_S$) and only stable periodic orbits of period $3 \cdot 2^k$ are detected. Also here the dynamics becomes chaotic provided x^* large enough.

In the case n = 3 (all age classes fertile) we find from the Jury criteria $x_F = 2(1 + P^2)(1 - P + P^2)^{-1}$ and $x_H =$

$P^{-2}(1 + P + 2P^2)$ and an easy argument shows that $x_F < x_H$ for all $0 < P < 1$. Hence, the flip bifurcation governs the nonstationary dynamics for any P, $0<P<1$ and the dynamics is qualitatively similar to the n = 2 case $0 < P < 1/2$. Since $x_F'(P) = 2(1 - P^2)(1 - P + P^2)^{-2} > 0$ we may also conclude (in contrast to the n = 2 case) that x^* is an increasing function of P at bifurcation threshold. In **Fig. 1** we plot the value of the equilibrium population at instability threshold as function of P in the n = 2 and n = 3 cases respectively.

Due to the complexity of the Jury criteria the analysis when n = 4 is more delicate. The value of x^* at instability is Equation 13:

$$\begin{aligned} x^* &= x_F = 2/(1-P) && 0 < P < P_c \\ x^* &= x_H && P_c < P < 1 \end{aligned} \tag{13}$$

where, $x_H = 1 + a_1(1 + P^2 + P^2 + P^3)$. a_1 is defined as the real solution of the Equation 14:

$$\begin{aligned} &P^3(1-P^2)(1+P^4)a_1^3 - \\ &P^2(1+P^2-P^4)a_1^2 + P(1+P^2)a_1 - 1 = 0 \end{aligned} \tag{14}$$

and $P_c \approx 0.61$. Consequently, the n = 4 case is similar to the n = 2 case except for the fact that the flip bifurcation determines the dynamics in a larger P interval.

Next, assume n arbitrary and P small. Then (9) implies $x^* \approx \ln(F(1 + P))$ and the general eigenvalue equation (10) may be written as Equation 15:

$$\lambda^2 - \frac{(1-x^*)}{1+P}\lambda - P\frac{(1-x^*)}{1+P} = \frac{(1-x^*)}{1+P}\sum_{i=1}^{n-1}\frac{P^{i+1}}{\lambda^i} \tag{15}$$

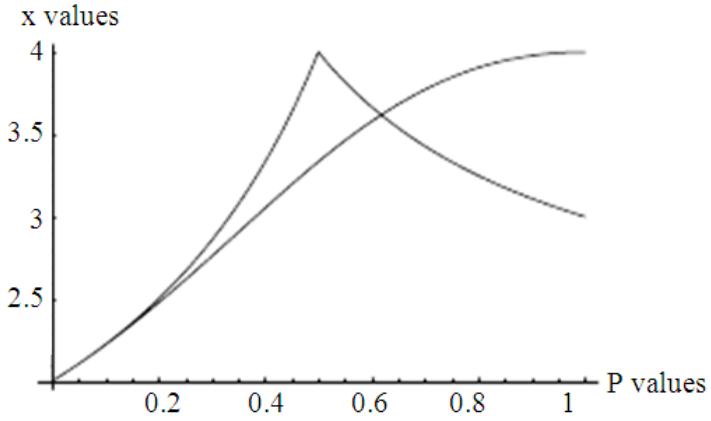

Fig. 1. The values of the equilibrium population x at instability threshold in the n = 2 and n = 3 cases. The monotonic increasing curve corresponds to n = 3

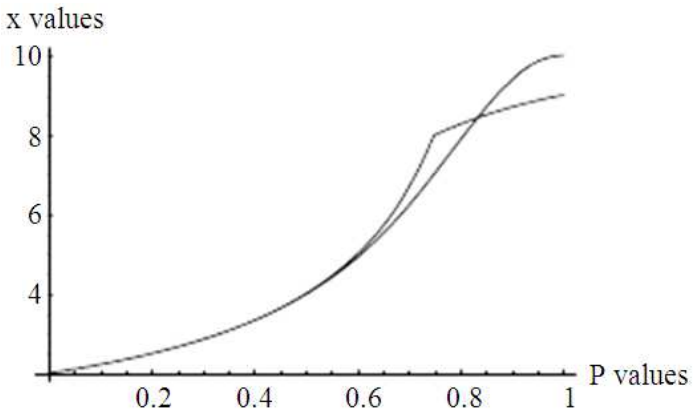

Fig. 2. The values of the equilibrium population x at instability threshold when n = 8 and n = 9. The "kinked" curve corresponds to n = 8

Now, the left hand side of (15), $g_2(\lambda)$ is nothing but the left hand side of (10) (n = 2) and from (12) it follows that the only modulus 1 solution of $g_2(\lambda) = 0$ is $\lambda = -1$ (and $x^* \to 2$ when $P \to 0$). This means that for λ close to -1 the dominant term on the right hand side of (15) will be of order P smaller than the left hand side which again implies that it will deviate O(P) from the solution of $g_2(\lambda) = 0$. Hence, we conclude that there will be no Hopf bifurcation in case of P small (and also P "moderate" as suggested by our n = 2, 3 and 4 analysis). The flip bifurcation threshold is found by letting $\lambda = -1$ in (10). Thus Equation 16:

$$x^* = x_F = \frac{2\sum_{i=0}^{k} P^{2i}}{\sum_{i=0}^{n-1}(-1)^i P^i} \tag{16}$$

where, k = (n − 1)/2 in case of n odd and k = (n − 2)/2 in case of n even.

Considering large P values it follows from (16) that $\lim_{P\to 1} x_F = n + 1$, n odd, while $\lim_{P\to 1} x_F \to \infty$, when n is even. Consequently, if n is even there will be no period doubling bifurcation when $P \to 1$. Moreover, when (n, P) = (2,1), $x^* = x_H = 3$ (cf. (12)). If (n, P) = (4,1) the solution of (14) is $a_1 = 1$ which implies $x_H = 5$ and if (n, P) = (3,1), then from (16) $x_F = 4$. Thus P = 1 seems to imply that $x^* = n + 1$ at instability threshold. A formal proof may be obtained in Wikan (2012a).

Based upon our findings above as well as lots of numerical experiments we conclude that (16) is the instability threshold for any P, $0<P\leq 1$, provided n is odd. Moreover, keeping n fixed, $x_F = x_F(P)$ (see (16)) is a monotonic increasing function of P, hence increasing the survival probabilities acts stabilizing. When n is even, (16) is the threshold whenever $0<P<P_c$, but in the interval $P_c<P<1$ the transfer from stability to instability occurs as (9) undergoes a Hopf bifurcation. P_c becomes larger as n is increased.

