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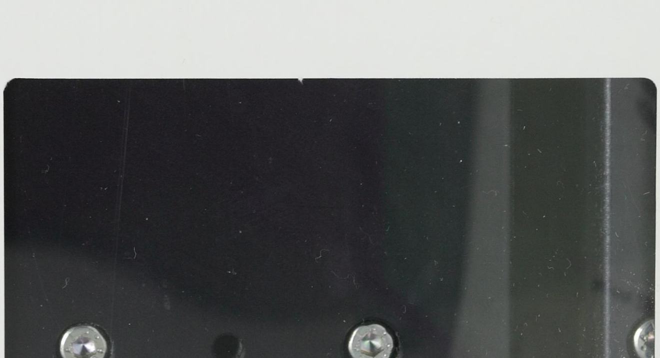

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<table>
<tr><td colspan="2">Tittel

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37</td></tr>
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</table>

Sammendrag/Abstract

The dynamical consequences of reproductive delay in Leslie Matrix models with nonlinear survival probabilities p are analysed. Considering two-age classes, we prove rigorously for a wide range of p functions that outside the strongly resonant cases, the transfer from stability to instability goes through a supercritical Hopf bifurcation and moreover that the nonlinear development has a strong resemblance of 3- or 4-cycles, either exact or approximate. In three-age class models we show that the tendency towards 4-periodical dynamics is even more pronounced, a qualitative finding which gradually disappears as we turn to the higher dimensional cases. We also prove that for models of any dimension $n > 1$ there are regions in parameter space where the equilibrium is unstable at its creation and we demonstrate that the dynamics in this age class extinguishing case is $2^k \cdot n$ cyclic.

Stikkord	population dynamics - density dependence - bifurcation - chaos	Key Words
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1 Introduction

In several papers on population dynamics the effect upon stability due to different delay mechanisms has been explored. Turning to the continuous case, the basic model for such considerations, in absence of migration, is the van Foerster equation

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(\cdot)n \tag{1}$$

$$n(0,t) = \int_0^\infty b(\cdot)n(t,a)da \tag{2}$$

See Caswell [7] or Murray [26], where $n(t,a)$ is the age density function, $\mu(\cdot)$ and $b(\cdot)$ are the density dependent death and birth rates respectively. For example, Cushing [14] used this approach to study the impact on stability in age-structured populations caused by varying gestation periods and age-specific reproductive rates, McNair [25] considered the impact of varying the length of the juvenile period, Bence and Nisbet [3] showed the importance of time delays in open systems and De Roos et al. [17] extended the model (1), (2) by also incorporating size structure in their Daphnia study.

By a direct forward difference discretization of (1),(2), see for example Guckenheimer et al. [20] or Caswell [7], we obtain the discrete analogue

$$\mathrm{x} \longrightarrow A\mathrm{x} \tag{3}$$

where $\mathrm{x} = (x_1, .., x_n)^T$ is a n-dimensional population vector and A the Leslie matrix

$$\begin{pmatrix} f_1 & \cdots & & & f_n \\ p_1 & 0 & & & 0 \\ 0 & \ddots & & & \vdots \\ \vdots & & \ddots & & \\ 0 & \cdots & 0 & p_{n-1} & 0 \end{pmatrix} \tag{4}$$

with fecundity elements f_i and year-to-year survival probabilities p_i. Ergodic properties of the map (3) in case of density independent matrix elements may be found in Cohen

[9]. In the nonlinear case the ergodic results obtained by Cushing [15,16] and Crowe [10] provide a basic setting to consider stability and bifurcation in matrix models.

When studying the system (3),(4) the usual approach has been to include density effects in the fecundity terms and not in the year-to-year survival probabilities. Especially in fishery models this has often been motivated by the fundamental assumption that most density effects occur within the first year of life, cf. Levin and Goodyear [23], Levin [22], Fisher and Goh [18], Bergh and Getz [5], Silva and Hallam [28,29], Wikan and Mjølhus [36], and again turning to delay considerations, it is in general demonstrated that a delay in reproduction (or generation delay, a term introduced in [23]) acts destabilizing. Similar conclusions have also been established in corresponding difference delay equation models of the form

$$x_{t+1} = x_t f(x_{t-T}) \tag{5}$$

See for example Levin and May [24], Clark [8], Botsford [6], Le Page and Curry [21]. For related models, cf. Nisbet and Onyiah [27], Tuljapurkar et al. [33].

Returning to the matrix model (3),(4), following Wikan and Mjølhus [35] and Wikan [34], the dynamical consequences of incorporating density dependence in the year-to-year survival probabilities instead of the fecundities are much less explored although it should be a fairly plausible assumption for may species. This brings us to the purpose of this paper, namely the role of reproductive delay in Leslie matrix models with nonlinear survival elements, and we shall ultimate impose the restriction $f_i = 0,\ i < n,\ f_n \neq 0$ in (4). In many respects this is the same strategy as in [18], but we shall not focus on global stability problems investigated in terms of Liapunov functions, instead our main concern is the description of the qualitative behaviour of the population in unstable and chaotic parameter regions, a strategy which is adopted by only a few of the papers quoted above.

Among our results are:

1. In case of two-age classes, using normal form calculations, see Guckenheimer and Holmes [19], we prove rigorously for large classes of nonlinear survival probability

[3]. In the nonlinear case the ergodic results obtained by Cushing [15,16] and Crowe [10] provide a basic setting to consider stability and bifurcation in matrix models.

When studying the system (3)-(4) the usual approach has been to include density effects in the fecundity terms and not in the year-to-year survival probabilities. Especially in fishery models this has often been motivated by the fundamental assumption that most density effects occur within the first year of life, cf. Levin and Goodyear [23], Levin [22], Fisher and Goh [18], Bergh and Getz [5], Silva and Hallam [33,34], Wikan and Mjølhus [35], and again turning to delay considerations, it is in general demonstrated that a delay in reproduction (or generation delay, a term introduced in [35]) acts destabilizing. Similar conclusions have also been established in corresponding difference delay equations of the form

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Returning to the matrix model (3)-(4), following Wikan and Mjølhus [35] and Wikan [34], the dynamical consequences of incorporating density dependence in the year-to-year survival probabilities instead of the fecundities are much less explored although it should be a fairly plausible assumption for many species. This brings us to the purpose of this paper, namely the role of reproductive delay in Leslie matrix models with nonlinear survival elements, and we shall ultimately impose the restriction $f_i = 0$, $i = 0, \ldots, T-1$ in (4). In many respects this is the same strategy as in [35], but we shall not focus on global stability problems investigated in terms of Liapunov functions. Instead our main concern is the description of the qualitative behaviour of the population in unstable and chaotic parameter regions, a strategy which is adopted by only a few of the papers quoted above.

Among our results are:

1. In case of teenage classes using classical ... (see ... and ...) we show ... for large classes of nonlinear survival probabilities

functions that the fixed point of (3),(4) in the generic case undergoes a supercritical Hopf bifurcation at instability threshold. We also show that there exist parameter values where the normal form also contains additional strong resonant terms, cf. Arnold [2], which in turn implies that there are large parameter regions where the dynamics beyond the bifurcation point has a strong resemblance of 3- or 4-cycles, either exact or approximate, a qualitative finding which takes over to the chaotic regime as well. This extends the results obtained in [34] and [35].

2. When $n = 3$ the tendency towards 4-periodically dynamics is even more pronounced.

3. We also demonstrate that for any $n > 1$ there exists a region in parameter space where the fixed point is unstable at its creation. This is valid both for overcompensatory and compensatory survival probabilities, hence we support the result obtained by [28] that the tendency for compensatory models to be stable does not always occur. The dynamics which is found in this part of parameter space is stable cycles of period $2^k \cdot n$, cf. Cull and Vogt [11,12,13] and especially Allen [1].

Finally we should stress that the analysis in this paper is pure theoretical and not related to any concrete species. Nevertheless, it is tempting to suggest that our results may apply to small rodent populations. For such species there are several examples of cycles comparable to our findings (Stenseth and Ims [32]) and there is a lack of pure density dependent models in the literature (Stenseth and Antonsen [30,31]).

The plan of the paper is as follows: In section 2 we present the model and describe equilibria and stability. In section 3 and 4 we present a detailed analysis of the dynamics in 2 and 3 dimensions respectively. In section 5 we extend results to higher dimensions.

2 Equilibria and Stability

Consider the map $f : \mathbb{R}^n \to \mathbb{R}^n$

$$\mathbf{x} \longrightarrow A\mathbf{x} \tag{6}$$

where $\mathbf{x}$ is a n-dimensional population vector and A a $n \times n$ Leslie matrix of the form

$$A = \begin{pmatrix} 0 & \cdots & & 0 & F_n \\ p & 0 & \cdots & & 0 \\ 0 & p & & & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & \cdots & 0 & p & 0 \end{pmatrix} \tag{7}$$

Here the capital F indicates density independent fecundity and we assume the same density-dependent survival probability $p = p(y)$ between any two-age classes where

$$y = \sum_{i=1}^{n} \alpha_i x_i \tag{8}$$

Further we require $p'(y) < 0$, thus except for depensatory effect [7] a rather general situation is under consideration.

Assuming $p(0) > F_n^{-\frac{1}{n-1}}$, at equilibrium

$$y^* = p^{-1}\left(F_n^{-\frac{1}{n-1}}\right) \tag{9}$$

and the unique nontrivial fixed point of (6) is given by

$$(x_1^*, x_2^*, ..., x_n^*) = \left(\frac{y^*}{K},\ p(y^*)\frac{y^*}{K},\ ...,\ p^{n-1}(y^*)\frac{y^*}{K}\right) \tag{10}$$

where $K = \sum_{i=1}^{n} \alpha_i p^{i-1}(y^*)$ (Silva and Hallam [29]). Using standard linearization techniques (see [7] or [23]) the eigenvalue equation may after some algebra be cast in the form

$$\lambda^n + \left(\sum_{i=2}^{n} \alpha_i p^{i-2}\right)\phi\lambda^{n-1} + \left(\sum_{\substack{i=1 \\ i\neq 2}}^{n} \alpha_i p^{i-2}\right)\phi\lambda^{n-2}$$
$$+ \left(\sum_{\substack{i=1 \\ i\neq 3}}^{n} \alpha_i p^{i-2}\right)\phi\lambda^{n-3} + \cdots + \left(\sum_{i=1}^{n-1} \alpha_i p^{i-2}\right)\phi = 1 \tag{11}$$

where the (positive!) parameter ϕ which will be our bifurcation parameter, is defined as

$$\phi = \phi(y^*) = -p'(y^*)\frac{y^*}{K} \tag{12}$$

The fixed point is locally stable as long as the spectral radius of (11) is less than unity.

