International Journal of Modern Physics B, Vol. 15, No. 4 (2001) 391–402

FLUCTUATIONS AND CORRELATIONS IN POPULATION MODELS WITH AGE STRUCTURE

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Received 8 December 2000

We study the fluctuations and correlations in a stochastic age-structured population model. Our model, which is closely related to certain "bit-string" models of evolution, incorporates survival probabilities that are density dependent, and also allows for varying reproductive probabilities as a function of age. We first solve for the simple steady-state of the deterministic version of our model, where all fluctuations and correlations are neglected. We then develop analytic techniques to calculate stochastic Gaussian corrections around this deterministic solution. This allows for a systematic, perturbative calculation of the population fluctuations and correlations. Away from the bifurcation point of the deterministic model we find good agreement with Monte–Carlo simulations.

1. Introduction

Discrete age-structured population models have been intensively studied since the pioneering work of Bernadelli,[1] Lewis,[2] and Leslie.[3] Models of this kind have now become very well established tools in population biology.[4–7] The population distribution as a function of age is encoded in a vector $\mathbf{n}(t) \equiv \{n_0(t), n_1(t), \ldots, n_D(t)\}$, where $n_a(t)$ is the number of individuals of age a at time t, D is the maximum age, and n_0 stands for the number of "newborns". The time evolution of these Leslie

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models is then given by $\mathbf{n}(t+1) = \mathbb{A}\mathbf{n}(t)$, where $\mathbb{A}$ is the Leslie matrix

$$\mathbb{A} = \begin{pmatrix} f_0 & f_1 & \dots & & f_D \\ v_0 & 0 & \dots & & 0 \\ 0 & v_1 & & & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & \dots & 0 & v_{D-1} & 0 \end{pmatrix}. \tag{1}$$

Here the elements f_a are the fecundities of individuals of age a, whereas the v_a (the Verhulst factors) represent the fraction of individuals of age a who survive to become age $a+1$. The original and simplest of these Leslie models is linear in $\mathbf{n}$, meaning that all the $\{f_a\}$ and $\{v_a\}$ are constants, independent of the density $\mathbf{n}$. However, many generalizations have since been made to density dependent factors,[4,8–15] so that the dynamics becomes inherently *nonlinear*. These nonlinear models split naturally into two further categories. The first of these are where the density effects are included in the fecundities $\{f_a\}$, but not in the survival probabilities $\{v_a\}$. For the case of fishery models, this approach has often been motivated by the assumption that all density dependent effects occur within the first year of life.[10] However, in other cases it may be more appropriate to assume that the density dependence can also occur in the survival probabilities, as in Tribolium Castaneum,[12] or semivoltine species.[14] These models may then be even further refined by the inclusion of additional features, such as reproductive delay.[15]

However one drawback of the models discussed hitherto is that they are deterministic. Real population systems are of course affected by random fluctuations, coming from the environment and/or from the intrinsic dynamics of the stochastic birth/death processes (see Ref. 16 and references therein). Such stochastic Leslie models have been intensively investigated.[5,16–19] For example, otherwise deterministic models conditioned on stochastic environmental variables have been studied.[17–19] In some of these models, further progress may potentially be made by invoking diffusion approximations.[19] However, the analysis for these cases depends on the birth/death probabilities being *independent* of the population vector $\mathbf{n}$. As emphasized by Engen and Sæther,[16] no information has been available regarding the more difficult case of *fluctuations* in stochastic age-structured models with *population dependent birth/death probabilities.* Further theoretical progress in this direction would be highly desirable,[16] and forms the object of this paper.

Population models have also been intensively studied by physicists in recent years; see, for example, Ref. 20. Particular attention has been paid to so-called "bit-string" models of evolution.[21] These models are based on the mutation accumulation hypothesis,[22] which assumes that during the aging process each individual accumulates exclusively late-acting deleterious genetic mutations. In "bit-string" models the genome of a particular species is encoded as a series of '0's and '1's (deleterious mutations), and as an individual ages the bits (genes) are activated one by one. When the accumulated sum of bad genes reaches a certain number the individual dies (although death may also occur at younger ages due to Verhulst competition). Note that the "bit-strings" of the offspring may differ from those of the parent due to additional beneficial ('1' → '0') or deleterious ('0' → '1') mutations. This type of model is clearly well suited to efficient computer simulation.[21] In its simplest case, where individuals die after the first deleterious mutation, "bit-string" models simply correspond to multiple genome population models with age structure, where the different genomes are distinguished by different maximum ages. Some analytic progress has already been made in deterministic versions of these models.[23] However, an analysis of the important role played by fluctuations has so far been lacking. Our calculations form the first step towards filling this gap.