Provided $n \geq 8$, x^* is a monotonic increasing function of P at bifurcation also in the even number of age class cases. When $P\to 1$ the size of x^* at threshold is a monotonic increasing function of n. Therefore, an enlargement of n acts stabilizing. In **Fig. 2** we show the equilibrium population at bifurcation threshold as function of P when n = 8 and n = 9. The different shapes of the stability curves for n = 2 and n large may be interpreted as a truncation effect. Indeed, following Wikan and Mjolhus (1996); see also Levin and Goodyear (1980), suppose that n is large. Then the contribution of new individuals from females in higher age classes is small provided P is small. Hence, in this case, $x^*(P)$ should be similar when n is large and n is small. Consequently, if we truncate a model with a large number of age classes, the effect on stability will be more or less negligible. However, if P is large, the contribution of new individuals from the higher age classes is large too. Therefore, it is natural to conclude that truncation will have a great impact on stability in this case. That is why the stability curves look different, thus the qualitative effect of truncation after a few age classes is that it causes decreasing stability beyond a certain value of P.

In the analysis presented above we assumed that each age class was fertile. Alternatively, we may consider biologically relevant n-age class models where individuals in the first n-i age classes do not reproduce. Such cases may be studied through the map Equation 17:

$$\begin{aligned} &x_1,\ldots,x_n \to (F\exp(-x)x_i + \\ &\cdots + F\exp(-x)x_n, Px_1 Px_2,\ldots,Px_{n-1}) \end{aligned} \tag{17}$$

where, i = (n + 1)/2, $n \geq 3$, n odd and i = n/2 ± 1, $n \geq 4$, n even. The total equilibrium population becomes Equation 18:

$$x^* = \ln\left(F\sum_{k=i-1}^{n-1} P^k\right) \tag{18}$$

and the associated eigenvalue equation may be cast in the form Equation 19:

$$\lambda^n + x_1^*\sum_{k=1}^{i-1} P^{k-1}\lambda^{n-k} + (x_1^* - Fe^{-x^*})\sum_{k=i}^{n} P^{k-1}\lambda^{n-k} = 0 \tag{19}$$

and (as before) $x_1^* = x^*(1 + P + \cdots + P^{n-1})^{-1}$.

As already shown, if n = 3 and all age classes are fertile the (flip) bifurcation threshold was found to be $x_{F1}^* = 2(1+P^2)/(1-P+P^2)$. A similar analysis of (17) where (n,i) = (3,2) yields $x_{F2}^* = 2P(1+P+P^2)/(1+P)(1-P+P^2)$ and since $x_{F1}^* - x_{F2}^* = 2/(1+P)(1-P+P^2) > 0$ it is natural to suggest that delayed recruitment acts destabilizing. Note however, that both stability thresholds are "flip thresholds", thus the dynamics in unstable parameter regions are periodic orbits of period 2^k in both cases.

If n is even it follows from (19) that $\lambda = -1$ gives birth to the threshold Equation 20:

$$x_F^* = \frac{2\left(\sum_{k=1}^{l} P^{2k-1}\right)\left(\sum_{k=0}^{n-1} P^k\right)}{\left(\sum_{k=0}^{n-1}(-1)^k P^k\right)\left(\sum_{k=0}^{n-i} P^k\right)} \quad (20)$$

where, l = (n − i)/2 when i is even and l = (n − i − 1)/2 when i is odd. Since $\lim_{P\to 1} x_F^* \to \infty$ we may exclude the flip if P becomes large. When (n,i) = (4,3) we may actually exclude the flip in case of P small as well. Indeed, by use of (19) and dividing by λ + 1 we arrive at Equation 21:

$$\lambda^3 + \frac{1+P^4}{Z(1+P)}\lambda^2 + \frac{2P-P^4-1}{Z(1+P)}\lambda + \frac{P(P^3+P^2+P-1)}{Z(1+P)} = 0 \quad (21)$$

where, Z = 1 − P + P² − P³ (cf. Wikan and Mjolhus (1996)). Here we notice that whenever P is small the dominant solution of (21) must be close to $(-1+\sqrt{5})/2$ which exceeds unity. Consequently, there exists a threshold $x_H^* < x_F^*$ (where x_F^* is given through (20)) where (21) has complex roots located on the boundary of the unit circle.

When n exceeds 4 it is difficult to give a thorough picture of the dynamics in unstable parameter regions due to the complexity of the Jury criteria but some information is still possible to obtain. If λ = −1 and n is even it follows from (19), (20) that Equation 22a and b:

$$x^* = \frac{2}{1-P} \quad \text{i odd} \quad (22a)$$

$$x^* = \frac{2P(1-P^{n-i})}{(1-P)(1-P^{n-i+1})} \quad \text{i even} \quad (22b)$$

Obviously, none of the expressions (22a, b) may be instability thresholds in case of P → 1. Moreover, assuming i odd $\lim_{P\to 0} x^* = 2$. Thus, according to our findings from the P → 0, (n, i) = (4,3) analysis, (22a) may not be the instability threshold in case of small P values either. Hence, a natural conjecture to propose is that whenever n is even and i is odd the dynamics in unstable parameter regions is governed by a Hopf bifurcation at a threshold lower than (22a).

On the other hand, assuming both n and i even, then from (22b) $\lim_{P\to 0} x^* = 0$. This fact together with the numerical findings from the (n,i) = (4,2) case which shows that (22b) is the instability threshold as long as P < 0.73 clearly suggests that the period doubling bifurcation governs the nonstationary dynamics provided P is not too close to unity.

If λ = −1 and n odd we arrive at the expressions Equation 23a and b:

$$x^* = \frac{2(1-P^{n-i+2})}{(1+P^n)(1-P^{n-i+1})}\left(\sum_{k=1}^{n} P^{k-1}\right) \quad \text{i odd} \quad (23a)$$

$$x^* = \frac{2P}{1+P^n}\left(\sum_{k=1}^{n} P^{k-1}\right) \quad \text{i even} \quad (23b)$$

Considering (23a) we find that P → 0 implies $x^* \to 2$ and P → 1 implies $x^* = n(n - i + 2)/(n - i + 1)$. Therefore whenever i > 1 the latter expression is larger than n + 1. This means that both in case of P small and P large (23a) is larger (or equal) than the instability threshold when there is no delay in reproduction (i.e., i = 1). This is not in agreement with our previous results (delayed recruitment acts destabilizing) so it is natural to conclude that (23a) is not the instability threshold for any value of P. Consequently, there exists a complex modulus 1 solution of the eigenvalue equation (19) which gives birth to a Hopf bifurcation threshold x_H^* which is smaller than (23a).