3 Two-Age Classes

Let $n = 2$ in (6). Then we are left with the map

$$f : \mathbb{R}^2 \longrightarrow \mathbb{R}^2 \qquad (x_1, x_2) \longrightarrow (F_2 x_2, p(y)x_1) \tag{13}$$

and (11) reduces to

$$\lambda^2 + \alpha_2\phi\lambda + \alpha_1 F_2 \phi - 1 = 0 \tag{14}$$

By applying the Jury criteria [26] the conditions for (x_1^*, x_2^*) to be locally stable are easily found to be

$$\phi(\alpha_1 F_2 + \alpha_2) > 0 \tag{15a}$$

$$\phi(\alpha_1 F_2 - \alpha_2) > 0 \tag{15b}$$

$$2 - \alpha_1 F_2 \phi > 0 \tag{15c}$$

First we consider the case $F_2 < \alpha_2/\alpha_1$. Then from (15b) there will be no stable equilibrium. Since (15b) is associated with the possibility of (x_1^*, x_2^*) to undergo a flip bifurcation it is natural to search for (stable) cycles of order 2. Hence, consider the second iterate:

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix}_{t+2} = \begin{pmatrix} F_2 p(y_t) & 0 \\ 0 & F_2 p(y_{t+1}) \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}_t \tag{16}$$

Clearly, one possibility is $F_2 p(y_t) = F_2 p(y_{t+1}) = 1$ which in turn implies $y_t = y_{t+1} = y^* = p^{-1}(1/F_2)$. Thus the 2-cycle is the trivial one where the unstable equilibrium is the only point in the cycle.

Another possibility is to assume a 2-cycle of the form $(\hat{x}_1, \hat{x}_2) = (A, 0)$ or $(0, B)$. Then from (16) we find that the system oscillates between the points

$$\left(\frac{1}{\alpha_1} p^{-1}(1/F_2), 0\right), \left(0, \frac{1}{\alpha_1 F_2} p^{-1}(1/F_2)\right) \tag{17}$$

In order to investigate stability we have computed the Jacobian of (16), used (17), and found the real eigenvalues to be

$$\mu_1 = 1 + F_2 p^{-1}(1/F_2) p'(y_t) \tag{18a}$$

$$\mu_2 = F_2 p(y_{t+1}) \tag{18b}$$

Since $F_2 p(y_t) = 1$, $y_{t+1} = (\alpha_2/\alpha_1 F_2) y_t > y_t \Rightarrow p(y_{t+1}) < p(y_t) = 1/F_2$. Consequently, $0 < \mu_2 < 1$ and for F_2 sufficiently close to 1, $|\mu_1| < 1$. Hence (17) is a stable 2-cycle for F_2 small.

It is further clear from (18a) that in the case $\alpha_2 \gg \alpha_1$, an increase of F_2 will eventually lead to a flip bifurcation creating a cycle of period 4. We emphasize that the form of the 4-cycle as well as the form of successive cycles of period 2^k, $k > 2$, which is the outcome of a further enlargement of F_2, has the same structure as the 2-cycle, a qualitative result which also takes over to the chaotic regime. Thus we have demonstrated numerically that the dynamics goes to the axes whenever $F_2 < \alpha_2/\alpha_1$.

Since we shall meet cycles like (17) also in models with more age classes it is convenient at this stage to define (17) as the 2-age class extinguishing cycle, and more generally, the cycle $(A, 0, ..., 0), (0, B, 0, ..., 0), ..., (0, ..., 0, N)$ in a model with n-age classes as the n-age class extinguishing cycle.

—ooo—

Next, consider the case $F_2 > \alpha_2/\alpha_1$. Then from (15c), $\phi(y^*) < 2/\alpha_1 F_2$ ensures that (x_1^*, x_2^*) is locally stable. Thus the only way for the nontrivial fixed point to become unstable is through a Hopf bifurcation at the threshold

$$\phi(y^*) = \frac{2}{\alpha_1 F_2} \tag{19}$$

where the corresponding modulus 1 solutions of the eigenvalue equation (14) are

$$\lambda = -\frac{\alpha_2}{\alpha_1 F_2} \pm \frac{1}{\alpha_1 F_2}\sqrt{(\alpha_1 F_2)^2 - \alpha_2^2}\, i \tag{20}$$

We shall now prove that outside the strongly resonant cases $F_2 = 2\alpha_2/\alpha_1$ or $\alpha_2 = 0$, the Hopf bifurcation is of the supercritical type (i.e. that there exists a stable attracting invariant curve surrounding (x_1^*, x_2^*) for $\phi > 2/\alpha_1 F_2$, $|\phi - \phi_c|$ small where ϕ_c is the ϕ value defined in (19)) for a large number of survival probability functions $p(y)$. The results will be stated as theorems, proofs of which may be found in the appendix.

Theorem 1.

Consider the map $f : \mathbb{R}^2 \to \mathbb{R}^2$

$$(x_1, x_2) \longrightarrow \left(F_2 x_2,\ P_1(1-\gamma y)^{1/\gamma} x_1\right) \tag{21}$$

under the restrictions $F_2 \neq 2\alpha_2/\alpha_1$, $\alpha_2 \neq 0$.

Assume $F_2 > \alpha_2/\alpha_1$. Then, for $\gamma > -\alpha_1 F_2/2(\alpha_1 F_2 + \alpha_2)$ the fixed point (x_1^*, x_2^*) of (21) will undergo a supercritical Hopf bifurcation at the threshold (19).

Theorem 2.

Consider the map $f : \mathbb{R}^2 \to \mathbb{R}^2$

$$(x_1, x_2) \longrightarrow \left(F_2 x_2,\ \frac{P_1}{1+y^\alpha} x_1\right) \tag{22}$$

under the restrictions $F_2 \neq 2\alpha_2/\alpha_1$, $\alpha_2 \neq 0$.

Assume $F_2 > \alpha_2/\alpha_1$. Then, for $\alpha > 2$ the fixed point (x_1^*, x_2^*) of (22) will undergo a supercritical Hopf bifurcation at the threshold (19).

Note that the strongly resonant cases $F_2 = 2\alpha_2/\alpha_1$ or $\alpha_2 = 0$ correspond to eigenvalues of third or fourth root of unity and that these cases require special treatment, see Arnold [2]. The survival probability defined in (21) is sometimes (especially in the fishery literature) referred to as a Deriso–Schnute relation [5,33], and the probability function in (22) is called a Shepard relation [5]. The classical overcompensatory Ricker relation is contained in (21) ($\gamma \to 0$), and the compensatory Beverton and Holt relation is contained in both (21) and (22) ($\gamma = -1$, $\alpha = 1$).

Our next goal is to discuss the dynamics beyond the bifurcation threshold, and in doing so we shall frequently refer to the survival probability functions in theorems 1 and 2.

We start with the interval $0 < \alpha_2 \leq \alpha_1$. Then from the theorems we know that (x_1^*, x_2^*) will undergo a supercritical Hopf bifurcation and by following Guckenheimer and Holmes [19], the dynamics on the invariant curve may be described by the rotation map

$$\theta \longrightarrow \theta + c - \frac{bd}{a}\mu \tag{23}$$

where b and $c = \arg\lambda$ give asymptotic information on rotation numbers, μ = bifurcation parameter, a is defined in appendix A and $d = d/d\mu|(\lambda(0))|$.

According to Wikan [34], see also the relations (A.9),(A.11) in appendix A, in case of $\gamma \leq 0$, $2 < \alpha \leq 3$ (which is the most interesting parameter intervals for the functions in theorem 1 and 2), F_1 is a large number at the bifurcation. Consequently, from (20), $\arg\lambda \approx \pi/2$, thus on the invariant curve, close to the bifurcation, the rotation number $\sigma \approx 1/4$. Hence the dynamics in the interval $0 < \alpha_2 \leq \alpha_1$, must be qualitative similar to the special case $\alpha_1 = \alpha_2$ which was extensively studied in [34]. There it was found large fecundity intervals where the dynamics was 4-periodical, either exact or approximate. In Figure 1 we show an exact 4-periodical orbit and in Figure 2 we demonstrate the 4-periodical structure in the chaotic regime. For further reading, cf. [34] and [35].

Theorem 1 and 2 do not apply in the strongly resonant case $\alpha_2 = 0$, but from our analysis above it is nevertheless natural to expect some kind of 4-periodical behaviour. Indeed, numerical simulations suggest that as the fixed point (x_1^*, x_2^*) fails to be stable, a stable 4-cycle on the form

$$(A, p(C)C),\ (A, p(A)A)\ (C, p(A)A)\ (C, p(C)C) \tag{24}$$

is created. We shall now demonstrate that for specific choices of $p(y)$, A and C may actually be computed. To this end, following the method of Levin [22] with $p(y) = P_1\exp(-y)$, we first observe that (13) implies

$$\begin{aligned} A &= F_2 P_1 e^{-\alpha_1 C} C \\ C &= F_2 P_1 e^{-\alpha_1 A} A \end{aligned} \tag{25}$$

Now define $x = A/C$. Then from (25)

$$F_2 = h(x) = \frac{1}{P_1} x^{(x+1)/(x-1)} \tag{26}$$

The graph of $h(x)$ is shown in Figure 3 and once x is found it is easy to compute A and C from (25).

where b and $c = \arg\lambda$ give asymptotic information on rotation numbers, γ = bifurcation parameter, a is defined in appendix A and $d = d(\arg(\lambda, 0))$.