The first step in our analysis involves setting up a rather general age-structured population model, with density dependent probabilities. We then rewrite this model by using a Markovian master equation formalism. This forms a complete description of the probabilistic dynamics of the model. With this equation as a starting point we first investigate the mean field version of the model, where all fluctuations and correlations between the populations at the various ages are neglected. Within this approximation the model simply reduces to a deterministic Leslie model with density dependent coefficients. In that case it is straightforward to calculate the steady-state values of the population as a function of age. We also investigate the stability of this solution, and demonstrate that for sufficiently high birth rates this simple steady-state solution becomes unstable and a bifurcation occurs.[24] In our case we show that the bifurcation is to an orbit with period 2. Subsequent bifurcations will then lead eventually to chaotic behavior. However, if the simple steady-state solution is stable then it is possible to expand around it using a Gaussian perturbation theory. This allows us to compute the stochastic Gaussian fluctuation corrections, using techniques based on those of Ref. 25. To the best of our knowledge, however, this is the first time these perturbative methods have been applied to stochastic age-structured population models, with an arbitrary number of age classes and density dependent probabilities. The Gaussian perturbation theory predicts that the size of the fluctuations increases as the deterministic bifurcation point is approached, with the fluctuations diverging exactly at the bifurcation, at which point the expansion breaks down entirely. We have compared these results with those from Monte–Carlo simulations of a simple (but still biologically applicable) version of our model. Away from the bifurcation point, we find very good agreement between theory and simulations. As the bifurcation point is approached, the agreement deteriorates, as expected. Of course, as our simulations show, the real fluctuations cannot diverge at the bifurcation point, but the magnitudes of the fluctuations can nevertheless become a substantial fraction of the mean population values.

2. The Model

We begin our analysis by defining our discrete time population model, with population vector $\mathbf{n}$. At each time step we compute the survival probability $V(\mathbf{n})$ and let each individual survive with probability V. Note that this survival probability is the same for all individuals regardless of their age. After this "pruning", each of the remaining individuals of age a may give birth to F_a offspring with probability r_a. At this point the remaining population is aged by one time step, with the exception of the new offspring who make up n_0. Individuals of age $D+1$ then die immediately and are removed from the system. Note that our model allows for a variable reproduction probability r_a as a function of age. However, we do assume that individuals of the same age who succeed in reproducing, produce an identical number (F_a) of offspring. Note that we are not restricting ourselves to specific forms for V, r_a, or F_a beyond some general features. These general features include $V, r_a \in [0,1]$, since they represent *probabilities*. Furthermore, we assume that V depends only on the *total* population $N \equiv \sum_a n_a$, via the ratio N/N_0, where N_0 represents a characteristic population size that the resources can support. Also, to be reasonable, V is assumed to be monotonically decreasing with N. For comparisons with simulations, we use $V = \exp(-N/N_0)$, a form frequently chosen in the biology literature.[26] In contrast, the algebraic form $V = 1-(N/N_0)$ is the favorite in the recent physics literature.[21,23] We prefer the exponential form, since absolute cut-offs seem unrealistic in a real population system.

As mentioned above, deterministic variants of this model have previously been investigated[11,12,14]; for example, the population dynamics of the semivoltine species studied in Ref. 14 is quite similar to a $D=1$ version of our model. Our goal is to go beyond these deterministic treatments and analyze the fluctuations and correlations in our system. Therefore, we need to consider $P(\mathbf{n},t)$, the probability of finding the population with a particular distribution $\mathbf{n}$ at time t. Its evolution obeys the master equation

$$\begin{aligned} P(\mathbf{n},t+1) = &\sum_{m_0,\ldots,m_D,n_{D+1}} P(\mathbf{m},t)\left[\prod_{a=1}^{D+1}\binom{m_a-1}{n_a} V^{n_a}[1-V]^{m_{a-1}-n_a}\right] \\ &\times\left[\prod_{a=1}^{D+1}\binom{n_a}{b_{a-1}} r_{a-1}^{b_{a-1}}[1-r_{a-1}]^{n_a-b_{a-1}}\right] \\ &\times\sum_{b_0,\ldots,b_D}\delta\left[n_0-\sum_{c=0}^{D}F_c b_c\right]. \end{aligned} \tag{2}$$