Regarding (23b), P → 0 implies $x^* \to 0$ and P → 1 implies $x^* \to n$, Moreover, we know from our (n,i) = (3,2) analysis that (23b) is the bifurcation threshold for any value of P. Therefore, it is tempting to conclude that (23b) is the instability threshold and additionally that an increase of the number of age classes acts stabilizing, especially when P becomes large.

The final age-structured case to discuss is the one where fertility is restricted to the last age class only. (Species which reproduce at the end of life is often referred to as semelparous species.) Therefore, consider the map Equation 24:

$$(x_1,...,x_n) \to (F\exp(-x)x_n, Px_1, Px_2, ..., Px_{n-1}) \quad (24)$$

At equilibrium $x^* = \ln(FP^{n-1})$. The eigenvalue equation becomes Equation 25:

$$\lambda^n + \frac{x^*}{K}\sum_{i=0}^{n-1} P^i \lambda^{n-1-i} - 1 = 0 \quad (25)$$

and when n is even and λ = −1 the left hand side of the equation may be expressed as Equation 26:

$$\frac{x^*}{K}\sum_{i=0}^{n}(-1)^{i+1}P^i \tag{26}$$

Now, (26) is clearly negative. Moreover, when $\lambda \to -\infty$ the left hand side of (25) $\to +\infty$. Hence, (25) has a root $\hat{\lambda} < -1$ from which we conclude that the nontrivial fixed point of (24) is always unstable. When n is odd it was proved by Wikan and Mjolhus (1996) that the nontrivial fixed point is unstable in case of small equilibrium populations x^*. Whenever x^* is large, that is $x^* > 2K(\sum_{i=0}^{n-1}(-P)^i)^{-1}$ we may use the same kind of consideration (Mjolhus *et al*., 2005) in order to conclude that (25) has a root $\tilde{\lambda} < -1$ too. In case of intermediate values of x^* the argument presented above does not work but extensively numerical simulations indeed suggest that the fixed point of (24) is unstable also here. However, if different survival probabilities P_i are assumed in (24), then there may exist small parameter windows where the nontrivial fixed point is stable. This is documented in Mjolhus *et al*. (2005) in case of n = 3.

Actually, the only dynamics which we find from map (24) is SYC (Single Year Class) dynamics, cf. Davydova *et al*. (2003) and Mjolhus *et al*. (2005), i.e., dynamics where only one age class is populated at each time. When n = 2 and $x^* = \ln(FP)$ is small (24) possesses a stable 2-cycle where the points in the cycle are $(P^{-1}\ln(FP),0)$, $(0,\ln(PF))$. When x^* increases, stable cycles of period 4, 8,… are introduced and beyond the accumulation point for the flip bifurcation sequence we observe chaotic dynamics. Note that all cycles as well as the dynamics in the chaotic regime are on SYC form. For arbitrary values of n and $x^* = \ln(FP^{n-1})$ small we find the stable n-cycle Equation 27:

$$\left(\frac{1}{P^{n-1}}x^*,0,...,0\right)\cdots \left(0,0,...,\frac{P^{i-1}}{P^{n-1}}x^*,0,...,0\right),\cdots(0,0,...,x^*) \tag{27}$$

and through an enlargement of x^* we find the same qualitative picture as in the n = 2 case.

Next, we turn to the difference delay equation (7). The nontrivial equilibrium is given as Equation 28:

$$x^* = \ln\left(\frac{F}{1-P}\right) \tag{28}$$

where, $F > 1 - P$ and $0 \le P < 1$ is necessary in order to ensure a biologically acceptable equilibrium. The linearization of (7) may be expressed as Equation 29:

$$\lambda^{T+1} - P\lambda^T - (1-P)(1-x^*) = 0 \tag{29}$$

and x^* is stable provided all the eigenvalues λ are located inside the unit circle.

Independent of the values of T we may use Rouche´s theorem to show (in a similar way as in the age-structured case) that $x^* < 2$ ensures that (28) is a stable equilibrium. Thus, rewrite (29) as $g(\lambda) + h(\lambda) = 0$ where $g(\lambda) = \lambda^{T+1}$ and $h(\lambda) = -P\lambda^T - (1 - P)(1 - x^*)$. Further, observe that g and h are analytic functions on and inside the unit circle and that the equation $g(\lambda) = 0$ has all its roots located inside the unit circle. On the boundary we have:

$$\begin{aligned}|h(\lambda)| &= |-P\lambda^T - (1-P)(1-x^*)| \le |P| + |(1-P)(1-x^*)| \\ &= P + (1-P)|1-x^*| < 1 = |g(\lambda)|\end{aligned}$$

as long as $x^* < 2$. Consequently, $g(\lambda) + h(\lambda) = 0$ has the same numbers of roots inside the unit circle as $g(\lambda) = 0$, namely T + 1 roots and (28) is stable.

Let us now focus on the nonstationary dynamics. First, assume T = 0 (no delay). Then, x^* is stable as long as $x^* < 2/(1-P)$ (note that $P \to 0 \Rightarrow x^* \to 2$) or alternatively $F < (1 - P)\exp(2/(1 - P))$ and $\lambda = -1$ at bifurcation threshold. Moreover, by use of the notation $f(x) = Px + Fe^{-x}x$ we find at bifurcation that the nondegeneracy condition becomes Equation 30a:

$$\frac{\partial f}{\partial F}, \frac{\partial^2 f}{\partial x^2} + 2\frac{\partial^2 f}{\partial x \partial F} = -2e^{-\frac{2}{1-P}} \neq 0 \tag{30a}$$

and that the stability coefficient a may be expressed as Equation 30b:

$$a = \frac{1}{2}\left(\frac{\partial^2 f}{\partial x^2}\right)^2 + \frac{1}{3}\frac{\partial^3 f}{\partial x^3} = P(2P-1) + \frac{1}{3} > 0 \tag{30b}$$

Hence, according to Theorem 3.5.1 in Guckenheimer and Holmes (1990) we conclude that the flip bifurcation is supercritical which means that when x^* fails to be stable, a stable period 2 orbit is created. If we continue to increase F (or x^*) stable orbits of period 2^k, k = 2,3,… are established. Eventually, in case of large x^* values the dynamics becomes chaotic.

