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Dormancy strategies in a random environment: Comparing structured and unstructured models

Michael R. Easterling[1,2]* and Stephen P. Ellner[1]

[1]Biomathematics Graduate Program, Department of Statistics, CB 8203, North Carolina State University, Raleigh, NC 27695-8203 and [2]Pharmacokinetics Branch, US Environmental Protection Agency, MD-74, Research Triangle Park, NC 27711, USA

ABSTRACT

Hatching strategies are studied in a model of population dynamics in a random environment. The strategies are the fraction of dormant eggs that hatch each year. A projection matrix with random elements describes the population dynamics. The model extends the density-independent model of Dan Cohen and the density-dependent model of Stephen Ellner by adding structure to the egg bank, such that a fraction of the dormant eggs are buried and unavailable for hatching each year. Differences between the structured and unstructured models are analysed by deriving a small variance approximation for the population's long-term growth rate and relating the growth rate to the egg bank structure and the environmental parameters. Tuljapurkar and Istock (1993) claimed that structured and unstructured models give very different predictions, especially when dormancy is high. We show that Tuljapurkar and Istock's conclusions are the result of the particular dormancy type in their model, in which the maximum duration of dormancy is 2 years, rather than the addition of population structure. Using parameters estimated from field and experimental studies of the freshwater copepod *Diaptomus sanguineus* in Bullhead Pond, RI, the density-dependent model correctly predicts that the population should maintain a long-term pool of diapausing eggs, whereas the density-independent model makes the incorrect prediction that all eggs should hatch at their first opportunity. If the per capita burial and emergence rates are low, as may be the case for many plant populations, the ESS optimal hatching strategy is nearly that of an unstructured model with the mortality of non-hatchers increased by the burial rate.

Keywords: copepod, dormancy strategies, evolutionarily stable strategy, moment closure, structured population model.

INTRODUCTION

Population growth can be affected by many factors, such as resource competition, predation, environmental fluctuations and unpredictable catastrophes. Organisms in a successful population must find ways to respond to these influences. One possible response

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* Address all correspondence to Michael R. Easterling, Pharmacokinetics Branch, US Environmental Protection Agency, MD-74, Research Triangle Park, NC 27711, USA. e-mail: easterling.michael@epa.gov

is a dormant stage in the life-cycle to avoid unfavourable conditions. The dormant stage may be in the form of an egg or seed and may last longer than one generation. The formation of a seed bank has been shown to be a mechanism of surviving in a random environment (Cohen, 1996) and a buffer against population fluctuations (Ellner, 1985a,b).

Most models for optimal seed dormancy in random environments represent the seed bank as an unstructured entity. Many models are structured spatially (Venable and Lawlor, 1980; Venable and Brown, 1988; Cohen and Levin, 1987; Rees, 1994), but none (Cohen, 1966; Bulmer, 1984; Ellner, 1985a,b; Brown and Venable, 1986; Tuljapurkar and Istock, 1993) includes structure that can force long-term dormancy. In all of these models, all seeds in the seed bank are available to germinate. The age of an egg or seed, or its depth of burial, might affect germination or hatching (Phillipi, 1993; Hairston *et al.*, 1995) and, in this case, a structured model is more suitable. Another case is a temporary pond where dormant individuals require water to break dormancy. The key feature of these situations is that all the seeds or eggs are not equally available all the time, which cannot be represented in an unstructured model.

Tuljapurkar and Istock (1993) analysed a stage structured model and an unstructured model for a population with variable diapause in a random environment. Their structured model behaves differently from the unstructured model with the greatest difference when diapause is high. They attribute their results to the effect of structure: there is extreme variability of the stage structure even for populations subject to small environmental variability, which cannot be present in an unstructured model. However, Tuljapurkar and Istock (1993) assumed a very specific type of dormancy when they constructed their structured model: a particular individual can only diapause once, and for only one time step.

Our particular motivation for a structured population model is copepod populations that possess an egg bank with the potential for long-term storage of dormant eggs. DeStasio (1989) showed that a population of *Diaptomus sanguineus* has an egg bank in Bullhead Pond, RI, with viable dormant eggs for at least 3 years. Hairston *et al.* (1995) suggested that the dormant eggs remain viable for much longer: eggs estimated to be over 100 years old were successfully hatched in the laboratory. Moreover, settling of eggs is greatest in the middle of the pond, while emergence is greatest near shore. This suggests that a structured model of the egg bank is necessary. The egg bank plays a very significant role in the population dynamics of *D. sanguineus* because active individuals are entirely eliminated from the water column each summer (Hairston and Munns, 1984). Because the bank contains the entire population for part of every year, the structure of the bank may be very important. One goal of this study was to predict what the *D. sanguineus* population in Bullhead Pond is doing: should the population have some extended dormancy?