This equation forms a complete and exact description of the probabilistic dynamics of the system. The first term in square brackets results from the probability (V) for each individual to survive. The second line gives the probability that, of the survivors, only a fraction of them (b_c individuals of age c) become parents, each of whom gives birth to F_c offspring. Thus, the total number of offspring is $\sum_c F_c b_c$. The δ function ensures that this is equal to n_0. Note that the n_{D+1} is just a "temporary" variable, which keeps track of the number of individuals of age D at time t who survive just long enough to reproduce before dying from old age.

As it stands above, this equation, although exact, is rather unwieldy. In practice, we would look for the simple steady-state distribution, $P_{ss}(\mathbf{n})$, by solving Eq. (2) with $P(\mathbf{n}, t+1) = P(\mathbf{n}, t) = P_{ss}(\mathbf{n})$. From this, the averages and higher moments can be computed. However, such a program is still unrealistically difficult. Nevertheless, we can still use Eq. (2) as a starting point for the derivation of more tractable equations and for carrying out our perturbative analysis.

3. Analysis

We begin by obtaining equations for the first moment of the population vector. Multiplying Eq. (2) by n_c and summing over all the other indices, we find

$$\langle n_a \rangle_{t+1} = \langle V(N) n_{a-1} \rangle_t \,, \qquad (a > 0)\,, \tag{3}$$

$$\langle n_0 \rangle_{t+1} = \sum_d F_d r_d \langle V(N) n_d \rangle_t \,, \tag{4}$$

where $\langle \bullet \rangle_t$ denotes the average of $\bullet$ over $P(\mathbf{n}, t)$. These equations are *exact*. However, since V is a function of $N \equiv \sum_a n_a$, all moments of P may be coupled together. If we now make the deterministic (or mean field) assumption that all fluctuations can be neglected, then we can replace the higher order moments by appropriate products of the first moment. Hence we find

$$\langle n_a \rangle_{t+1}^{\mathrm{MF}} = \left[V \left(\sum_c \langle n_c \rangle_t^{\mathrm{MF}} \right) \right] \langle n_{a-1} \rangle_t^{\mathrm{MF}} \,, \qquad (a > 0)\,, \tag{5}$$

$$\langle n_0 \rangle_{t+1}^{\mathrm{MF}} = \left[V \left(\sum_c \langle n_c \rangle_t^{\mathrm{MF}} \right) \right] \sum_d F_d r_d \langle n_d \rangle_t^{\mathrm{MF}} \,, \tag{6}$$

where, to be clear, we have written the explicit expression for N, and labeled the deterministic (or mean field) quantities as $\langle \bullet \rangle^{\mathrm{MF}}$.

Even at this level these nonlinear mean field equations are known to contain a rich variety of behavior, depending on the details of F_c, r_c, and V. If, however, we assume the existence of a *simple* steady-state solution where $\langle n_a \rangle_{t+1}^{\mathrm{MF}} = \langle n_a \rangle_t^{\mathrm{MF}}$, then, dropping the time subscripts, we can substitute the relation $\langle n_a \rangle^{\mathrm{MF}} = V^a \langle n_0 \rangle^{\mathrm{MF}}$ into Eq. (6). In that case Eqs. (5) and (6) are easily solved to give

$$\langle n_a \rangle^{\mathrm{MF}} = N(z) \frac{z^a (1 - z)}{(1 - z^{D+1})} \,. \tag{7}$$

Here z is the unique, positive, real root of the equation $\sum_c F_c r_c z^{c+1} = 1$, and $N(z)$ is the steady-state total population, given by the value that satisfies $V(N) = z$.

This solution is similar to that given in Ref. 11, although in our case we have not specified the functional form for V.