Next, consider T = 1 (small delay). The eigenvalue equation (29) may be written as Equation 31:

$$\lambda^2 - P\lambda - (1-P)(1-x^*) = 0 \quad (31)$$

and from the Jury criteria it is straightforward to show that $x^* < (2 - P)/ (1-P)$ guarantees a stable equilibrium. At instability threshold $x^* = (2-P)/(1-P)$ and the modulus 1 solution of (31) may be written as Equation 32:

$$\lambda = \frac{P}{2} \pm \frac{\sqrt{4-P^2}}{2} i = \frac{P}{2} \pm \frac{b}{2} i \quad (32)$$

Hence (in contrast to the T = 0 case) x^* undergoes a Hopf bifurcation at instability.

In order to determine the nature of the bifurcation, first observe that Equation 33:

$$\frac{d}{dt}|\lambda| = \frac{1}{2} e^{\frac{2-P}{1-P}} > 0 \quad (33)$$

at bifurcation from which we conclude that the eigenvalues leave the unit circle through an increase of F. Further, by defining $y_t = x_t$ and $z_t = x_{t+1}$ we may rewrite (7) (T = 1) as a first order system Equation 34:

$$\begin{pmatrix} y \\ z \end{pmatrix} \to \begin{pmatrix} 0 & 1 \\ Fe^{-y} & P \end{pmatrix} \begin{pmatrix} y \\ z \end{pmatrix} \quad (34)$$

with corresponding fixed point Equation 35:

$$(y^*, z^*) = \left(\ln\left(\frac{F}{1-P}\right), \ln\left(\frac{F}{1-P}\right) \right) \quad (35)$$

Now, following the procedure outlined in Wikan (1997) we find after a long and tedious calculation that the stability coefficient a in the normal form of (34) may be expressed as Equation 36:

$$a = \frac{P^2(P^2 - P - 3)}{16b^2} - \frac{1}{8}\frac{P^2}{b^2} - \frac{1}{16}\frac{P^2}{b^2} - \frac{1}{16}(1-2P) \quad (36)$$

Clearly, a < 0 if $0 < P \leq 1/2$. If $1/2 < P < 1$ we may write (36a) as Equation 37:

$$a = \frac{1}{16b^2}\left[(P^4 - 3P^3) + (-5P^2 + 8P) - 4 \right] \quad (37)$$

The term P^4-$3P^3$ is always negative. The max value of $-5P^2 + 8P$ is 16/5 and since 16/5 < 4, a < 0 in this case too.

Consequently, when (35) fails to be stable due to an increase of F, the dynamics is a quasiperiodic orbit restricted to an invariant curve which surrounds (35). This is displayed in **Fig. 3**. If we continue to increase F the invariant curve becomes kinked which signals that we are on the onset to chaos as shown in **Fig. 4**.

Turning to the T = 2 case we find from (29) and the Jury criteria that the fixed point is stable as long as Equation 38:

$$x^* < \frac{2 - 3P + \sqrt{P^2 + 4}}{2(1-P)} \quad (38)$$

Instability is introduced by increasing F such that (37) becomes equality and just as in the T = 1 case the eigenvalues at bifurcation threshold are complex conjugated and may be expressed as Equation 39:

$$\lambda = \frac{1}{4}\left\{ P + \sqrt{4 + P^2} \pm \sqrt{16 - (P + \sqrt{4 + P^2})^2}\, i \right\} \quad (39)$$

Further, the maximum stable population size in the T = 2, T = 1 and T = 0 cases clearly satisfies Equation 40:

$$\frac{2 - 3P + \sqrt{P^2 + 4}}{2(1-P)} < \frac{2-P}{1-P} < \frac{2}{1-P} \quad (40)$$

which suggests that delayed maturity acts destabilizing.

Now, assuming T arbitrary (T > 0) our findings above imply that it is natural to suppose that $\lambda = \exp(i\theta)$ at bifurcation threshold. Then from (29) Equation 41:

$$1 = Pe^{-i\theta} + (1-P)(1-x^*)e^{-i(T+1)\theta} \quad (41)$$

and by separating into real and imaginary parts we arrive at Equation 42a and b:

$$1 = P\cos\theta + (1-P)(1-x^*)\cos(T+1)\theta \quad (42a)$$

$$0 = -P\sin\theta - (1-P)(1-x^*)\sin(T+1)\theta \quad (42b)$$

Squaring and adding now yields Equation 43:

$$\cos T\theta = \frac{1 + P - (1-P)(1-x^*)^2}{2P(1-x^*)} \quad (43)$$

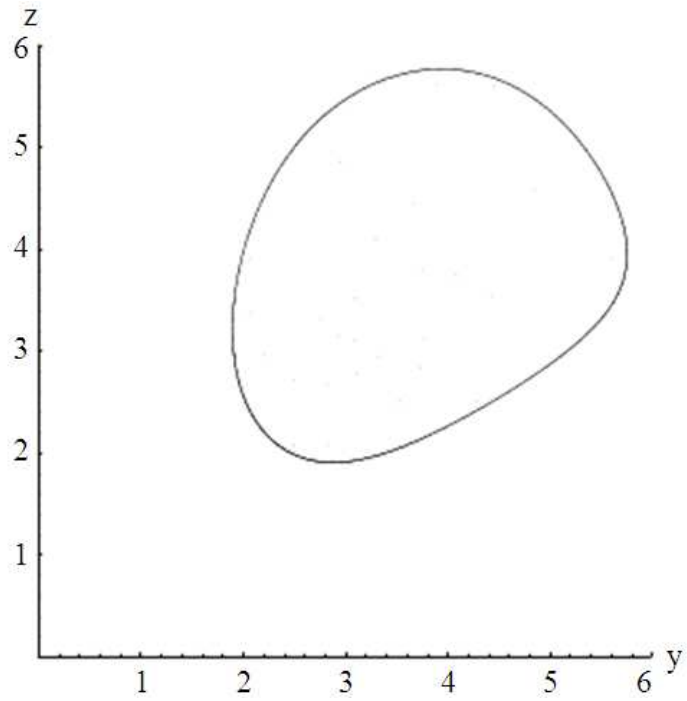

Fig. 3. An invariant curve (together with some initial transitions) generated by (34). Parameter values (F, P) = (14,0.5)