The growth rate of the population is needed to compare the structured and unstructured models and to determine optimal dormancy strategies. The average growth rate of the population is defined according to Tuljapurkar (1989) as

$$\lambda = E \ln \left\{ \frac{\text{eggs at time } t+1}{\text{eggs at time } t} \right\} \tag{1}$$

so that $\exp(\lambda)$ is the population's geometric mean growth rate (note that equation 1 defines λ as the population's *instantaneous* rate of increase). A long-run growth rate is derived for the density-independent model and an evolutionarily stable strategy (ESS) analysis is used with the density-dependent model. In both models, a small-variance approximation of λ is derived, and the approximation of λ is used to determine optimal or ESS dormancy strategies. The small-variance approximation is an example of what are now called 'moment closure' methods (Pacala and Levin, 1997), which proceeds by deriving an infinite hierarchy of equations for stationary moments, which is closed by setting third and higher moments to zero.

We present and analyse models for a population with a structured egg bank in a random environment. The models are the matrix analogs of Cohen's density-independent seed bank model and Ellner's density-dependent seed bank model. First, the questions related to a structured copepod egg bank are addressed by deriving an approximate growth rate for a model with density-independent yield. The effects of model parameters on the growth rate and optimal dormancy strategies are analysed. Second, a more realistic and robust density-dependent model is analysed. Results for evolutionarily stable strategies in the density-dependent model are very similar to results for optimal strategies in the density-independent model. Third, the density-independent model is used to compare structured and unstructured models with an emphasis on similar comparisons made by Tuljapurkar and Istock (1993). We show that their results are due to the specific type of dormancy in their model, rather than the addition of structure. Finally, predictions are made and tested about hatching strategies of the Bullhead Pond copepod population.

DENSITY-INDEPENDENT MODEL

We view the egg bank as a structure with two components: a shallow bank and a deep bank (Fig. 1). A fraction (s) of the eggs in each bank survives, and this fraction is assumed to be constant and the same in each bank. Additions to the bank are initially deposited in the shallow bank. The source of eggs for the deep bank is a constant fraction (d) of the eggs in the shallow bank. Each year the entire shallow bank is exposed to favourable hatching conditions, while only a variable fraction (c_t) of the deep bank is exposed. Deep bank eggs that are exposed to hatching conditions but do not hatch are mixed upward to the shallow bank. The fraction of the deep bank that is exposed depends on the environment in the current year. It is assumed the fractions of the eggs that hatch (h) in each bank are the same (this assumption will be relaxed later). Each hatched egg has a per capita yield Y_t of eggs back to the bank that is assumed to depend on the environmental conditions of the current year. The population dynamics are then

$$\begin{bmatrix} X_s(t+1) \\ X_d(t+1) \end{bmatrix} = \begin{bmatrix} hY_t + s(1-d)(1-h) & hc_tY_t + (1-h)sc_t \\ sd(1-h) & s(1-c_t) \end{bmatrix} \begin{bmatrix} X_s(t) \\ X_d(t) \end{bmatrix} \tag{2}$$

where $X_s(t)$ and $X_d(t)$ are the number of eggs at time t in the shallow and deep banks respectively. The model assumes that survival and hatching fractions in each bank are independent of egg age, egg density and environmental conditions. We assume that the yield of a hatched egg is independent of where the egg hatched from, the age of the egg and the density of eggs.