According to Wiles [24], see also the relations (A.9)–(A.11) in appendix A, in case of $\gamma \leq 0$, $2 < \alpha \leq 3$ (which is the most interesting parameter intervals for the functions in theorem 1 and 2), F_2 is a large number at the bifurcation. Consequently, from (20), $\arg\lambda \approx \pi/2$, thus on the invariant curve, close to the bifurcation, the rotation number $\sigma \approx 1/4$. Hence the dynamics in the interval $2 < \alpha_1 \leq \alpha_2$ must be qualitative similar to the special case $\alpha_1 = \alpha_2$ which was extensively studied in [9]. There it was found large fecundity intervals where the dynamics was 4-periodical, either exact or approximate. In Figure 1 we show an exact 4-periodical orbit and in Figure 2 we demonstrate the 4-periodical structure in the chaotic regime. For further readings, cf. [24] and [6].

Theorem 1 and 2 do not apply in the strongly resonant case $\alpha_1 = 0$, but from our analysis above it is nevertheless natural to expect some kind of 4-periodical behaviour. Indeed, numerical simulations suggest that as the fixed point (x^*, x^*) fails to be stable, a stable 4-cycle on the form

$$(A, C)(C, B)(B, C)(C, A) \qquad (24)$$

is created. We shall now demonstrate that for specific choices of x_0, A, B and C may actually be computed. To this end, following the method of Levin [12] with $\exp(\mu) = F_1\exp(-\gamma)$, we first observe that (11) implies

$$A = F_1 C e^{-\mu C}$$

(25)

$$C = F_2 e^{-\mu A} A$$

Now define $z = A/C$. Then from (25)

$$C = B(z) = \frac{1}{z} e^{(\ln z)/(\mu z)} \qquad (26)$$

The graph of $B(z)$ is shown in Figure 3 and once z is found it is easy to compute A and C from (25).

Finally, $x = 1$ implies $A = C$ which means that the 4-cycle degenerates to only one point in this case. Further by L'hopital's rule:

$$\lim_{x \to 1} h(x) = \frac{1}{P_1} e^2 \qquad \lim_{x \to 1} h'(x) = 0 \tag{27}$$

where $(1/P_1)e^2$ is recognized as the F_2 value where (x_1^*, x_2^*) goes unstable. Thus we have shown that the stable small amplitude 4-cycle evolves directly from the point where (x_1^*, x_2^*) bifurcates. Although the bifurcation described here clearly should not be called supercritical it is definitely of local nature in contrast to the strongly resonant cases discussed in [20], [22] and [36].

Finally, let us turn to the qualitative behaviour when $\alpha_1 < \alpha_2$. We deal separately with the cases

$$\text{(A)} \quad \alpha_2/\alpha_1 = d \quad d > 1 \quad d \text{ small}$$

$$\text{(B)} \quad \alpha_2/\alpha_1 = d \quad d > 1 \quad d \text{ large}$$

Considering (A), Eq. (20) implies that the difference $\arg \lambda - (\pi/2)$ becomes large, thus the 4-periodicity vanishes. Consequently, in accordance with simulation results, quasiperiodic orbits is the only outcome in the unstable parameter regions. The route to chaos also differs from the previous case. For sufficiently large values of F_2 we first experience that the invariant curve becomes kinked and then it breaks up into a number of separate clouds, a situation somewhat akin to the description of the Dubois and Bergé model in [7]. An example of the chaotic attractor is given in Figure 4.

Whenever d is large, (B), at bifurcation, the difference $F_2 - 2\alpha_2/\alpha_1$ becomes small, thus we are close to the second strong resonance $\lambda^3 = 1$. From [20], [22] and [36] we know that this opens for multiple attractors in a certain interval $F_s \leq F_2 \leq F_k$. Indeed, if $F_2 = F_s$, we have by adopting the same technique as in [36] verified numerically for selected values of different survival probabilities, that the third iterate $g = f \circ f \circ f$ undergoes a saddle node bifurcation, creating 3 branches of stable and 3 branches of unstable equilibria. Hence, whenever $F_s \leq F_2 < F_c$ where F_c is the F_2 value implicitly defined in (19), the stable large amplitude 3-cycle and (x_1^*, x_2^*) coexists. Further from

Finally, $x = 1$ implies $A = C$ which means that the 4-cycle degenerates to only one point in this case. Further by L'Hopital's rule

$$\lim_{x \to 1} h(x) = \frac{1}{P_1} [illegible] \lim_{x \to 1} [illegible] \qquad (2[illegible])$$

where $(1/P_1)e^{[illegible]}$ is recognised as the P_1 value where (x_1^*, x_2^*) goes unstable. Thus we have shown that the stable small amplitude 4-cycle evolves directly from the point where (x_1^*, x_2^*) bifurcates. Although the bifurcation described here clearly should not be called supercritical it is definitely of local nature in contrast to the strongly resonant cases discussed in [20], [22] and [30].

Finally, let us turn to the qualitative behaviour when $\sigma_1 < \sigma_2$. We deal separately with the cases

(A) $\sigma_2/\sigma_1 = d$, $d > 1$, d small

(B) $\sigma_2/\sigma_1 = d$, $d > 1$, d large.

Considering (A), Eq. (20) implies that the difference $\arg \lambda - 2\pi/2$ becomes large, thus the 4-periodicity vanishes. Consequently, in accordance with simulation results, quasiperiodic orbits is the only outcome in the unstable parameter regions. The route to chaos also differs from the previous case. For sufficiently large values of P_1 we first experience that the invariant curve becomes kinked and then it breaks up into a number of separate clouds, a situation somewhat akin to the description of the Aronson and Bruce model in [7]. An example of the chaotic attractor is given in Figure 4.

Whenever d is large (B), at bifurcation, the difference $P_1 - 2\sigma_1/\sigma_2$ becomes small, thus we are close to the second strong resonance $\lambda^2 = 1$. From [20], [22] and [30] we know that this opens for multiple attractors in a certain interval $P_b \leq P_1 \leq P_c$. Indeed, if $P_b = P_c$, we have by adopting the same technique as in [30] verified numerically for selected values of different survival probabilities, that the third iterate $q = 1 \circ f \circ f$ undergoes a saddle node bifurcation, creating 3 branches of stable and 3 branches of unstable equilibria. Hence whenever $P_b < P_1 < P_c$ where P_c is the P_1 value implicitly defined in (19), the stable large amplitude 3-cycle and (x_1^*, x_2^*) coexists. Further from theorem 1 and 2 it must also exist an interval $F_c \leq F_2 \leq F_k$ where the coexistence is between the 3-cycle and the invariant curve emerged from (x_1^*, x_2^*). This is exemplified in Figure 5. At $F_2 = F_k$ there is a global bifurcation which makes the stable invariant curve vanish, leaving the stable 3-cycle as the only stable attractor. The bifurcation occurs as the 3 branches of unstable equilibria of g "hit" the invariant curve. Numerically we have shown this by finding the point z on the invariant curve where x takes its maximum value and verified that $g(z) = z$.

The route to chaos is not through period doublings, as in the above quoted papers. Rather, by computing the eigenvalues of the Jacobian of g, we have found numerical evidence that there exists a critical $F_2 > F_k$ where the fixed points of g to through a Hopf bifurcation establishing 3 invariant curves which are visited once every third iteration. This is exemplified in Figure 6. Hence, in sharp contrast to the case $\alpha_2 \leq \alpha_1$, we have demonstrated that $\alpha_2 \gg \alpha_1$ leads to a qualitative finding of 3-cycles, either exact or approximate in a large parameter region.

4 Three-Age Classes

By an ultimate application of the Jury criteria, see Murray [26], p. 704, on the eigenvalue equation (11) ($n = 3$), it is clear that the fixed point (x_1^*, x_2^*, x_3^*) will be stable whenever

$$\phi(y^*) < \frac{1}{\alpha_2} \tag{28a}$$

$$0 < \phi(y^*) < \frac{2p}{\alpha_1 + p\alpha_2} \tag{28b}$$

$$(\alpha_1 - p^2\alpha_3)\phi(y^*) < \frac{p(\alpha_1 + p\alpha_2 - 2p^2\alpha_3)}{\alpha_1 + p\alpha_2} \tag{28c}$$

($p = p(y^*)$). First assume $\alpha_1 + p\alpha_2 = p^2\alpha_3$. Then (28a),(28c) may be written as

$$\phi(y^*) < \frac{p}{p^2\alpha_3 - \alpha_1}, \qquad \phi(y^*) > \frac{p}{p^2\alpha_3 - \alpha_1}$$

respectively. Thus the equilibrium is unstable at its creation in this case, a result which easily may be extended to the parameter region

$$\alpha_1 + p\alpha_2 \leq p^2\alpha_3 \tag{29}$$

Assuming (29), in case of F_3 small, the only stable attractor found through numerical experiments, is the age class extinguishing cycle

$$(A, 0, 0),\ (0, B, 0),\ (0, 0, C) \tag{30}$$

but in contrast to the two-age class study, A, B and C must be computed by means of numerical methods. For the possibility of period doubling and chaotic dynamics, we have found the same qualitative behaviour as in the two-dimensional analysis.

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Next, consider the parameter region

$$\alpha_1 + p\alpha_2 > p^2\alpha_3 \tag{31}$$

Then there exists a stable fixed point for $\phi(y^*)$ sufficiently small. If $\alpha_1 \ll \alpha_2$, (x_1^*, x_2^*, x_3^*) undergoes a (supercritical) flip bifurcation at the threshold

$$\phi(y^*) = \frac{1}{\alpha_2} \tag{32a}$$

otherwise, the fixed point goes through a (supercritical) Hopf at the threshold

$$\phi(y^*) = \frac{p(\alpha_1 + p\alpha_2 - 2p^2\alpha_3)}{(\alpha_1 + p\alpha_2)(\alpha_1 - p^2\alpha_3)} \tag{32b}$$

Considering the latter situation first, the complex modulus 1 solutions of the eigenvalue equations may be expressed as

$$\lambda_{1,2} = -\frac{p^2\alpha_3}{\alpha_1 + p\alpha_2} \pm \sqrt{1 - \frac{p^4\alpha_3^2}{(\alpha_1 + p\alpha_2)^2}}\, i \tag{33}$$

Assuming $\alpha_3 \neq 0$ (the strongly resonant case), it is clear from (33) that there exists a large parameter region where $\lambda_{1,2}$ are located close to the imaginary axis, thus there is also here a strong indication of 4-periodical dynamics. In fact, several numerical simulations suggest that the 4-periodicity is even more pronounced here than in the two-age class model. For example, it is possible to find frequency locking into an exact 4-periodic orbit also in the case $\alpha_1 < \alpha_2 < \alpha_3$. This is shown in Figure 7.