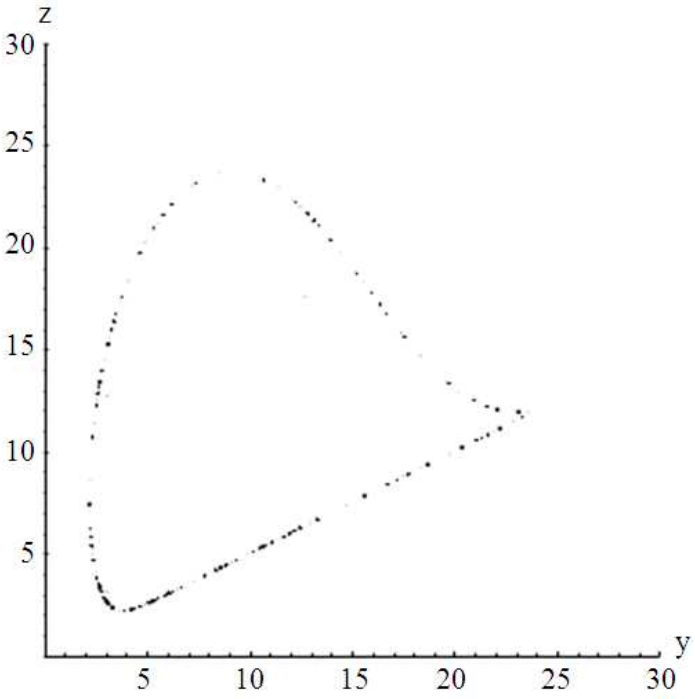

Fig. 4. The invariant curve has been kinked and has started to break up. Parameter values (F, P) = (80,0.5)

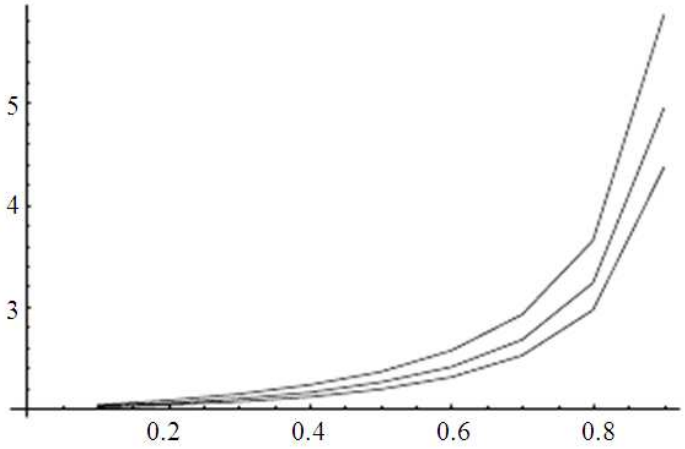

Fig. 5. The maximum stable equilibrium population. From top to bottom the curves correspond to T = 3, 4 and 5

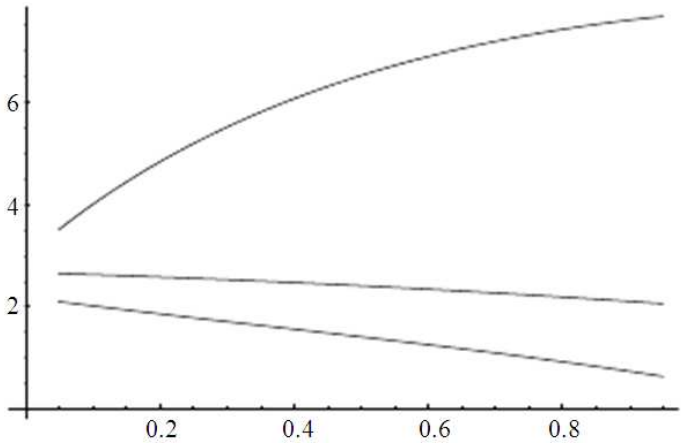

Fig. 6. The equilibrium population at bifurcation threshold as function of p. Upper curve corresponds to $\mu_2 = 0.9$, middle curve $\mu_2 = 0.5$ and bottom curve $\mu_2 = 0.1$

Thus, for given values of T and P, $\theta = \theta(x^*)$ may be obtained from Equation 44:

$$\theta = \frac{1}{T}\arccos\left\{\frac{1+P-(1-P)(1-x^*)^2}{2P(1-x^*)}\right\} \quad (44)$$

and Equation 45:

$$P\sin\theta = -(1-P)(1-x^*)\sin(T+1)\theta \quad (45)$$

From (43), (44) we may compute the value of x^* at bifurcation threshold. In **Fig. 5** we show the maximum stable equilibrium in the T = 3, 4 and 5 cases respectively. From top to bottom the curves correspond to T = 3, 4 and 5 and the stable region is located below the curves. Clearly, an increase of T acts destabilizing here too, just as we found in the T = 0, 1 and 2 cases. Also, cf. (37), (39) and **Fig. 5**, that x^* (T fixed) is an increasing function of P at instability threshold, hence increased adult survival acts in a stabilizing fashion. Since all instability thresholds ($T \geq 1$) are Hopf bifurcation thresholds it means that when F is increased to a level where x^* fails to be stable, quasiperiodic orbits are established. This does not exclude the possibility of exact or approximate periodic orbits as we penetrate deeper into the unstable parameter region. Indeed, such orbits may be created through frequency locking, see Wikan and Mjolhus (1996). In the model at hand we have not detected much periodicity. One exception is when

T = 1 and P → 1. Then arg λ ≈ π/3 (see (32)) and we observe six periodical dynamics. Through further increase of F the dynamics becomes chaotic. A final comment is that if T is increased beyond 1 (T≥2) it follows from (43) that θ becomes smaller. Thus as T grows, possible periodic dynamics will have longer and longer periods.

Finally, let us turn to the stage-structured model (8). Assuming $\mu_1 p > (1 - \mu_2)[1 - \mu_1(1 - p)]$ which ensures that the origin is an unstable fixed point we find that the nontrivial fixed point of (8) may be expressed as (cf. Neubert and Caswell (2000)) Equation 46:

$$(x_1^*, x_2^*) = \left(\frac{1-\mu_2}{1-\mu_2+\mu_1 p} x^*, \frac{\mu_1 p}{1-\mu_2+\mu_1 p} x^* \right) \quad (46)$$

where the total equilibrium population is Equation 47:

$$x^* = \ln\left\{ \frac{\mu_1 pf}{(1-\mu_2)\left[1-\mu_1(1-p)\right]} \right\} \quad (47)$$

Now, denote the Jacobian of (8) as J. Then the following inequalities (Neubert and Caswell (2000)) (I) 1 − tr J + |J| > 0, (II) 1+ tr J + |J| > 0, (III) 1 − |J| > 0 must be satisfied in order for (45) to be a stable fixed point. (I) may be written as Equation 48a:

$$(1-\mu_2)\left[1-\mu_1(1-p)\right]x^* > 0 \quad (48a)$$

and is always satisfied. (II) may be expressed as Equation 48b:

$$x^* = x_F^* < \frac{2(\mu_1+\mu_2-\mu_1 p)(1-\mu_2+\mu_1 p)}{(1-\mu_2)(1+\mu_2-\mu_1 p)\left[1-\mu_1(1-p)\right]} \quad (48b)$$