Approximating the population growth rate

The population's long-run growth rate λ (equation 1) is the centre of our analysis. The growth rate λ is the stochastic analog of the dominant eigenvalue from a traditional Leslie

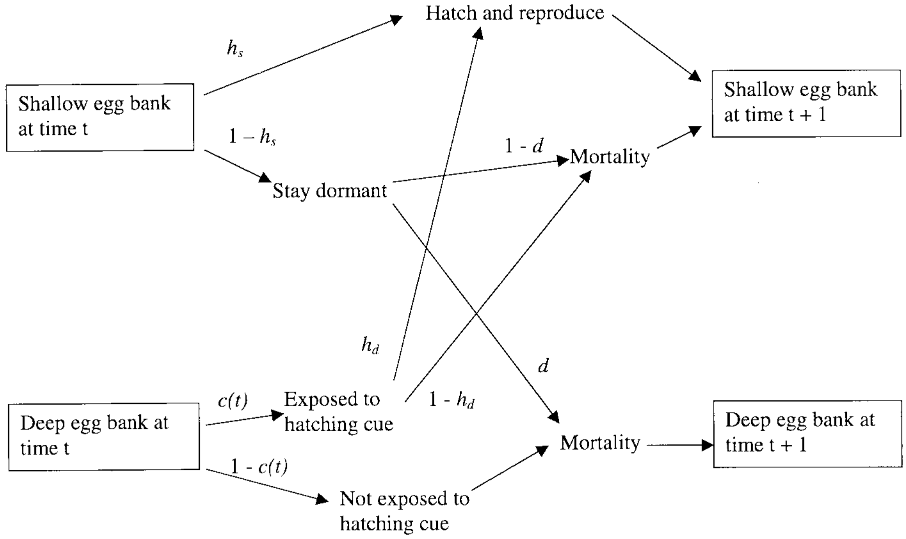


Fig. 1. Diagram of the population with a structured egg bank in the model.

matrix model. The growth of the population is described by a product of random matrices (equation 2). An expression for λ would allow us to relate the population growth rate to environmental parameters, but an exact expression only exists in special cases, so an approximation is needed (Tuljapurkar, 1990). Tuljapurkar (1984) introduced a 'ratio' method which casts the system dynamics in terms of the ratio of eggs in the shallow bank to eggs in the deep bank. This reduces the matrix difference equation (2) to a one-dimensional difference equation. The analysis relies on the ratio of age classes converging to a stationary distribution. However, when $h = 1$ in our model, the deep bank is empty and so the 'ratio' approximation becomes inaccurate as $h \to 1$. This same problem arises when using the ratio of the deep bank to the shallow bank.

The matrix equation can also be reduced to a one-dimensional difference equation by writing the model in terms of the fraction of eggs in one egg bank. This casts the system dynamics (2) in terms of the fraction of eggs in one bank, $\Phi_s = X_s/(X_s + X_d)$ for the shallow bank or $\Phi_d = X_d/(X_s + X_d)$ for the deep bank, and yields a one-dimensional difference equation of the form

$$\Phi(t+1) = F(\Phi(t), c_t, Y_t) \tag{3}$$

Expression (3) and the growth rate (equation 1) are used to derive the small-variance approximation of the population growth rate.

The stationary first and second moments of $\Phi(t)$ were calculated using Bartlett's approximation (Bartlett, 1957; Ellner, 1985), as described in the Appendix. It is assumed $c_t = \bar{c} + O(\varepsilon)$ and $Y_t = \bar{Y} + O(\varepsilon)$, that c_t and Y_t are independent of $\Phi(t)$ and of each other ($E[(c_t - \bar{c})(Y_t - \bar{Y})] = 0$), and that $E[\Phi(t)] = E[\Phi(t+1)]$. The growth rate λ is defined for the total population, but the growth rate of either egg bank is the same as the growth rate of the total population because of the exchange of eggs between banks. It is convenient, for simplifying the algebra, to use

$$\lambda = E \ln \left\{ \frac{\text{\# of eggs in deep bank at } t+1}{\text{\# of eggs in deep bank at } t} \right\} = E \ln \left\{ \frac{X_d(t+1)}{X_d(t)} \right\} \quad (4)$$

and let Φ be the fraction of eggs in the deep bank. The ratio of eggs in (4) is expressed in terms of Φ and the population projection matrix (2). The logarithm in (4) is expanded in a Taylor series to second order in ε and the expectation is taken. Substituting in the moments derived above, the result is an expression for λ in terms of $h, s, d, \bar{c}, \sigma_c, \bar{Y}$ and σ_Y,

$$\lambda = G(h, s, d, \bar{c}, \sigma_c, \bar{Y}, \sigma_Y) \quad (5)$$

These calculations were performed using the symbolic software Maple. Equation (5) allows us to numerically compare dormancy strategies and determine optimal strategies. Later, a similar expression in the density-dependent model determines whether a 'rare' invader population is successful.