We now briefly consider the stability properties of this simple mean field steady state. Firstly, it is straightforward to show that, if the reproductive rates are too low with $\sum_c F_c r_c < 1$, then no nontrivial steady-state is possible and the population will eventually die out. On the other hand, if the reproductive rates are large enough, the population will display period doubling bifurcations (cf. Ref. 24). To see this, we need to analyze the properties of the stability matrix $\mathbb{S}$ associated with the simple mean field steady-state given in Eq. (7). The stability matrix $\mathbb{S}$ given by

$$S_{ab} = \frac{\partial[V n_{a-1}]}{\partial n_b}\,, \qquad S_{0b} = \sum_c F_c r_c \frac{\partial[V n_c]}{\partial n_b}\,, \qquad (a > 0)\,, \tag{8}$$

may also be written as $\mathbb{S} = \mathbb{L} + \mathbb{V}$, where $\mathbb{L}$ is the deterministic Leslie matrix defined by Eqs. (5) and (6) and $\mathbb{V}$ is a matrix defined by $V_{ab} = V' n_a / V$. Here V' denotes the derivative of V with respect to n_b, a quantity which is the same for all b. The eigenvalues and eigenvectors of $\mathbb{L}$ can easily be calculated, where one finds that the largest eigenvalue λ_0 is equal to unity. The associated eigenvector is, of course, just given by $\mathbf{n}$. Excepting some special cases, all the other (in general complex) eigenvalues λ_k, $(k > 0)$, can be shown to lie within the unit circle. Considering now the full stability matrix $\mathbb{S}$, this turns out to have the *same eigenvectors* as $\mathbb{L}$ with exactly the same eigenvalues λ_k, $(k > 0)$, except for λ_0 which now has the value $\lambda_0 = 1 + NV'/V$. With the assumption that V is a monotonically decreasing function, this eigenvalue must be less than unity. Since all the other eigenvalues generically lie within the unit circle, we find that the simple steady-state solution will be stable, provided $\lambda_0 > -1$. When the eigenvalue λ_0 reaches -1, we expect that the simple steady-state solution will undergo a bifurcation into an orbit with period 2.

Now that we have completed our mean field and stability analysis, our principal objective is to investigate fluctuations and correlations, i.e. the second moments of the population distribution function P. Thus, we multiply Eq. (2) by $n_a n_b$ and sum over all the other indices, giving

$$\langle n_a n_b \rangle_{t+1} = \langle V^2 n_{a-1} n_{b-1} \rangle_t + \delta_{ab} \langle V(1-V) n_{a-1} \rangle_t\,, \qquad (a, b > 0)\,, \tag{9}$$

$$\langle n_a n_0 \rangle_{t+1} = \sum_c F_c r_c \langle V^2 n_{a-1} n_c \rangle_t + F_{a-1} r_{a-1} \langle V(1-V) n_{a-1} \rangle_t\,, \quad (a > 0)\,, \tag{10}$$

$$\langle n_0 n_0 \rangle_{t+1} = \sum_{c,d} F_c r_c F_d r_d \langle V^2 n_c n_d \rangle_t + \sum_c [F_c^2 (r_c \langle V n_c \rangle_t - r_c^2 \langle V^2 n_c \rangle_t)]\,. \tag{11}$$

Note that, like Eqs. (3) and (4), these equations are *exact*. Assuming $N_0 \gg 1$, and that the system is well away from "critical" points (e.g. the survival/extinction transition), it is reasonable to postulate a Gaussian distribution $P^*_{ss}(\mathbf{n})$ with width of $O(\sqrt{N_0})$. Rewriting Eqs. (3), (4) and (9)–(11) for $\langle \bullet \rangle^*_{ss}$, we then have a closed set of equations for the first and second moments. This approach should form the first step in a systematic expansion of all quantities in decreasing powers of N_0. Furthermore, since we have assumed that $N_0 \gg 1$, we will allow $\mathbf{n}/N_0$ to assume *continuous* values. Using this perturbative formalism we will derive analytic expressions for the fluctuations and correlations in our model. In Sec. 4, these results will then be compared with Monte–Carlo simulations, for a simple case.