Regarding (III), whenever $\mu_2 > \mu_1 p$ Equation 48c:

$$2-(\mu_1+\mu_2-\mu_1 p)+(\mu_2-\mu_1 p)e^{-x^*}x_2^* > 0 \quad (48c)$$

which is obviously satisfied. If $\mu_2 < \mu_1 p$ we may write condition (III) as Equation 48d:

$$x^* = x_H^* < \frac{\left[2-(\mu_1+\mu_2-\mu_1 p)\right](1-\mu_2+\mu_1 p)}{(1-\mu_2)(\mu_1 p-\mu_2)\left[1-\mu_1(1-p)\right]} \quad (48d)$$

and since:

$$x_F^* - x_H^* = \frac{1-\mu_2+\mu_1 p}{(1-\mu_2)\left[1-\mu_1(1-p)\right]}$$
$$\left\{ \frac{2(\mu_1+\mu_2-\mu_1 p)}{1+\mu_2-\mu_1 p} - \frac{2-(\mu_1+\mu_2-\mu_1 p)}{\mu_1 p-\mu_2} \right\} < 0$$

we conclude that the stability threshold is found when the inequality sign in (48b) becomes an equality. Thus the period doubling bifurcation governs the dynamics as we penetrate into the unstable parameter region.

In **Fig. 6** we show the total equilibrium population x^* at bifurcation threshold (48b) as a function of the fraction p of the immature population which survives to become adult for different values of the adult survival μ_2. What **Fig. 6** clearly demonstrates is that an enlargement of μ_2 leads to an increase of x^* at instability threshold. Hence, increased adult survival which means that individuals live through several years as adults which again leads to repeated reproduction (iteroparous species) possess better stability properties than species which reproduces only once, ($\mu_2 \to 0$) (semelparous species). Moreover, in the iteroparous case (large μ_2 values) we find that x^* is an increasing function of p at instability. Hence, species with precocious iteroparous life histories ($p \to 1$, $\mu_2 \to 1$) are more stable than species with delayed iteroparous life histories ($0<p<1$, $\mu_2 \to 1$). Regarding semelparous species an opposite tendency seems to be the case. The delayed case ($0 < p < 1$, $\mu_2 \to 0$) appears to be more stable than the precocious case ($p \to 1$, $\mu_2 \to 0$). These findings confirm the results obtained by Neubert and Caswell (2000).

Turning to the nonstationary dynamics we find in case of small μ_2 values (both in the precocious and delayed cases) orbits of period 2^k as well as chaotic dynamics. There are no qualitative differences between the dynamics in precocious and delayed cases. Considering large μ_2 values (iteroparity), the delayed case exhibits the same dynamics as we found in the semelparous cases. On the other hand, when $p \to 1$ and μ_2 large (precocious iteroparity) the dynamics is not so rich. We have observed period 2 orbits but not orbits of period 2^k, $k > 1$, nor chaotic dynamics. This reflects the fact that x^* at instability threshold is larger here than in the delayed case, see **Fig. 6**.

Without repeating results from the detailed analysis of (6), (7) and (8) we find it natural to suggest that species who possess iteroparous life histories tend to be more stable than species with semelparous life histories. In the stage-structured model by Neubert and Caswell (2000) focus was also on submodels where μ_1 and p

respectively (see (5)) were density dependent and based upon the analysis of these submodels as well as on (8) they conjectured that it is a fairly general ecological principle that iteroparous species are more stable than species with semelparous life histories. By including the results of the analysis of (6) and (7) we feel that this conjecture has become significantly more robust.

Let us now focus on iteroparity in somewhat more detail. Assuming all age classes fertile, our analysis of the age-structured model (6) shows that there will always be a stable fixed point provided the total equilibrium population $x^* < 2$. Moreover, the nonstationary dynamics depends on both the number of age classes n and the year to year survival probability P. When n is sufficiently large, $x^*(P)$ at instability is an increasing function of P. Small survival probabilities imply that the transfer from stability to instability goes through a flip bifurcation independent of the number of age classes. The same is true when P is large provided n is odd. However, when n is even the transfer from stability to instability goes through a Hopf bifurcation. In all cases, an enlargement of n acts stabilizing if P is large enough.

If we shall compare the findings above with the outcomes of the stage-structured model (8) it must be with the case $\mu_2 \to 1$ (large adult survival) and $p \to 1$ (a large fraction of the immature population survives to become adults). Since large μ_2 values combined with large p values acts stabilizing (**Fig. 6**) the results here are in excellent agreement with the results of the age-structured model with respect to stability. Considering the nonstationary dynamics there is a fairly good agreement between the findings of (8) and the outcomes of (6) when there are an odd number of age classes. In both models the period doubling bifurcation governs the dynamics, but the difference is that while the stage-structured model exhibits period 2 orbits only beyond threshold (47b) the dynamics of the age-structured model is richer in the sense that there are stable orbits of period 2^k, $k > 1$ and chaotic dynamics as well. Therefore, from the discussion above, we find it fair to say that models (6) and (8) show much of the same qualitative picture when they are applied on species with precocious iteroparous life histories. However, when there are an even number of age classes in (6) there is a certain mismatch. The nonstationary dynamics in the age-structured case is now determined by a Hopf bifurcation which means that beyond instability threshold the dynamics is restricted to an invariant curve which surrounds the unstable fixed point. The parameter region where we have this discrepancy between (6) and (8) becomes smaller as n (n even) becomes larger. The worst case is n = 2. Then $1/2 < P < 1$ results in a Hopf bifurcation (see (12)).