S. Tuljapurkar (personal communication) has noted that the small-fluctuations approximation for λ can be derived more elegantly from his general results (Tuljapurkar, 1990, eq. 12.1.16). However, this derivation does not extend to the density-dependent model, whereas Bartlett's moment-closure method can be applied to both models in very similar ways.

Testing the accuracy of the approximation

The growth rate λ can be compared exactly when $h = 1$, and this provides a check for the general approximation. The comparison will show the approximation is correct to second order. When $h = 1$, all the eggs in the shallow bank hatch, and the deep bank does not receive new eggs, so the deep bank empties by eggs hatching or dying. The dynamics of the vanishing deep bank are $X_d(t+1) = s(1 - c_t)X_d(t)$ and the growth rate is $\lambda_d = E \ln \{s(1 - c_t)\}$. The small-variance approximation for the growth rate of the deep bank is

$$\lambda_d = \ln(s(1 - \bar{c})) - \frac{\operatorname{var}(c_t)}{2(1 - \bar{c})^2} \quad (6)$$

With the deep bank empty, the model reduces to $X_s(t+1) = Y_t X_s(t)$. In this case,

$$\lambda_s = E \ln \left\{ \frac{X_s(t+1)}{X_s(t)} \right\} = E \ln\{Y_t\}$$

The small-variance approximation for λ_s is

$$\lambda_s = \ln \bar{Y} - \frac{1}{2\bar{Y}^2} \operatorname{var}(Y_t) \quad (7)$$

These answers are consistent with the λ derived from the full model when the fractions in each bank are used. When equation (5) is derived in terms of the fraction in the deep bank or the shallow bank, the expressions for λ at $h = 1$ simplify to λ_d (7) or λ_s (6) respectively. Additionally, a dormancy condition similar to Cohen's can be derived. Dormancy is favoured if

$$\left. \frac{\partial \lambda}{\partial h} \right|_{h=1} < 0 \quad (8)$$

The structured egg bank is a single unstructured bank if $d = 0$ or $\bar{c} = 1$; when equation (8) is evaluated at either of these values, we get Cohen's condition for dormancy from our structured model dormancy condition.

When $h \neq 1$, the approximation to λ is not as simple as equation (6) or (7) and must be evaluated numerically. The analytic growth rate λ is compared to the growth rate from a simulated population to evaluate the accuracy of the approximation (Fig. 2). In the simulations, the yield $Y(t)$ is log-normally distributed and the fraction of the deep bank that is exposed to favourable hatching conditions c_t is distributed uniformly. The simulated population was run for 100 generations, then a population growth rate was determined for the next 19,900 generations. Simulated and analytic growth rates were calculated for 1944 parameter combinations. The parameters $\bar{c}$ and d take all combinations of the values 0.2, 0.5 and 0.8, while σ_c is 0.01, 0.09, 0.17 and 0.25. The value of 0.25 for σ_c is not used when $\bar{c}$ is 0.2 or 0.8 because the fraction c_t must be inside the range [0,1]. These parameter values cover the range of possible egg bank types from almost no movement between banks to rapid exchange of eggs between banks. Survival of dormant eggs is high (Hairston *et al.*, 1995), so parameter s takes the values 0.9, 0.94 and 0.98. Per capita yields are close to or equal to 1 and the variances cover coefficients of variation between 0.0 and 0.32. For these parameter ranges, typical values of λ range from –0.07 to 0.09.

The mean errors between simulated and approximated growth rates are on the order of 10^{-4} to 10^{-5} and the variances of these errors are on the order of 10^{-7} to 10^{-10} (Fig. 2). The larger error variances correspond to larger variance of $Y(t)$; the variability in $c(t)$ has no effect on the accuracy of the approximation (Fig. 2). The small difference between the simulated and approximate growth rates validates use of the approximation to study the behaviour of the system.