Unlike the corresponding two-age class case, the route to chaos does not go through period doublings, cf. [35]. Here we have shown numerically by computing the Jacobian of the fourth iterated map $h = f \circ f \circ f \circ f$ that h undergoes a Hopf bifurcation as the exact 4-cycle fails to be stable. This extends the result in the simpler model studied by Wikan [34]. Consequently, there exists a region in parameter space where the stable attractor consists of 4 disjoint "circles" which are visited once in each "topological" 4-cycle. This is exemplified in Figure 8.

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If $\alpha_3 = 0$, $\lambda = \pm i$ at bifurcation threshold. Numerically, we have verified that as (x_1^*, x_2^*, x_3^*) fails to be stable, an exact small amplitude 4-periodical orbit is introduced. Hence, the qualitative behaviour here is in many respects similar to what was found in the corresponding strongly resonant case in the previous section. However, a computation of the points in the cycle is out of reach.

Finally, in case of α_2 large, the instability threshold is given by (32a). Thus there exists a parameter region where a 2-cycle is the only stable attractor. However, this region is very small since the composite $g = f \circ f$ almost immediately undergoes a Hopf bifurcation giving birth to 2 disjoint "circles". This is shown in Figure 9.

Hence, to summarize: Compared with the two-age class study, the tendency towards 4-periodical dynamics is even more pronounced here in 3 dimensions. The main difference is the behaviour in case of large values of α_2. In the two-age class model we found 3-periodical dynamics either exact or approximate. Here the dynamics has a strong resemblance of 2 cycles.

5 Discussion

In chapter 3 and 4 we showed that there exist parameter regions where the equilibrium is unstable at its creation. Instead we found the stable age class extinguishing 2-cycle (17) in case of $n = 2$ and the corresponding cycle $(A, 0, 0)$, $(0, B, 0)$, $(0, 0, C)$ in case of $n = 3$. We shall now extend these results.

Unlike the corresponding two-age class case, the route to chaos does not go through period doublings, cf. [33]. Here we have shown numerically by computing the Jacobian of the fourth iterated map $h = f \circ f \circ f \circ f$ that h undergoes a Hopf bifurcation as the exact 4-cycle fails to be stable. This extends the result in the simpler model studied by Wikan [34]. Consequently, there exists a region in parameter space where the stable attractor consists of 4 disjoint "circles" which are visited once in each "generation" 4-cycle. This is exemplified in Figure 8.

If $\alpha_1 = 0$, $\lambda = \lambda_H$ at bifurcation threshold. Numerically, we have verified that as (x_1^*, x_2^*, x_3^*) fails to be stable, an exact small amplitude 4-periodical orbit is introduced. Hence, the qualitative behaviour here is in many respects similar to what was found in the corresponding strongly seasonal case in the previous section. However, a computation of the points in the cycle is out of reach.

Finally, in case of α_2 large, the instability threshold is given by (22a). Thus there exists a parameter region where a 2-cycle is the only stable attractor. However, this region is very small since the composite map $f \circ f$ almost immediately undergoes a Hopf bifurcation giving birth to 2 disjoint "circles". This is shown in Figure 9.

Hence, to summarize: Compared with the two-age class study, the tendency towards periodical dynamics is even more pronounced here in 4 dimensions. The main difference is the behaviour in case of large values of α_2. In the two-age class model we found 2-periodical dynamics either exact or approximate. Here the dynamics has a strong resemblance of 2 cycles

5 Discussion

In chapter 3 and 4 we showed that there exist parameter regions where the equilibrium is unstable "at its creation". Instead we found the stable age class extinguishing 2-cycle (A, 0) in case of $n = 2$ and the corresponding cycle (A, 0, 0), (0, B, 0), (0, 0, C) in case of $n = 3$. We shall now extend these results.

First, assume that n is even. Then by applying the Jury criterion $(-1)P(\lambda = -1) > 0$, where P is the eigenvalue polynomial defined in (11), it is straightforward to show that $(x_1^*, ..., x_n^*)$ always is unstable at its creation in the region

$$\sum_{j=1}^{n-1} (-1)^{j-1} p^{j-2} \alpha_j \leq p^{m-2} \alpha_n \tag{34}$$

Assuming $n = 4$, Eq. (34) does not necessarily imply that the age class extinguishing 4-cycle $(A, 0, 0, 0), ..., (0, 0, 0, D)$ is the only stable attractor in case of small F_4 values. Indeed a 4-cycle of the form $(A, B, 0, 0), ..., (0, 0, C, D)$ is definitely also a possibility, but this cycle as well as the other possibilities have all by means of numerical experiments been found to be unstable, leaving the age class extinguishing cycle as the only stable attractor. For a more thorough discussion of such cycles we refer to [36] where density dependent fecundity and density independent survival terms are considered.

Next, assume n odd, Clearly $\phi = 0$ implies that all solutions $\lambda_0 = e^{i\varphi}$, $\varphi = 2\pi k/n$, $k = 0, 1, ..., n-1$ of (11) are located on the unit circle. Further, in case of $\phi > 0$, ϕ small, assume the expansion

$$\lambda = \lambda_0 + \phi \lambda_1 + \cdots$$

This yields

$$\lambda_1 = -\frac{1}{n} \left\{ \sum_{j=2}^{n} \alpha_j p^{j-2} + \left(\sum_{\substack{j=1 \\ j \neq 2}}^{n} \alpha_j p^{j-2} \right) \lambda_0^{-1} + \cdots + \left(\sum_{j=1}^{n-1} \alpha_j p^{j-1} \right) \lambda_0^{-(n-1)} \right\}$$

Now, regarding the complex numbers λ_0, λ_1 as two-dimensional vectors $\vec{\lambda_0}$ and $\vec{\lambda_1}$, the sign of the product

$$\vec{\lambda_0} \cdot \vec{\lambda_1} = \frac{1}{2}(\lambda_0 \lambda_1^* + \lambda_0^* \lambda_1) = -\frac{1}{n} \sum_{j=1}^{n} \left(\sum_{\substack{k=1 \\ k \neq j}}^{n} \alpha_k p^{k-2} \right) \cos j\,\varphi \tag{35}$$

where * denotes complex conjugation) will decide whether an eigenvalue will leave the unit circle or not as the parameter ϕ is increased.

Now, assume (cf. (29))

$$\sum_{j=1}^{n-1} p^{j-2}\alpha_j \leq p^{n-2}\alpha_n \tag{36}$$

Our goal is to show that the right hand side of (35) is positive under the restriction (36). To this end suppose

$$\frac{p\alpha_{i+1}}{\alpha_i} = m > 1$$

Then (35) becomes

$$\begin{aligned}\vec{\lambda}_0 \cdot \vec{\lambda}_1 &= -\frac{\alpha_1}{pn}\left[2m^{n-1}\sum_{j=1}^{n}\cos j\varphi - \sum_{j=1}^{n} m^{j-1}\cos j\varphi\right] \\ &= -\frac{\alpha_1}{p}\left[0 - \frac{(\cos\varphi - m)(1-m^n)}{(1-m\cos\varphi)^2 + (m\sin\varphi)^2}\right]\end{aligned}$$

which clearly is positive. Hence, the fixed point $(x_1^*, ..., x_n^*)$ is also here unstable at its creation. Again, this does not actually prove that the age class extinguishing attractor $(A, 0, ..., 0), ...(0, ..., 0, N)$ is the only stable cycle under the restriction (36), but as in the case of n odd, such a cycle is the only one found through numerical simulations.

—ooo—

In the rest of this section we shall deal exclusively with the dynamics outside the parameter regions defined in (34) and (36).

One of our most significant results obtained from our two- and three-dimensional analyses was that there exist large parameter regions where the dynamics is 4-periodical, either exact or approximate. This is due to the fact that the eigenvalues cross the unit circle close to the imaginary axis at bifurcation. Hence, we are close to the strong resonance $\lambda = \pm i$ which occurs when $\alpha_2 = 0$, $\alpha_1 \neq 0$ in the 2-dimensional case, and $\alpha_3 = 0$, $\alpha_1, \alpha_2 \neq 0$, in the 3-dimensional case.

Motivated by this, turning to 4-age classes, it is natural to search for a possible strong resonance under the restriction $\alpha_4 = 0$, $\alpha_i \neq 0$, $i < 4$. The corresponding eigenvalue equation may now be cast in the more simple form

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0 \tag{37}$$

where the coefficients a_i, $i < 4$ may be obtained from (11). One of the Jury criteria which must be satisfied in order to ensure that $(x_1^*, ..., x_4^*)$ is locally stable, is

$$|(1-a_4^2)^2 - (a_3 - a_4 a_1)| > |(1-a_4^2)(a_2 - a_4 a_2) - (a_3 - a_4 a_1)(a_1 - a_4 a_3)| \tag{38}$$

cf. Murray [26], and by applying this on (37) we obtain $\phi < 0$ which actually excludes the possibility of a stable fixed point as well as a strong resonance.

From this we conclude that the tendency towards 4-periodical dynamics must be much less pronounced here than in the 2- and 3-dimensional cases. Further, since (38) is a Hopf criterion (it is easy to show (Jury) that the real solutions of (37) in case of $\phi > 0$, ϕ small, have modulus less than unity) the only possible dynamics in case of ϕ small is quasiperiodic orbits. This is exemplified in Figure 10.

For other values of the weight factors it is still possible to obtain a stable equilibrium. For example, if $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = \alpha$, we obtain from (38) that the fixed point is stable whenever

$$\alpha\phi(y^*) < \frac{1 + bp + 5p^2 + bp^3 - \sqrt{1 + 12p + 14p^3 + p^4 - 4p^5 + 4p^6}}{4(1 + p + p^2)} \tag{39}$$

but the real part of the corresponding modulus 1 eigenvalues at bifurcation is now positive which clearly is different from the cases $n = 2$, $n = 3$, and again there is no sign of orbits of finite period.

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To investigate the case $n > 4$ we may by assuming ϕ small use the same technique as at the beginning of this section and once again appeal to formula (35).