Proceeding, let us write down the general form for our Gaussian probability distribution P^*_{ss}

$$P^*_{ss}(\mathbf{n}) = \left(\frac{1}{2\pi N_0}\right)^{(D+1)/2} \frac{1}{\sqrt{\det \mathbb{G}}} \exp\left[-\frac{1}{2N_0}\sum_{c,d}(n_c - \bar{n}_c)G^{-1}_{cd}(n_d - \bar{n}_d)\right] , \quad (12)$$

where we expect the unknown (to be determined) parameters $\bar{\mathbf{n}}$ and $\mathbb{G}$ to be of $O(N_0)$ and $O(1)$, respectively. Note that we will integrate $\mathbf{n}$ from $-\infty \to \infty$ rather than from $0 \to \infty$, a simplification which will introduce only negligible errors of $O(\exp[-N_0])$. Averages can now be computed using

$$\langle f(n_a)\rangle^*_{ss} = f(\bar{n}_a) + \frac{1}{2}\sum_{c,d}\frac{\partial^2 f}{\partial\bar{n}_c\partial\bar{n}_d}N_0 G_{cd} + \cdots . \quad (13)$$

Note that the second term in Eq. (13) is expected to be suppressed by a factor of $O(1/N_0)$ compared to the first term $f(\bar{n}_a)$. This ordering allows us to set up a systematic perturbation theory, which can be pushed to higher orders if desired.

From now on we drop the bars and angled brackets for clarity. Applying Eq. (13) to Eqs. (3) and (4) gives

$$n_a = Vn_{a-1} + \frac{1}{2}\sum_{c,d}\frac{\partial^2[Vn_{a-1}]}{\partial n_c\partial n_d}N_0 G_{cd}\,, \qquad (a > 0)\,, \quad (14)$$

$$n_0 = V\sum_d F_d r_d n_d + \frac{1}{2}\sum_{c,d,e} F_c r_c \frac{\partial^2[Vn_c]}{\partial n_d\partial n_e}N_0 G_{de}\,. \quad (15)$$

With the assumptions $\mathbf{n} \sim O(N_0)$ and $\mathbb{G} \sim O(1)$, the last terms in each of Eqs. (14) and (15) represent $O(1/N_0)$ corrections to the mean field results, while the remaining (lowest order) terms make up the mean field Eqs. (5) and (6). Writing a perturbative expansion: $n_a = n_a^{(0)} + n_a^{(1)} + \ldots$ (with $n_a^{(k)} \sim O(N_0^{1-k})$), we see that at zeroth order we have simply recovered the mean field equations: $n_a^{(0)}$ with $a > 0$ is given by Eq. (5), while $n_0^{(0)}$ is given by Eq. (6). Defining $\mathbb{I}$ as the unit matrix, the first order result is

$$n_a^{(1)} = \sum_c([\mathbb{I} - \mathbb{S}]^{-1})_{ac}U_c\,, \quad (16)$$

with

$$S_{ab} = \frac{\partial[Vn_{a-1}]}{\partial n_b}\,, \qquad U_a = \frac{1}{2}\sum_{c,d}\frac{\partial^2[Vn_{a-1}]}{\partial n_c\partial n_d}N_0 G_{cd}\,, \qquad (a > 0)\,, \quad (17)$$

$$S_{0b} = \sum_c F_c r_c \frac{\partial [V n_c]}{\partial n_b}\,, \qquad U_0 = \frac{1}{2} \sum_{c,d,e} F_c r_c \frac{\partial^2 [V n_c]}{\partial n_d \partial n_e} N_0 G_{de}\,. \tag{18}$$

Here $\mathbb{S}$ is the matrix associated with linear stability analysis around the deterministic or mean field stationary solution (see above). Note that in order to compute the first order corrections, we need only evaluate $\mathbb{S}$ and U at zeroth order.

Applying the same analysis to the second moments, we obtain, after some lengthy algebra,

$$G_{ab} - \sum_{c,d} S_{ac} S_{bd} G_{cd} = K_{ab}\,, \tag{19}$$

where

$$K_{ab} = \delta_{ab}(1 - V)\frac{n_a}{N_0}\,, \qquad (a, b > 0)\,, \tag{20}$$

$$K_{a0} = K_{0a} = F_{a-1} r_{a-1} (1 - V)\frac{n_a}{N_0}\,, \qquad (a > 0)\,, \tag{21}$$

$$K_{00} = \frac{1}{N_0} \sum_b V F_b^2 r_b n_b (1 - V r_b)\,. \tag{22}$$

Again, all quantities need to be evaluated only at the zeroth order, so that, e.g. V is just z. In compact form this equation can be written as $\mathbb{G} - \mathbb{S}\mathbb{G}\mathbb{S}^T = \mathbb{K}$, which may be solved by series

$$\mathbb{G} = \mathbb{K} + \mathbb{S}\mathbb{K}\mathbb{S}^T + \mathbb{S}^2\mathbb{K}(\mathbb{S}^T)^2 + \cdots = \sum_n \mathbb{S}^n \mathbb{K} (\mathbb{S}^T)^n\,. \tag{23}$$