Results: Density-independent model

We now consider how the model parameters affect λ and the optimal hatching fraction. One case of interest is when d and c are both small: most eggs or seeds do not get deeply buried, but those that do are unlikely ever to emerge. The size of the egg or seed bank may nonetheless be large if s is high, because even with small burial rate d, buried individuals can accumulate over many years. This case is probably relevant to many plant species, where deep burial and emergence would only occur as a result of occasional large disturbances to the soil. For this case, we can approximate λ by a joint expansion in c, d and the variance in Y, as in Ellner (1996, section 4). The result is $\hat{\lambda} = \hat{\lambda}_0 + ds(h-1)$, where $\hat{\lambda}_0$ is the approximate λ for $d = c = 0$. We see from this expression that the population growth rate is decreased (to leading order) by an egg bank with small burial and emergence, and that the optimal value of h is increased. These results are, in retrospect, intuitive: if d and c are both $O(\varepsilon)$, then the loss rate to burial (eggs per year) is $O(\varepsilon)$, while the return rate from burial is $O(\varepsilon^2)$. Consequently, the population growth rate is decreased, and it pays to avoid burial, so the optimal h goes up.

For larger d and c, we used simulations to compute the partial derivatives of the approximation of λ (5) with respect to each parameter, at 911,250 parameter combinations covering the range of the fractions for $\bar{c}$, d, s and h. The parameters $\bar{c}$, d and s take the values from 0.1 to 0.9 in increments of 0.1. Mean yield takes the values 1.0 to 1.5 in increments of 0.1 and the coefficient of variation of the yield and $\bar{c}$ ranges between 0.007 and 0.17. The derivatives reveal that the approximation of λ is increasing in s, $\bar{c}$ and $\bar{Y}$, whereas it is

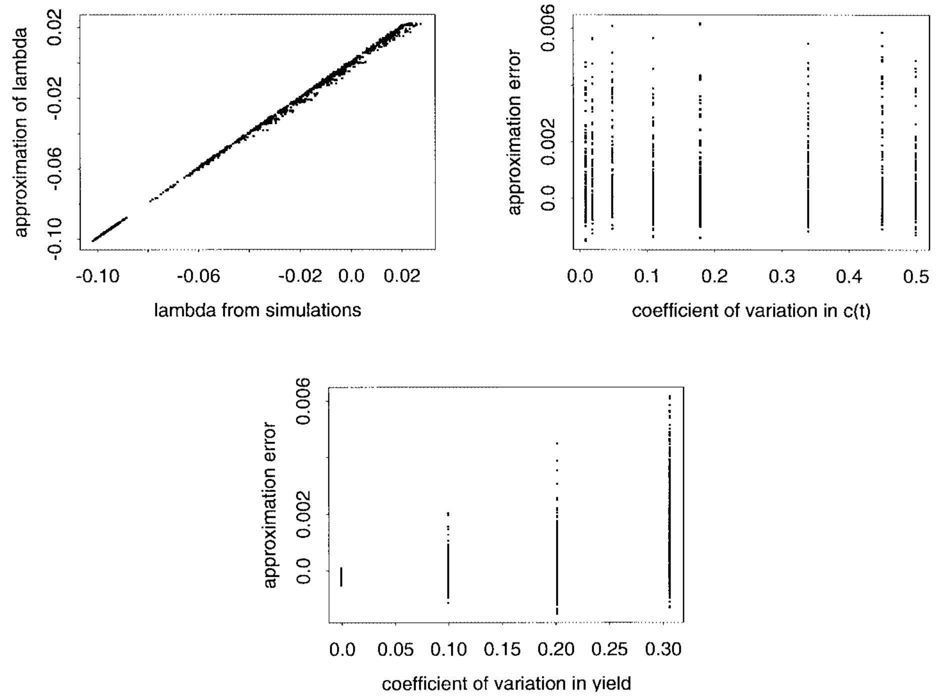


Fig. 2. Comparison of the small-variance approximate growth rate for the density-independent model with the observed growth rate in simulations. Approximation errors (simulation – analytic) as a function of the variability in $c(t)$ and $Y(t)$.

decreasing in σ_c^2, σ_Y^2 and d, over the entire range of parameters examined. The growth rate decreasing in σ_c^2 and σ_Y^2 implies a more variable environment is bad for the population. The results for s and $\bar{Y}$ are expected; higher survival or per capita yield benefits the population. The effects of d and c on λ show the negative effect of long-term storage of eggs. The growth rate λ is increasing in $\bar{c}$ and this implies that the fewer eggs in long-term storage the better. The growth rate λ decreasing in d shows that eggs moving into long-term storage is detrimental to the population.