Now, considering 5-age classes ($n = 5$), assuming $k = 2$, (35) may be written as

$$\vec{\lambda_0} \cdot \vec{\lambda_1} = -\frac{1}{5}\left[\frac{1}{4}\left(1 - \sqrt{5}\right)\left(\frac{1}{4}\alpha_1 + p^2\alpha_4\right) + \frac{1}{4}\left(1 + \sqrt{5}\right)(\alpha_2 + p\alpha_3) - p^3\alpha_5\right] \tag{40}$$

and in case of $\alpha_i \approx \alpha_j$ and p sufficiently small, $\vec{\lambda_0} \cdot \vec{\lambda_1} > 0$. Hence, the destabilizing effect due to generation delay, cf. [23], [28], [29], [35] and [36] has now become so severe that where the coefficients $a_i, i \le 4$ may be obtained from (31). One of the Jury criteria which must be satisfied in order to ensure that $(x_1^*, ..., x_5^*)$ is locally stable is

$$|(1-a_4^2)^2 - (a_2 - a_4 a_0)^2| > |(1-a_4^2)(a_3 - a_4 a_1) - (a_2 - a_4 a_0)(a_1 - a_4 a_3)| \quad (38)$$

cf. Murray [26], and by applying this on (37) we obtain $\alpha \le 2$ which actually excludes the possibility of a stable fixed point as well as a strong resonance.

From this we conclude that the tendency towards a periodical dynamics must be much less pronounced here than in the 2- and 3-dimensional cases. Further, since (38) is a Jury criterion (it is easy to show (Jury) that the real solutions of (37) in case of $\alpha > 2$, α small, have modulus less than unity) the only possible dynamics in case of α small is quasiperiodic orbits. This is exemplified in Figure 10.

For other values of the weight factors it is still possible to obtain a stable equilibrium. For example, if $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = \alpha$, we obtain from (38) that the fixed point is stable whenever

$$\alpha\psi(\eta^*) < \frac{1 + 4\eta + 5\eta^2 + 4\eta^3 - \sqrt{1 + 12\eta + 14\eta^2 + 12\eta^3 + \eta^4}}{2\eta(1+\eta+\eta^2)} \quad (39)$$

but the real part of the corresponding modulus 1 eigenvalues at bifurcation is now positive which clearly is different from the cases $n = 2$, $n = 3$. And again there is no sign of orbits of finite period.

—ooo—

To investigate the case $n \ge 4$ we may by assuming α small use the same technique as at the beginning of this section and once again appeal to formula (30).

Now, considering 5-age classes ($n = 5$), assuming $k = 2$, (30) may be written as

$$\lambda_0 - \lambda_1 = -\frac{x}{5}\left[\frac{1}{4}\left(1 - \sqrt{5}\right)\left(\frac{1}{4}\alpha_1 + p^2\alpha_3\right) + \frac{1}{4}\left(1 + \sqrt{5}\right)(\alpha_1 + p\alpha_3) - p^2\alpha_3\right] \quad (40)$$

and in case of $\alpha_1 = \alpha_3$ and p sufficiently small, $\lambda_0 - \lambda_1 > 0$. Hence, the destabilizing effect due to generation delay, cf. [23], [25], [30], [35] and [36] has now become so severe that there is no stable equilibrium which is in contrast to the corresponding case in the 4-age class model, cf. (39). Again, we find that the dynamics is quasiperiodic in case of ϕ small.

Thus, what these findings indicate is that outside the age class extinguishing parameter regions (34),(36), orbits of finite periods, especially orbits of period 4, are restricted to two- and three-generation models. Further we have demonstrated that the parameter region which permits a stable fixed point shrinks as n is increased and finally that as n exceeds 3 the outcome is quasistationary behaviour in larger and larger parameter intervals.

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Appendix A

In this appendix we shall prove theorem 1 and theorem 2 in the main text.

First we consider the general map (13). From the main text, the eigenvalues of the linearized map at bifurcation may be expressed as

$$\lambda = -\frac{\alpha_2}{\alpha_1 F_2} \pm \frac{1}{\alpha_1 F_2} bi \tag{A.1}$$

where $b = \sqrt{(\alpha_1 F_2)^2 - \alpha_2^2}$.

Next, define the matrix

$$T = \begin{pmatrix} -\frac{\alpha_2}{\alpha_1} & -\frac{b}{\alpha_1} \\ 1 & 0 \end{pmatrix} \tag{A.2}$$

which columns are the real and imaginary parts of the eigenvectors belonging to (A.1).

Then, after expanding the second component of (13) up to third order, applying the change of coordinates $(\hat{x}_1, \hat{x}_2) = (x_1 - x_1^*,\ x_2 - x_2^*)$ (in order to translate the bifurcation to the origin) together with the transformations

$$\begin{pmatrix} \hat{x}_1 \\ \hat{x}_2 \end{pmatrix} = T \begin{pmatrix} u \\ v \end{pmatrix} \qquad \begin{pmatrix} u \\ v \end{pmatrix} = T^{-1} \begin{pmatrix} \hat{x}_1 \\ \hat{x}_2 \end{pmatrix}$$

(13) may be cast into standard form at the bifurcation as

$$\begin{pmatrix} u \\ v \end{pmatrix} \longrightarrow \begin{pmatrix} -\frac{\alpha_2}{\alpha_1 F_2} & -\frac{b}{\alpha_1 F_2} \\ \frac{b}{\alpha_1 F_2} & -\frac{\alpha_2}{\alpha_1 F_2} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} f(u,v) \\ g(u,v) \end{pmatrix} \tag{A.3}$$

where the nonlinear terms are

$$f(u,v) = -\frac{\alpha_2 b}{\alpha_1} p'(y^*)uv + \frac{b^2}{\alpha_1} Av^2 - \frac{1}{2}\frac{\alpha_2 b^2}{\alpha_1} p''(y^*)uv^2 + \frac{b^3}{\alpha_1} Bv^3$$

$$g(u,v) = \frac{\alpha_2}{b} f(u,v)$$

with

$$A = p'(y^*) - \frac{p''(y^*)}{F_2 p'(y^*)} \qquad B = \frac{1}{2}p''(y^*) - \frac{1}{3}\frac{p'''(y^*)}{F_2 p'(y^*)}$$

Following Guckenheimer and Holmes [19] (theorem 3.5.2) defining

$$\begin{aligned}
\xi_{20} &= \tfrac{1}{8}\left[(f_{uu} - f_{vv} + 2g_{uv}) + i(g_{uu} - g_{vv} - 2f_{uv})\right] \\
\xi_{11} &= \tfrac{1}{4}\left[(f_{uu} + f_{vv}) + i(g_{uu} + g_{vv})\right] \\
\xi_{02} &= \tfrac{1}{8}\left[(f_{uu} - f_{vv} - 2g_{uv}) + i(g_{uu} - g_{vv} + 2f_{uv})\right] \\
\xi_{21} &= \tfrac{1}{16}\left[(f_{uuu} + f_{uvv} + g_{uuv} + g_{vvv}) + i(g_{uuu} + g_{uvv} - f_{uuv} - f_{vvv})\right]
\end{aligned} \tag{A.4}$$

the bifurcation will be of the supercritical type whenever

$$\frac{d}{d\phi}|\lambda(\phi(y^*)| > 0 \tag{A.5}$$

and that the stability coefficient

$$a = -\mathrm{Re}\left\{\frac{(1-2\lambda)\bar{\lambda}^2}{1-\lambda}\xi_{11}\xi_{20}\right\} - \frac{1}{2}|\xi_{11}|^2 - |\xi_{02}|^2 + \mathrm{Re}(\bar{\lambda}\xi_{21}) \tag{A.6}$$

in the normal form of (A.3) is negative. Clearly, from (14) and (19):

$$\frac{d}{d\phi}|\lambda(\phi(y^*))| = \frac{1}{2}\alpha_1 F_2 > 0$$

Hence, the eigenvalues leave the unit circle at bifurcation.

Further, from (A.3), (A.4) may (at bifurcation) be expressed as

$$\begin{aligned}
\xi_{20} &= -\frac{1}{4\alpha_1}\left[(b^2 A + \alpha_2^2 p') + i\alpha_2 b(A - p')\right] \\
\xi_{11} &= \frac{bA}{2\alpha_1}\left[b + i\alpha_2\right] \\
\xi_{02} &= -\frac{1}{4\alpha_1}\left[(b^2 A - \alpha_2^2 p') + i\alpha_2 b(A + p')\right] \\
\xi_{21} &= -\frac{b}{16\alpha_1}\left[\alpha_2 b(p'' - 6B) + i(\alpha_2^2 p'' + 6b^2 B)\right]
\end{aligned}$$

and finally, by substituting into (A.6), we have after some algebra

$$a = -\frac{(b^2+\alpha_2^2)}{16\alpha_1^2}\left[6b^2A^2 + \frac{6b^2B}{F_2} + \alpha_2^2 p'^2 - \frac{\alpha_2 b^2 p' A}{\alpha_1 F_2 + \alpha_2}\right] \tag{A.7}$$

We are now ready to prove theorem 1 and theorem 2 in the main text.

We start with theorem 1 and consider the survival probability function

$$p(y) = P_1(1 - \gamma y)^{1/\gamma}$$

Now, in order to have a Hopf bifurcation at all, it follows from (19) that

$$\gamma > -\frac{\alpha_1 F_2}{2(\alpha_1 F_2 + \alpha_2)} \tag{A.8}$$

Further, at bifurcation

$$P_1 = \frac{1}{F_2}\left[1 + \gamma\,\frac{2(\alpha_1 F_2 + \alpha_2)}{\alpha_1 F_2}\right]^{1/\gamma} = \frac{1}{F_2} D^{1/\gamma} \tag{A.9}$$

and by using this expression in the computations of p', A and B the stability coefficient becomes

$$a = -\frac{D^2}{16}\left\{b^2(2\gamma+1)(\gamma+1) + \alpha_2\left[\alpha_2 - \gamma(\alpha_1 F_2 - \alpha_2)\right]\right\} \tag{A.10}$$

which clearly is negative under the restriction (A.8). Hence, theorem 1 is proved.