Next, assume that individuals of a species may live through several age classes before maturity and then survive to reproduce for many years, i.e., we are considering species with delayed iteroparous life histories. By comparing the analysis of this case (see (17)) with the analysis of the precocious iteroparous case (6) we conclude that the precocious case seems to be more stable than the delayed case. As we have shown, when (n, i) = (3, 3) the stable parameter region is larger than in the case (n, i) = (3, 2). The dynamics beyond the instability thresholds are qualitatively similar. Still considering the delayed case (17), whenever $n \geq 4$ the Hopf bifurcation gives birth to the dynamics in unstable parameter regions in large P intervals. Hence, the size of the stable parameter regions as well as the dynamics in unstable regions are different in (17) and (6). Now, turning to the stage-structured model (8), delayed iteroparity is characterized by $\mu_2 \to 1$ and $0 < p < 1$. As **Fig. 6** demonstrates the value of x^* at instability in this case is smaller than in the precocious iteroparous case ($\mu_2 \to 1$, $p \to 1$). Based upon this, Neubert and Caswell (2000) proposed that species with precocious iteroparous life histories tend to be more stable than species with delayed iteroparous life histories. Our analysis of (6), (17) and (8) both confirm and strengthen their conclusion. It appears to be a general ecological principle that delayed iteroparous species possess poorer stability properties than precocious iteroparous species. On the other hand, regarding the nonstationary dynamics, the outcomes of (17) and (8) are different. Indeed, while the nonstationary dynamics generated by (8) is periodic orbits of period 2^k, $k = 1,2,\ldots$ or chaotic dynamics beyond the point of accumulation for the flip bifurcation sequence we observe that the dynamics generated by (17) is different. In case of $n > 4$ numerical simulations show that the fixed point of (17) (see (18)) undergoes a (supercritical) Hopf bifurcation at instability threshold in large P intervals. This gives birth to quasiperiodic orbits restricted to invariant curves. Whenever F is large the dynamics may be chaotic but the structure of the chaotic attractor is not the same as the structure of the corresponding attractor generated by (8).

Finally, considering semelparous species, according to our analysis of the difference delay equation model (7) there always exists a stable equilibrium if $x^* < 2$. Moreover, cf. (39) and **Fig. 5**, an enlargement of the delay T acts destabilizing. Consequently, it is natural to conclude the precocious semelparous species have better stability properties than species with delayed

semelparous life histories. The results of the semelparous age-structured case (24) are special (SYC dynamics), but our treatment of the delayed case (17) supports the findings of (7) with respect to the size of the stability region as well as the dynamics beyond the instability threshold. Also, note that if we allow a small fecundity F_{n-1} in age class n-1 (see (24)) it was shown in Wikan and Mjolhus (1996) the existence of a stable nontrivial fixed point $(x_1^*,\ldots,x_n^*)$ in case of small equilibrium population x^*. This strengthens the conclusions above too. On the other hand, still assuming semelparity, the stage-structured model (8) does not support any of the results of (6) and (7). Indeed, from **Fig. 6** we now conclude that species who possess delayed semelparous life histories are more stable than species who have precocious semelparous life histories and as we have shown, cf. (48b), periodic behaviour of period 2^k, $k \geq 1$, as well as chaotic dynamics are the only possible outcomes beyond (48b).

It is not obvious why (6), (7) and (8) in some cases give similar results and in other cases not. Considering species with iteroparous life histories the agreement between the outcomes of the age-structured model (6) and the stage-structured model (8) appears to be good. Regarding semelparous species the agreement is much poorer, hence it is natural to search for factors linked to delayed recruitment in order to explain the differences. Now, in (6) and (7) sexual maturity is triggered at a specific age which allow us to think of recruitment as a birth pulse. Moreover, as we know from several scientific branches, delay effects very often act destabilizing and lead to nonstationary phenomena. Therefore, we find it plausible to propose that it is the combined effect of abrupt delay and birth pulses which leads to the dynamics observed in (6) and (7). On the other hand, in the stage-structured case (8), it is hard to think of recruitment as a pulse and even harder to link it to a small time interval (unless $\mu_2 \to 0$).

2. CONCLUSION

Assuming overcompensatory recruitment functions we have by use of a variety of different discrete nonlinear population models (which rest on different prerequisites) been able to suggest some important ecological principles with respect to stability and dynamic behaviour. On a few occasions, the dynamic outcomes of the models do not match. Typically, this occurs when we study populations who possess semelparous life histories.

3. REFERENCES

Alm, G., 1959. Connection between maturity, size and age in fishes. Drottningholm Instit. Freshwater Res., Report, 40: 5-145.

Beland, P., 1974. On predicting the yield from brook trout populations. Trans. Am. Fish Soc., 103: 353-355. DOI: 10.1577/1548-8659(1974)103<353:OPTYFB>2.0.CO;2

Bellows, Jr., T.S., 1986. Impact of development variance on behaviour of models for insect populations. I Models for populations with unrestricted growth. Res. Populat. Ecol., 28: 53-62. DOI: 10.1007/BF02515535

Botsford, L.W., 1986. Population dynamics of the Dungeness crab (Cancer magister). Can. Spec. Publ. Fish. Aquat. Sci., 92: 140-153.

Botsford, L.W., 1992. Further analysis of Clark's delayed recruitment model. Bull. Math. Biol., 54: 275-293. DOI: 10.1016/S0092-8240(05)80027-8

Campbell, A. and M.D. Eagles, 1983. Size at maturity and fecundity of rock crabs, 'Cancer irroratus', from the bay of fundy and Southwestern Nova Scotia. Fishery Bull., 81: 357-362.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis and Interpretation. 2nd Edn., Sinauer Associates, Sunderland, Massachusetts, ISBN-10: 0878930965, pp: 722.

Clark, C.W., 1976. A delayed recruitment model of population dynamics with an application to baleen whale population. J. Math. Biol., 3: 381-391. DOI: 10.1007/BF00275067

Cooke, D. and J.A. Leon, 1976. Stability of population growth determined by 2×2 Leslie matrix with density dependent elements. Biometrics, 32: 435-442. DOI: 10.2307/2529512

Costantino, R.F., R.A. Desharnais, J.M. Cushing and B. Dennis, 1997. Chaotic dynamics in an insect population. Science, 275: 389-391. DOI: 10.1126/science.275.5298.389

Crowe, K.M., 1994. A nonlinear ergodic theorem for discrete systems. J. Math. Biol., 32: 179-191. DOI: 10.1007/BF00163877

Cushing, J.M., 1987. An Introduction to Structured Population Dynamics. 1st Edn., SIAM, Philadelphia, ISBN-10: 0898714176, pp: 200.

Cushing, J.M., 1988. Nonlinear matrix models and population dynamics. Nat. Res. Mod., 2: 539-580.

Cushing, J.M., 1989. A strong ergodic theorem for some nonlinear matrix models for the dynamics of structured populations. Nat. Res. Mod., 3: 331-357.

Cushing, J.M., B. Dennis and R.F. Costantino, 1996. An interdisciplinary approach to understanding nonlinear ecological dynamics. Ecol. Model, 92: 111-119. DOI: 10.1016/0304-3800(95)00170-0

Darwin, J.H. and R.M. Williams, 1964. The effect of time of hunting on the size of a rabbit population. New Zealand J. Sci., 7: 341-352.