More important than changes in the growth rate is how the optimal hatching fraction is affected by the model parameters (Table 1). The derivatives of the optimal hatching fraction with respect to each parameter were evaluated numerically, at the parameter combinations described above. Structuring the egg bank does not change Cohen's (1966) main results: increased survival or environmental variability favours more dormancy, and increased mean yield favours decreased dormancy (Fig. 3). The parameters d and $\bar{c}$ affect the nature of the egg bank. An increase in the fraction (d) of eggs in the shallow bank moving to the deep bank increases h_{opt} and the increase is greatest for small $\bar{c}$ (Fig. 3). Conversely, increasing $\bar{c}$ decreases h_{opt} with the most change occurring when d is large. When $\bar{c}$ is small, eggs that move to the deep bank have fewer opportunities to hatch and the deep egg bank is a 'strong' bank. Increasing the burial rate (d) increases the number of unhatched eggs moving to the 'strong' long-term bank and the increase in h_{opt} can be interpreted two ways. First, eggs in

Table 1. Effects of changes in model parameters on the optimal hatching fraction in the density-independent model[a]

Parameter	Change in parameter	Change in h_{opt}
d	↑	↑
$\bar{c}$	↑	↓
σ_c^2	↑	none
s	↑	↓
$\bar{Y}$	↑	↑
σ_Y^2	↑	↓

[a] Parameter definitions are as follows (see also Fig. 1): d is the fraction of non-hatching shallow eggs that sink into the deep egg bank; c is the fraction of deep eggs that are exposed to the hatching cue by being mixing upward into the shallow egg bank; s is the survival probability of eggs (deep or shallow); Y is the per capita yield of eggs (eggs produced per hatched egg). Overbars denote means and σ^2 indicates the variance.

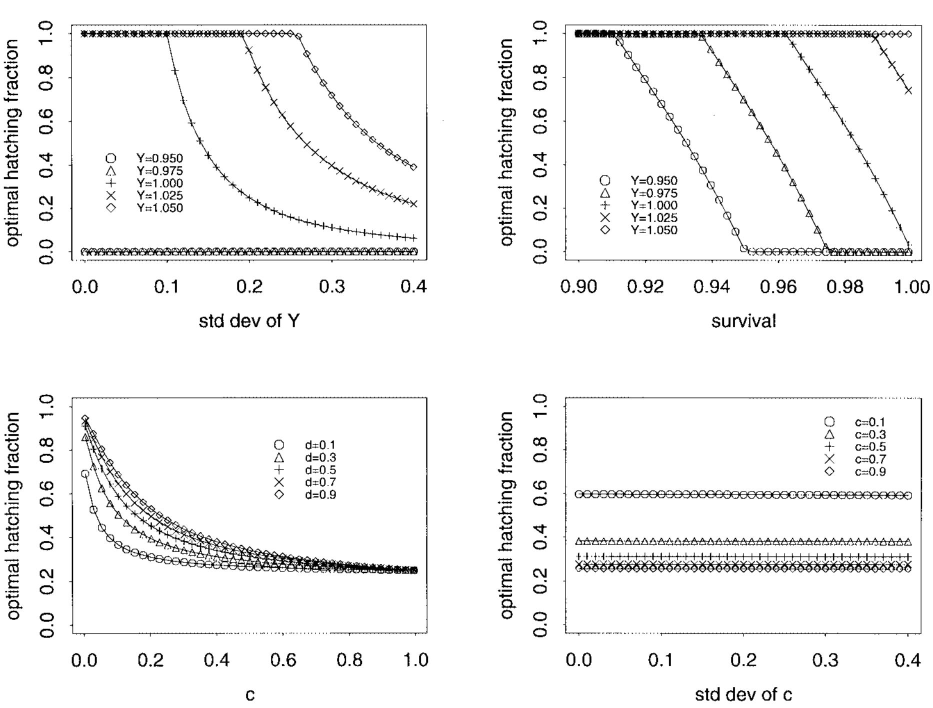


Fig. 3. Optimal hatching fractions for the density-independent model as functions of model parameters. Unless otherwise noted in the legends, the parameter values are $d = 0.5$, $\bar{c} = 0.5$, $\sigma_c = 0.1$, $\bar{Y} = 1.0$, $\sigma_Y = 0.2$, $s = 0.99$.

the shallow bank should hatch before moving to the deep where hatching opportunities may be rare. Second, as d increases, more dormant eggs are in the deep bank and those eggs should hatch when the rare favourable conditions are available. Increasing $\bar{c}$ increases the frequency of good hatching conditions in the deep bank and the threat of not surviving to the next reproductive opportunity is lower, resulting in dormancy being favoured. Increasing the variability of the yield decreases h_{opt}, but changing σ_c^2 does not have a significant effect on h_{opt} (Fig. 3).