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Repeating the analysis above for the function

$$p(y) = \frac{P_1}{1 + y^\alpha} \qquad \alpha > 0$$

in theorem 2 it is clear from (19) (see also Wikan [34]) that the Hopf bifurcation is restricted to $\alpha > 2$, and that the relation between the parameters at bifurcation is:

$$P_1 = \frac{1}{F_2}\,\frac{\alpha\alpha_1 F_2}{(\alpha - 2)\alpha_1 F_2 - 2\alpha_2} = \frac{1}{F_2} G \tag{A.11}$$

The stability coefficient now becomes

$$a = -\frac{(G-1)^{-2/\alpha}}{16G^2}(V + W) \tag{A.12}$$

where

$$V = (\alpha - 1)b^2 G\left[(\alpha - 2)G + 3\alpha\right]$$

$$W = \alpha\alpha_2(G-1)\left[(\alpha\alpha_2 + \alpha_1 F_2 - \alpha_2)G - \alpha\alpha_1 F_2\right]$$

$V > 0$ for any $\alpha > 2$. $W > 0$ for any (finite) $\alpha > 2$ if $d = F_2 - \alpha_2/\alpha_1$ is sufficiently small. Thus in this case a is clearly negative. W may become negative for large values of d, but then, $b > \alpha_1 F_2 \Rightarrow V > |W| \Rightarrow a < 0$. This completes the proof of theorem 2.

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Figure Captions

Figure 1. An exact 4-periodical orbit in the two-generation case. $\alpha_1 = \alpha_2$, $\gamma = -0.45$, $p(y) = P_1(1-\gamma y)^{1/\gamma}$.

Figure 2. The "4-periodical" attractor in the chaotic regime. $\gamma = -0.10$. $\alpha_1 = \alpha_2$.

Figure 3. The graph $F_2 = h(x) = (1/P_1)x^{(x+1)/(x-1)}$ $(P_1 = 1.)$

Figure 4. The map (21) in the chaotic regime. $\alpha_1 < \alpha_2$.

Figure 5. Coexisting attractors in the case $\alpha_1 \ll \alpha_2$. Depending on the initial condition the ultimate fate of an orbit is either a large amplitude exact 3-cycle or an almost 3-periodical orbit restricted on a small invariant curve.

Figure 6. 3 invariant curves which are visited once every third iteration. The third iterate g of (21) has gone through a (supercritical) Hopf bifurcation. $\alpha_1 \ll \alpha_2$.

Figure 7. An exact 4-periodical orbit in the 3-generation case $\alpha_1 < \alpha_2 < \alpha_3$.

Figure 8. The map $(x_1, x_2, x_3) \to (F_3 x_3, p(y)x_1, p(y)x_2)$ after the secondary Hopf bifurcation. $\alpha_1 < \alpha_2 < \alpha_3$.

Figure 9. 2-periodical dynamics in the 3-age class model. $\alpha_1 \ll \alpha_2$.

Figure 10. A quasiperiodic orbit in the 4-generation case $\alpha_1 = 1$, $\alpha_2 = \alpha_3 = \alpha_4 = 0$.

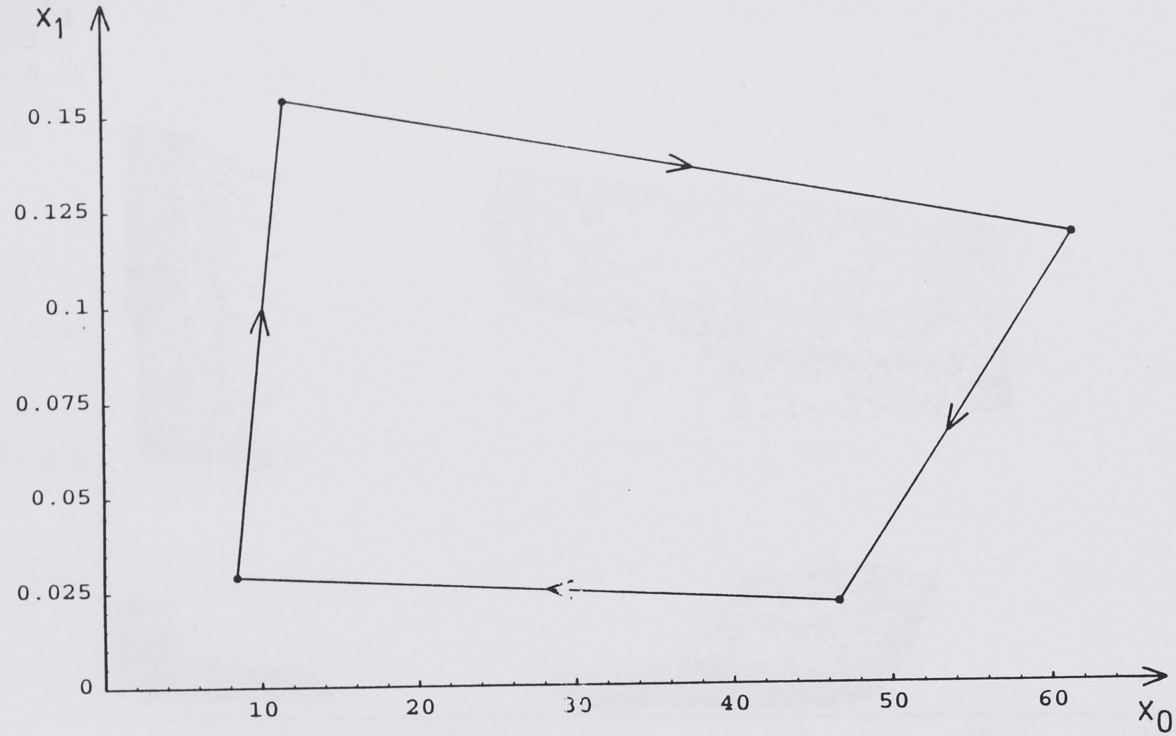
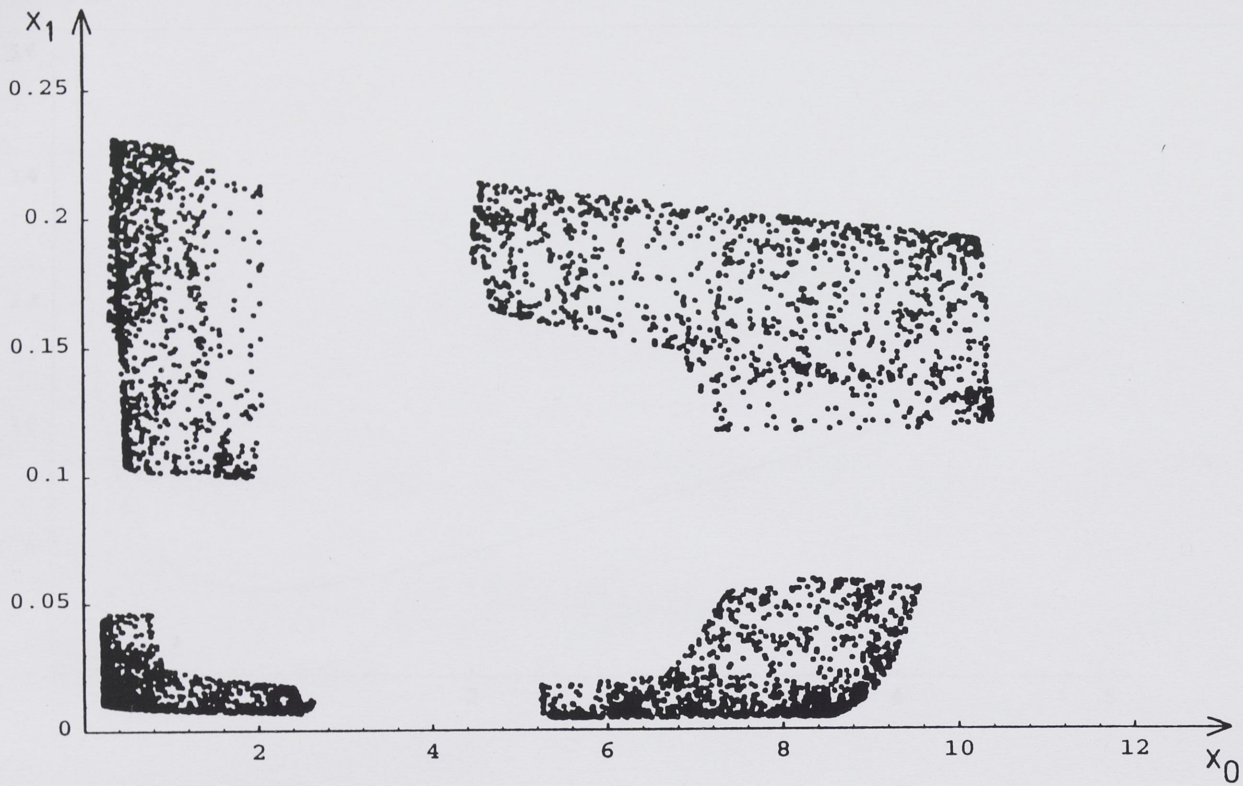


Fig. 1



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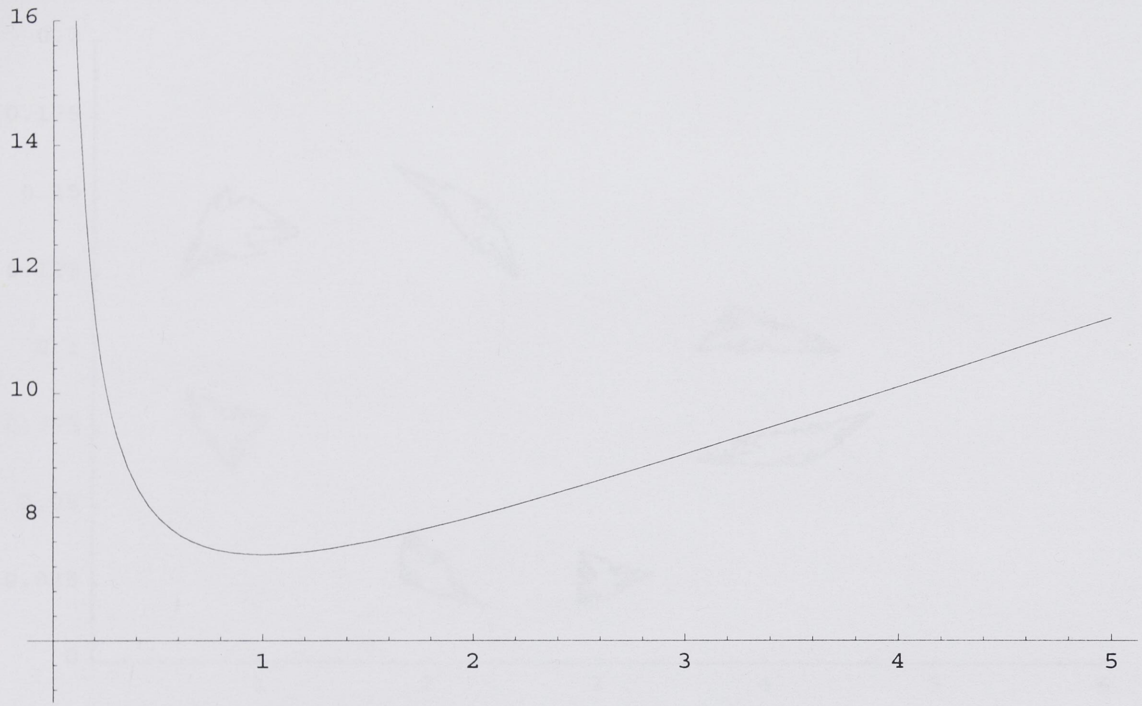