Davydova, N.V., O. Diekman and S.A. Van Gils, 2003. Year class coexistence or competitive exclusion for strict biennials. J. Math. Biol., 46: 95-131. DOI: 10.1007/s00285-002-0167-5

Dennis, B., R.A. Desharnais, J.M. Cushing and R.F. Costantino, 1997. Transition in population dynamics: Equilibria to periodic cycles to aperiodic cycles. J. Anim. Ecol., 6b: 704-729. DOI: 10.2307/5923

Desharnais, R.A. and L. Liu, 1987. Stable demographic limit cycles in laboratory populations of Tribolium Castaneum. J. Anim. Ecol., 56: 885-906. DOI: 10.2307/4955

Gourley, S.A. and Y. Kuang, 2004. A stage structured predator-prey model and its dependence on maturation delay and death rate. J. Math. Biol., 49: 188-200. DOI: 10.1007/s00285-004-0278-2

Guckenheimer, J. and P. Holmes, 1990. Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields. 3rd Edn., Springer-Verlag, New York, ISBN-10: 3540908196, pp: 459.

Guckenheimer, J., G. Oster and A. Ipaktchi, 1977. The dynamics of density dependent population models. J. Math. Biol., 4: 101-147. DOI: 10.1007/BF00275980

Gurtin, M.E. and R.C. MacCamy, 1974. Non-linear age-dependent population dynamics. Arch. Rational Mech. Anal., 54: 281-300. DOI: 10.1007/BF00250793

Hastings, A., 1984. Age dependent predation is not a simple process. II. Wolves, Ungulates and a discrete time model for predation on juveniles with a stabilizing tail. Theor. Pop. Biol., 26: 271-282. DOI: 10.1016/0040-5809(84)90033-9

Higgins, K., A. Hastings and L.W. Botsford, 1997. Density dependence and age structure: Nonlinear dynamics and population behavior. Am. Nat., 149: 247-269. DOI: 10.1086/285989

Huang, X.C., 1990. An age-dependent population model and its operator. Phys. D: Nonlinear Phenomena, 41: 356-370. DOI: 10.1016/0167-2789(90)90004-9

Klinkhamer, P.G.L., T.J. de Jong and E. Meelis, 1987a. Delay of flowering in the 'biennal' Cirsium vulgare: Size effects and devernalization. Oikos, 49: 303-308. DOI: 10.2307/3565765

Klinkhamer, P.G.L., T.J. de Jong and E. Meelis, 1987b. Life-history variation and the control of flowering in short-lived monocarps. Oikos, 49: 309-314. DOI: 10.2307/3565766

Kon, R., Y. Saito and Y. Takeuchi, 2004. Permanence of single-species stage-structured models. J. Math. Biol., 48: 515-528. PMID: 15133621

Lefkovitch, L.P., 1965. The study of population growth in organisms grouped by stages. Biometrics, 21: 1-18. DOI: 10.2307/2528348

Leslie, P.H., 1945. On the use of matrices in certain population mathematics. Biometrika, 33: 183-212.

Levin, S.A. and P.H. Goodyear, 1980. Analysis of an age-structured fishery model. J. Math. Biol., 9: 245-274. DOI: 10.1007/BF00276028

Longstaff, B.C., 1977. The dynamics of collembolan populations: A matrix model of single species population growth. Can. J. Zool., 55: 314-324. DOI: 10.1139/z77-043

Mjolhus, E., A. Wikan and T. Solberg, 2005. On synchronization in semelparous populations. J. Math. Biol., 50: 1-21. DOI: 10.1007/s00285-004-0275-5

Murray, J.D., 2003. Mathematical Biology. 3rd Edn., Springer, New York, ISBN-10: 0387952284, pp: 811.

Myers, R.A., B.R. MacKenzie, K.G. Bowen and N.J. Barrowman, 2001. What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. Can. J. Fish. Aquat. Sci., 58: 1464-1476.

Neubert, M.G. and H. Caswell, 2000. Density-dependent vital rates and their population dynamic consequences. J. Math. Biol., 41: 103-121. DOI: 10.1007/s002850070001

Neubert, M.G., 1997. A simple population model with qualitatively uncertain dynamics. J. Theor. Biol., 189: 399-411. DOI: 10.1006/jtbi.1997.0258

Pennycuick, L., 1969. A computer model of the Oxford great tit population. J. Theor. Biol., 22: 381-400. DOI: 10.1016/0022-5193(69)90011-3

Silva, J.A. and T.G. Hallam, 1993. Effects of delay, truncation and density dependence in reproduction schedules on stability of nonlinear Leslie matrix models. J. Math. Biol., 31: 367-395. DOI: 10.1007/BF00163922

Tuljapurkar, S., C. Boe and K.W. Wachter, 1994. Nonlinear feedback dynamics in fisheries: Analysis of the Deriso-Schnute model. Can. J. Fish. Aquat. Sci., 51: 1462-1473. DOI: 10.1139/f94-146

Wagner, T.L., H.I. Wu, P.J.H. Sharpe, R.M. Schoofield and R.N. Coulson, 1984. Modeling insect development rates: A literature review and application of a biophysical model. Annals Entomol. Soc. Am., 77: 208-225.

Webb, G.F., 1985. Theory of Nonlinear Age-Dependent Population Dynamics. 1st Edn., Marcel Dekker, New York, ISBN-10: 0824772903, pp: 294.

Werner, P.A., 1975. Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). Oecologia, 20: 197-201. DOI: 10.1007/BF00347472

Wikan, A. and A. Eide, 2004. An analysis of a nonlinear stage-structured cannibalism model with application to the northeast Arctic cod stock. Bull. Math. Biol., 66: 1685-1704. DOI: 10.1016/j.bulm.2004.03.005

Wikan, A. and E. Mjolhus, 1995. Periodicity of 4 in age-structured population models with density dependence. J. Theor. Biol., 173: 109-119. DOI: 10.1006/jtbi.1995.0048

Wikan, A. and E. Mjolhus, 1996. Overcompensatory recruitment and generation delay in discrete age-structured population models. J. Math. Biol., 35: 195-239. DOI: 10.1007/s002850050050

Wikan, A., 1997. Dynamic consequences of reproductive delay in Leslie matrix models with nonlinear survival probabilities. Math. Biosci., 146: 37-62. DOI: 10.1016/S0025-5564(97)00074-6

Wikan, A., 2012a. Age or stage structure? Bull. Math. Biol., 74: 1354-1378. DOI: 10.1007/s11538-012-9715-3

Wikan, A., 2012b. On nonlinear age- and stage-structured population models. J. Math. Stat., 8: 311-322. DOI: 10.3844/jmssp.2012.311.322