The conclusion that σ_c^2 has almost no effect on λ or h_{opt} appears to be very general. We used simulations, as above, to compare the population growth rate under two extreme assumptions about $c(t)$: $c(t)$ held constant at $\bar{c}$, and $c(t)$ taking the values 1 with probability $\bar{c}$ and 0 with probability $1 - \bar{c}$. Simulations were run for all combinations of d and $\bar{c}$ running from 0.1 to 0.5, h running from 0.2 to 0.8, and s running from 0.2 to 0.9, each in increments of 0.1. Simulations were paired, in that the same random sequence of $Y(t)$ values was used for corresponding runs with constant and variable $c(t)$ [$\log(Y)$ normally distributed with $\mu = 0.1$, $\sigma = 0.3$, and a second set with $\mu = 0.3$, $\sigma = 0.5$]. Population growth rates for variable c were lower on average, but only by a tiny amount. The relative errors between the finite rates of increase $\exp(\lambda)$ for variable and constant c had a mean magnitude of 0.22%, and a maximum magnitude of 2.8%. So, even for the situation where emergence from the deep bank only occurs as a result of occasional large-scale disturbance, the model behaves in the long run as if the emergence rate were constant.

DENSITY-DEPENDENT MODEL

An evolutionarily stable strategy analysis is used for the density-dependent model. The ESS analysis evaluates when a rare invader with a given hatching strategy can invade an established population with a different strategy. The established population's strategy is evolutionarily stable for a given environment and egg bank structure if no other strategy can invade. The fraction method is extended to derive an approximation to λ for a rare population invading an established population.

We now consider a population with a density-dependent yield of eggs. The model is the same as equation (2) apart from two changes. First, the yield of eggs is density-dependent. Second, the density-independent model showed that variability in $c(t)$, the faction of the deep bank exposed to favourable hatching conditions, had no effects, so $c(t)$ is changed to a constant c in the density-dependent model. This results in the following population dynamics:

$$X_{s,i}(t+1) = s(1-d)(1-h_i)X_{s,i}(t) + sc(1-h_i)X_{d,i}(t) + h_i(X_{s,i}(t) + cX_{d,i}(t))Y(t) \qquad (9)$$

$$X_{d,i}(t+1) = sd(1-h_i)X_{s,i}(t) + s(1-c)X_{d,i}(t) \qquad (10)$$

where $X_{s,i}$ and $X_{d,i}$ are the number of eggs with hatching strategy h_i in the shallow and deep banks respectively.

For the yield of eggs to the egg bank, we use the 'saturating yield' model of Levin *et al.* (1984). We assume that the total yield of eggs each year is a random variable $K(t)$, with mean $\bar{K}$ and variance σ_K^2. Yield is defined as the number of eggs deposited to the egg bank. By the saturating yield model, the per capita yield of type i eggs is

$$Y_i(t) = \frac{K(t)}{\sum_j (h_j X_{s,j}(t) + h_j c X_{d,j}(t))} \tag{11}$$

To find the ESS hatching fraction, consider a 'rare' invader invading an established population. The populations are identical except for the hatching fraction of dormant eggs, with the established and invading populations having hatching fractions H and h respectively. The invasibility analysis is based on the boundary growth rate of each competitor $\lambda(h, H)$ defined such that $e^{\lambda(h, H)}$ is the geometric mean growth rate of type h invading type H. The invasibility of a population of type H can then be described by:

if $\lambda(h, H) < 0$, then h cannot invade H

if $\lambda(h, H) > 0$ and $\lambda(H, h) > 0$, then h and H co-exist

Thus a hatching fraction H^* is an ESS if $\lambda(h, H^*) < 0$ for all $h \neq H^*$.