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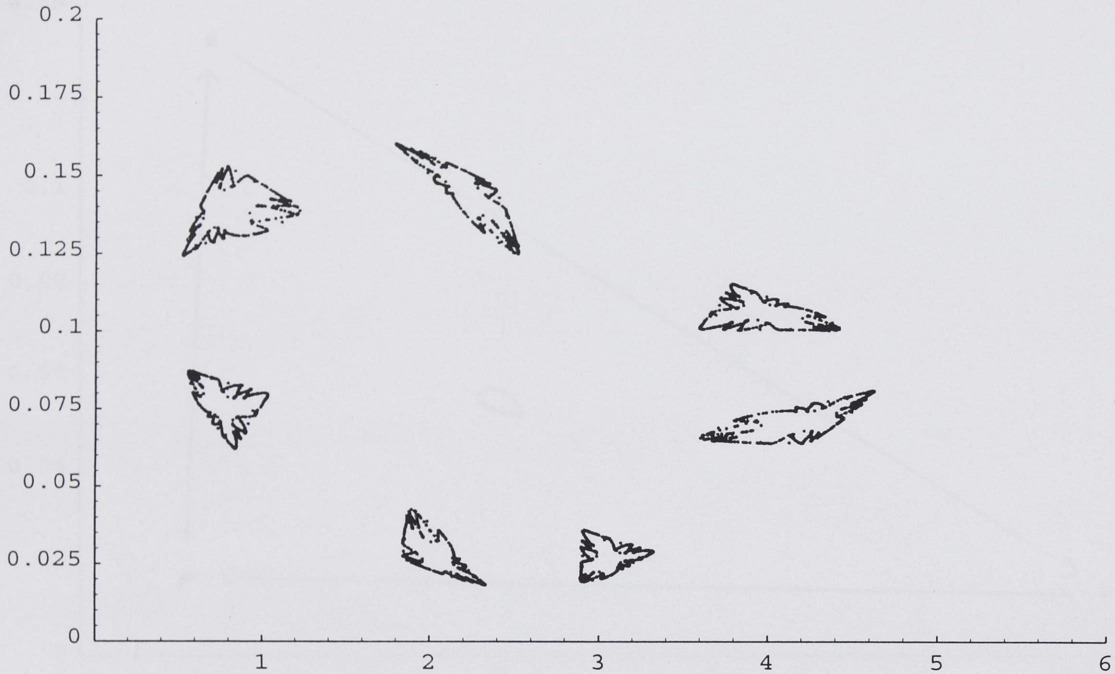

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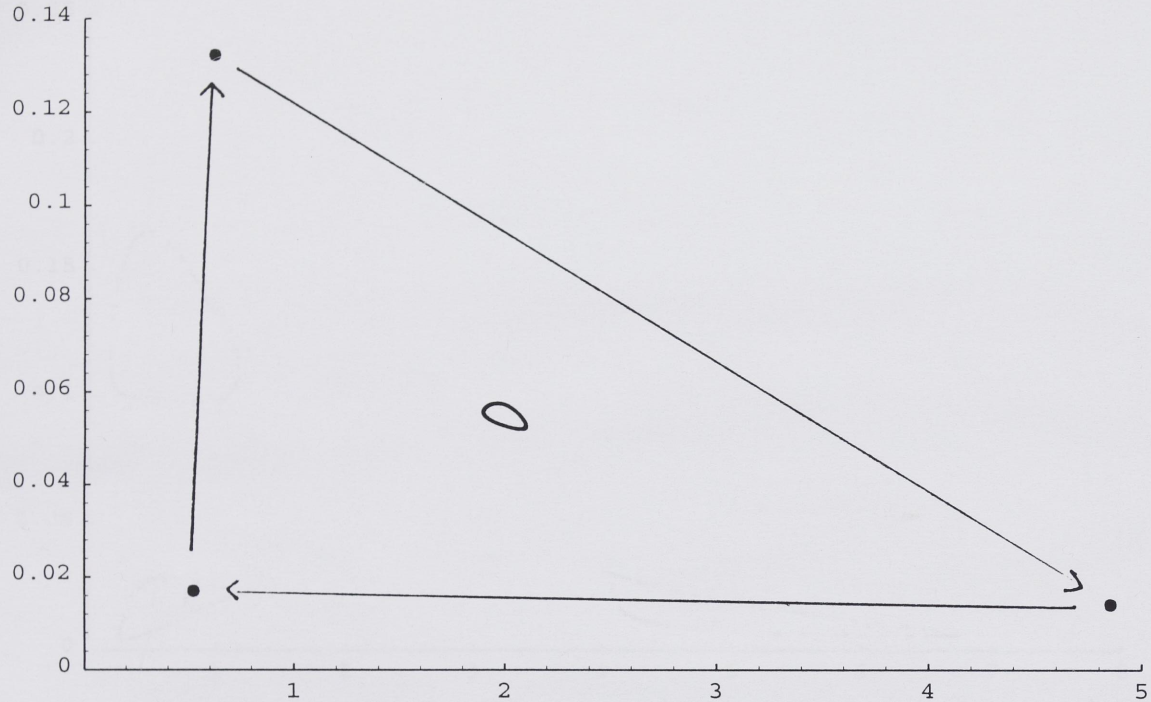
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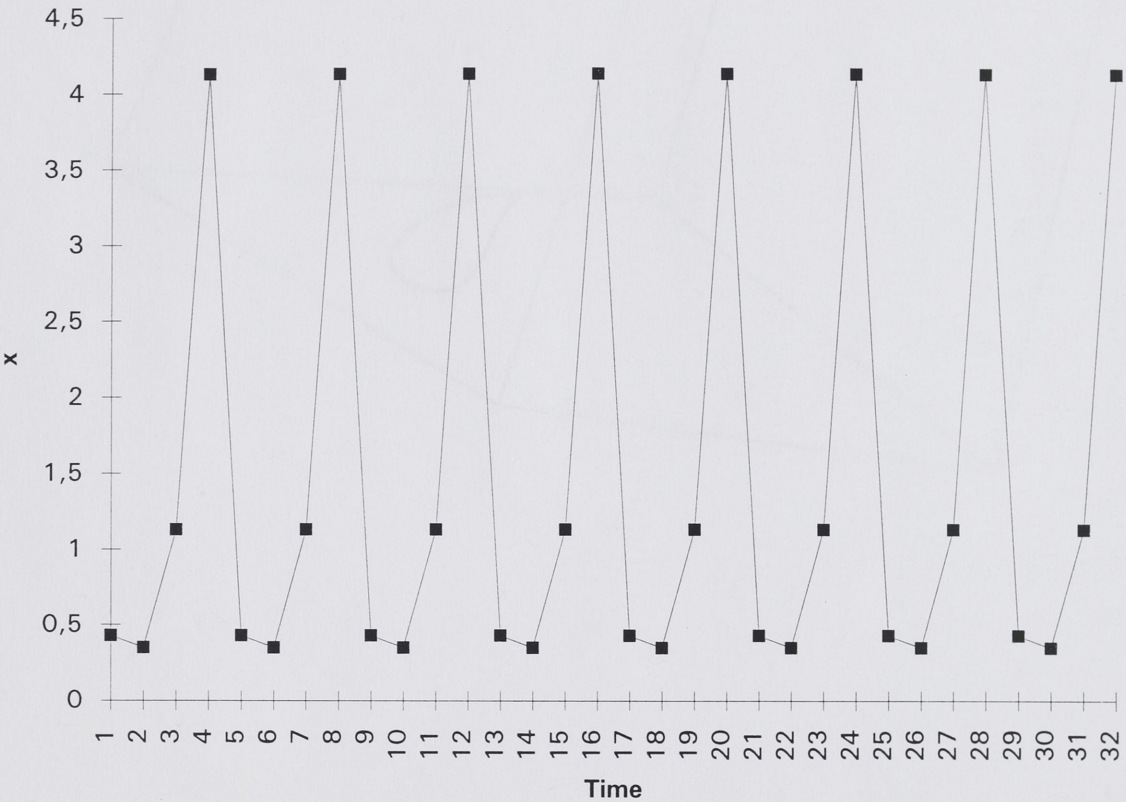
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Fig 7