Since the eigenvalues and eigenvectors of $\mathbb{S}$ are known, let us write $\mathbb{S} = \mathbb{M}\mathbb{E}\mathbb{M}^{-1}$, where $\mathbb{E}$ is in Jordan form, with the eigenvalues on the diagonal, and $\mathbb{M}$ is the matrix (with its *columns*) composed of the corresponding *right* eigenvectors. Note that $\mathbb{M}$ is not necessarily orthogonal or unitary. If we define $\tilde{\mathbb{G}} = \mathbb{M}^{-1}\mathbb{G}(\mathbb{M}^T)^{-1}$ and $\tilde{\mathbb{K}} = \mathbb{M}^{-1}\mathbb{K}(\mathbb{M}^{-1})^T$, then it is straightforward to show that $\tilde{\mathbb{G}} = \sum_n \mathbb{E}^n \tilde{\mathbb{K}} \mathbb{E}^n$. For simplicity, let us focus on the case where $\mathbb{E}$ is diagonal. Then the sum is easily performed, so that

$$\tilde{G}_{ab} = \frac{\tilde{K}_{ab}}{1 - e_a e_b}\,, \qquad (\text{no sum})\,, \tag{24}$$

where the $\{e\}$ are the eigenvalues. Since $\mathbb{G} = \mathbb{M}\tilde{\mathbb{G}}\mathbb{M}^T$, we can directly obtain the matrix $\mathbb{G}$ and with it all the information about the Gaussian probability distribution (12). The explicit formula for computing $\mathbb{G}$ is our principal result. Given a particular form of $V(N)$ and reproductive parameters r_a, F_a, we can compute $\mathbb{G}$ and find the fluctuations in, as well as the correlations between, the populations of various ages.

The result (24) contains a further appealing feature: the signal of bifurcation. From our earlier stability analysis, we know that period doubling emerges when the eigenvalue associated with $\delta n_a \propto n_a$ reaches -1. Examining Eq. (24), we see that it is precisely this feature which signals the breakdown of the Gaussian approximation.

However, before that point is reached, our perturbative expansion predicts that the fluctuations will become large. This is not unexpected — close to the bifurcation point the eigenvalue farthest from 0 will be close to (but slightly larger than) -1. Hence the deterministic "return force" to the stable solution will be rather weak. On the other hand the system will constantly be being "kicked" by random fluctuations. Hence, as we will see from the simulations in the next section, the stochasticity can be rather important in this regime of parameter space.

Finally, we briefly discuss the case where the probability of reproduction r_a falls to zero for all ages $M \leq a \leq D$. In that case, it turns out that the matrix $\mathbb{E}$ is no longer diagonal, meaning that the final expression for $\tilde{\mathbb{G}}$ is somewhat more complicated. Nevertheless, our above conclusions remain qualitatively unchanged.

4. Simulations

To check the above analysis, we consider a very simple 2 age system (i.e. $D = 1$). Note, however, that despite their simplicity such 2 age systems have been extensively studied (see, for example, the analysis in Ref. 14 for semivoltine species). In our case, we have selected the exponential form for V, with $N_0 = 1000$ and then investigated three sets of parameter values:

- $r_a = r = 0.75$ and $F_a = F = 1$.
  For the deterministic version of this simple model, our earlier stability analysis predicts a bifurcation to an orbit with period 2 when $NV'/V = -2$, which is solved by $rF = e^4/(1 + e^2) \approx 6.5083$. Hence, for these parameter values we are well away from the bifurcation point of the deterministic version of the model, and hence we expect the Gaussian perturbation expansion to work well. The deterministic theory yields $n_0^{(0)} = 157.3$ and $n_1^{(0)} = 119.3$. Performing our perturbative analysis, we arrive at the first order corrections to n_0 and n_1, the fluctuations in the populations of each age, and the correlation between the populations of the two ages. The results are listed in Table 1, alongside those from Monte–Carlo simulations.[27] The agreement is indeed excellent, validating our approach. Note that the corrections $n_a^{(1)}/n_a^{(0)}$ are less than 1%, vindicating our assertion that they should be $O(1/N_0)$.
- $r_a = r = 0.7$ and $F_a = F = 8$.
  These parameters now place the system much closer to the deterministic bifurcation point. A comparison between the simulations and perturbation theory is given in Table 2. The results are still in reasonable agreement, although the errors (of around 10%) are larger than in the previous case. Note that the values for $\langle n_0 \rangle$, $\langle n_1 \rangle$ are not given, since they are within about 0.2% of their mean field values of $n_0^{(0)} = 1616.6$, $n_1^{(0)} = 250.0$.
- $r_a = r = 0.65$ and $F_a = F = 10$.
  These parameters now place the system very close to the deterministic bifurcation point. The results from simulations are shown in Table 3. The discrepancy between the simulations and perturbative results (not shown in Table 3) is now

Table 1. Comparison of results for the 2 age model with $r_a = 0.75$, $F_a = 1$, $N_0 = 1000$.

	Gaussian approximation	Simulations
$\langle n_0 \rangle$	156.80	156.80
$\langle n_1 \rangle$	118.90	118.90
$\sqrt{\langle n_0^2 \rangle - \langle n_0 \rangle^2}$	11.05	11.05
$\sqrt{\langle n_0 n_1 \rangle - \langle n_0 \rangle \langle n_1 \rangle}$	7.99	8.01
$\sqrt{\langle n_1^2 \rangle - \langle n_1 \rangle^2}$	8.36	8.37

Table 2. Comparison of results for the 2 age model with $r_a = 0.7$, $F_a = 8$, $N_0 = 1000$.

	Gaussian approximation	Simulations
$\sqrt{\langle n_0^2 \rangle - \langle n_0 \rangle^2}$	208.0	191.0
$\sqrt{\langle n_0 n_1 \rangle - \langle n_0 \rangle \langle n_1 \rangle}$	77.5	70.6
$\sqrt{\langle n_1^2 \rangle - \langle n_1 \rangle^2}$	30.8	28.1

Table 3. Simulation results for the 2 age model with $r_a = 0.65$, $F_a = 10$, $N_0 = 1000$.

	Simulations
$\sqrt{\langle n_0^2 \rangle - \langle n_0 \rangle^2}$	347.0
$\sqrt{\langle n_0 n_1 \rangle - \langle n_0 \rangle \langle n_1 \rangle}$	124.0
$\sqrt{\langle n_1^2 \rangle - \langle n_1 \rangle^2}$	45.8

very large, indicating that very close to the deterministic bifurcation point the Gaussian perturbation expansion is no longer useful. Nevertheless, the fluctuations are clearly quite large here (much bigger than $O(\sqrt{N_0})$). Despite this, the values for $\langle n_0 \rangle$, $\langle n_1 \rangle$ are still in very good agreement with their mean field values of $n_0^{(0)} = 1760.4$, $n_1^{(0)} = 238.5$, the error being less than 0.2%.

5. Conclusion

In this paper, we have, for the first time, studied fluctuation effects in a general class of stochastic population models with age structure and with density dependent probabilities. We have shown that these fluctuation effects can be handled using Gaussian perturbative expansions, and that away from deterministic bifurcation points, considerable analytic progress towards the calculation of fluctuations and correlations can be made. We also note that the size of the fluctuations can become rather large in the regions close to deterministic bifurcation points. Hence we see that it is perfectly possible for purely *demographic* stochasticity (as defined in Ref. 16) to have a major impact on the dynamics of age-structured population models.

Improving on the Gaussian perturbation theory outlined here, and obtaining a better description of the role of fluctuations close to deterministic bifurcation points, remains a challenging problem. We hope that this paper will stimulate further work on the application of perturbative methods to stochastic density dependent Leslie models. Ultimately one would also like to understand the role of stochasticity in otherwise chaotic regions of parameter space. However, these issues remain beyond the scope of the present paper.

Acknowledgments

We thank R. Desai, B. Schmittmann, and U. C. Täuber for illuminating discussions, and also R. J. Astalos for sharing simulation results prior to publication. One of us (RKPZ) thanks H. W. Diehl for his hospitality at the University of Essen. This research has been supported in part by NSERC of Canada and by the US National Science Foundation through the Division of Materials Research.

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