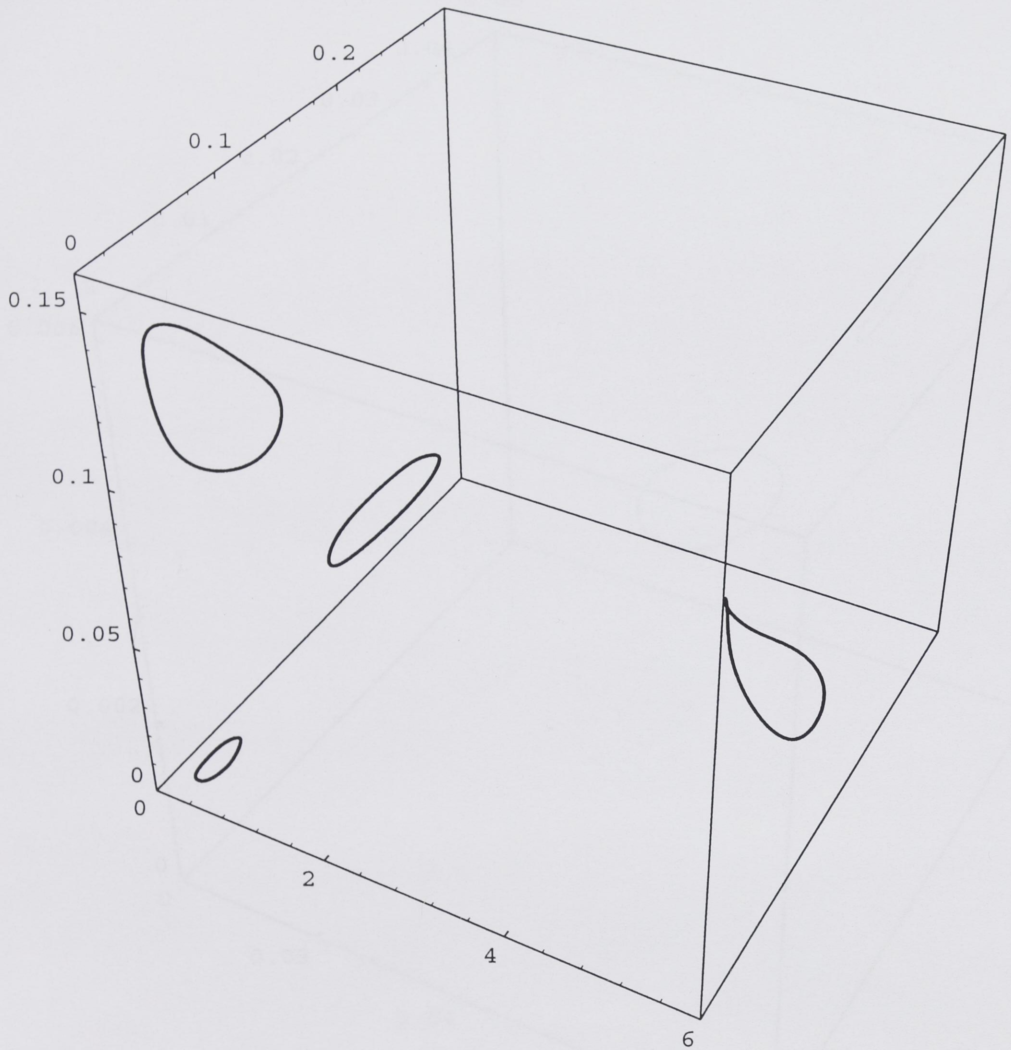


Fig 8

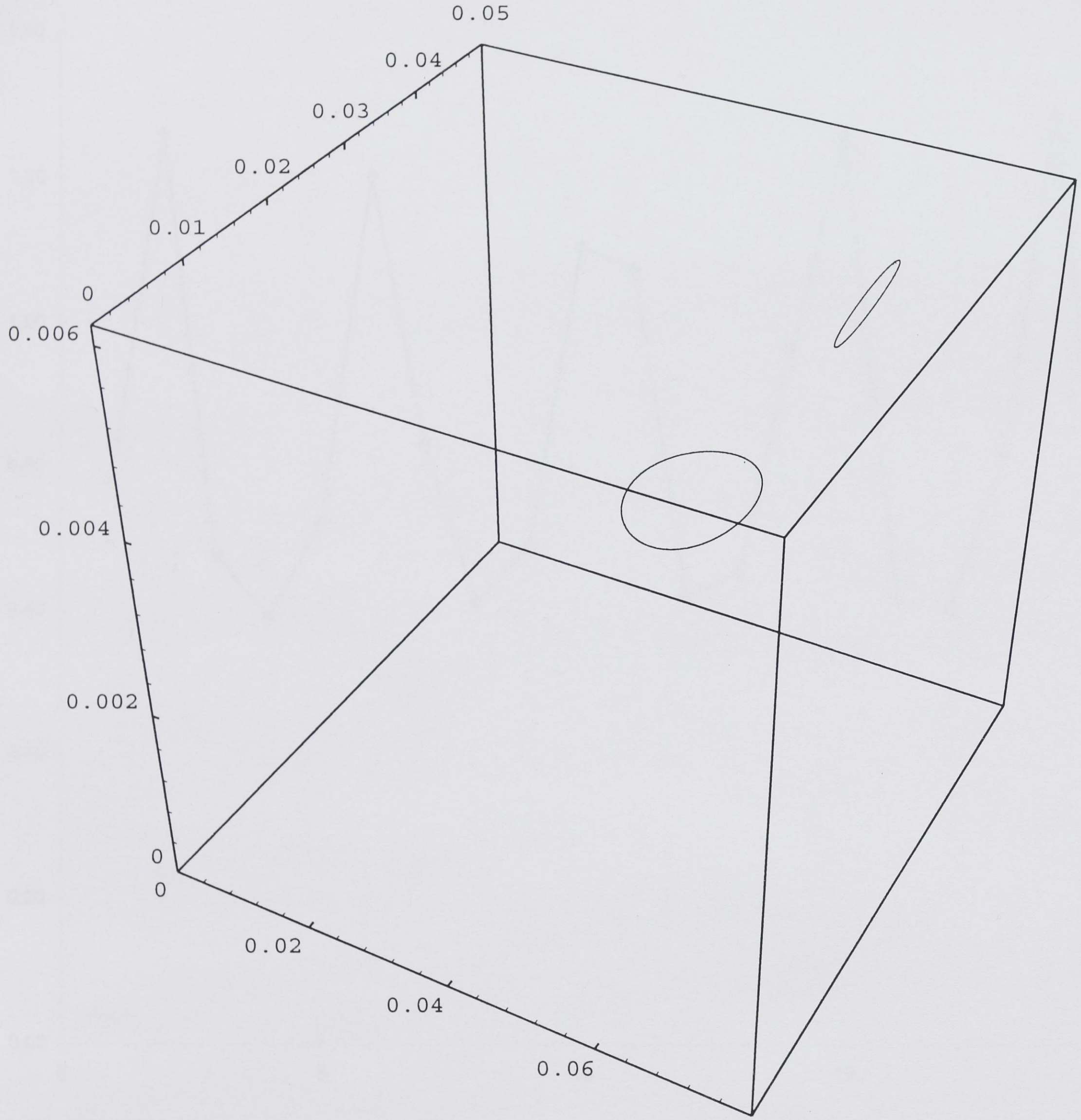
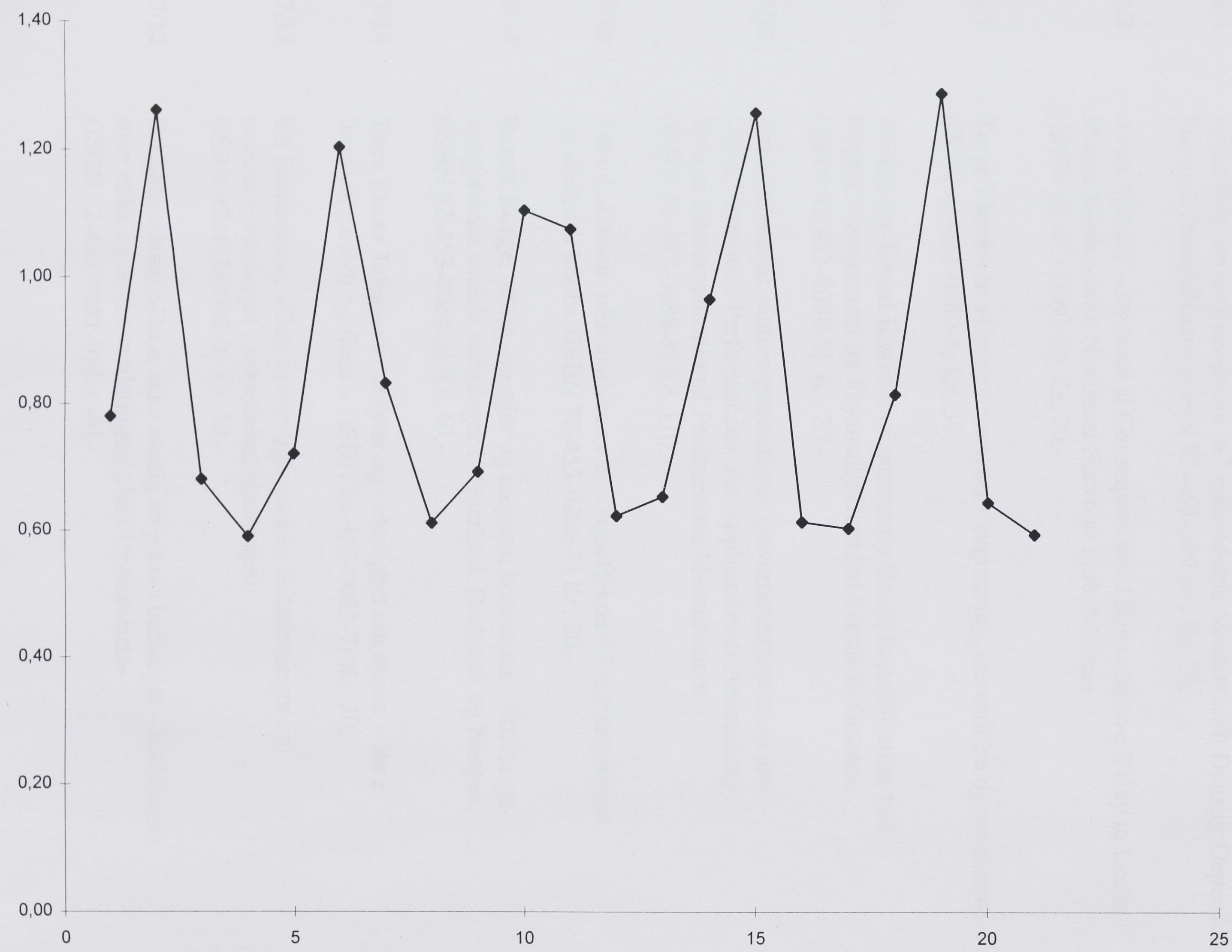


Fig 9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