We approximate λ as follows. The boundary growth rate $\lambda(h, H)$ is defined as

$$\lambda(h, H) = E \ln \left\{ \frac{X_{d,\text{inv}}(t+1)}{X_{d,\text{inv}}(t)} \right\} \tag{12}$$

The approximation of (12) closely follows the derivation of λ in the density-independent model, which assumes that Y_t is independent of $X_s(t)$ and $X_d(t)$. This assumption applies to both the invader (X_{inv}) and established (X_{est}) populations and to the eggs in either egg bank. The invader is density-independent and the yield depends only on the density of the established population. For the invader, (9) and (10) simplify to

$$\begin{bmatrix} X_{s,\text{inv}}(t+1) \\ X_{d,\text{inv}}(t+1) \end{bmatrix} = \begin{bmatrix} s(1-d)(1-h) + hY_h(t) & sc(1-h) + hcY_h(t) \\ sd(1-h) & s(1-c) \end{bmatrix} \begin{bmatrix} X_{s,\text{inv}}(t) \\ X_{d,\text{inv}}(t) \end{bmatrix} \tag{13}$$

where

$$Y_h(t) = \frac{K(t)}{H(X_{s,\text{est}}(t) + cX_{d,\text{est}}(t))} \tag{14}$$

If equation (13) is written in terms of the variable $P(t)$, where

$$P(t) = \frac{X_{s,\text{inv}}(t)}{X_{s,\text{inv}}(t) + X_{d,\text{inv}}(t)} \tag{15}$$

the result is a one-dimensional equation:

$$P(t+1) = F(P(t), X_{s,\text{est}}(t), X_{d,\text{est}}(t), K(t)) \tag{16}$$

Note from equations (14) and (16) that $P(t)$ depends on the number of eggs from the established population in each bank. The variances of $X_{s,\text{est}}(t)$ and $X_{d,\text{est}}(t)$ and their covariance are therefore needed in the approximation of λ (equation 16). To get these values, note that for a single established type the dynamics of (9, 10) simplify to

$$\begin{bmatrix} X_{s,\text{est}}(t+1) \\ X_{d,\text{est}}(t+1) \end{bmatrix} = \begin{bmatrix} s(1-d)(1-H) & sc(1-H) \\ sd(1-H) & s(1-c) \end{bmatrix} \begin{bmatrix} X_{s,\text{est}}(t) \\ X_{d,\text{est}}(t) \end{bmatrix} + \begin{bmatrix} K(t) \\ 0 \end{bmatrix} \tag{17}$$

Equation (17) is a linear system with known solution, from which the variances and covariance of $X_{s,\text{est}}(t)$ and $X_{d,\text{est}}(t)$ can be derived (see Appendix). The result is $\lambda(h, H)$ as a function of the model parameters:

$$\lambda(h, H) = F(s, c, d, \bar{K}, \sigma_K, h, H) \tag{18}$$

Testing the accuracy of the approximation

In Fig. 4, the approximate invader growth rate $\lambda(h, H)$ is compared to simulations, as was done above for the density-independent model. Altogether, 2160 parameter combinations are used to determine the growth rate for the invading population by simulation and by the analytic approximation. The same values used to check the density-independent model are used for the parameters s, d and c in the density-dependent model. Mean yield $\bar{K}$ is between 8000 and 9000 eggs and the coefficient of variation of $K(t)$ takes values between 0.0 and 0.42. Five different hatching fractions are used for the invader (0.1 to 0.9 at intervals of 0.2) and established (0.15 to 0.95 at intervals of 0.2) populations. The simulations run for 200 generations to let the established population converge to its stationary distribution, and then the mean growth rate of the invader is calculated over the next 14,800 generations. The small-variance approximation has an error on the order of 10^{-3} for a coefficient of variation of 0.3 on the yield, and the approximation and simulation are very close ($< 10^{-4}$) for coefficients of variation of 0.01 (Fig. 4).

Results: Density-dependent model

On the merits of the comparison to simulations, $\lambda(h, H)$ is used to investigate the behaviour of the ESS hatching fraction H^* under various parameter combinations (Table 2). The main issue is the effect of the structured egg bank. Increasing the fraction d of eggs moving from the shallow to the deep bank increases H^* (Fig. 5). The increase in H^* indicates there is a penalty for not hatching and staying in the bank. There are two interpretations of this result. One is that the penalty of being trapped in the deep bank is great enough that more individuals should hatch after one season of dormancy and avoid the potential misfortune of being moved to the deep bank. The other is that, with an increase of eggs moving to the deep bank, eggs in the deep bank should hatch when exposed to hatching conditions. The magnitude of the increase in H^* depends on the fraction c of the deep bank that is exposed

Table 2. Effects of changes in model parameters on the ESS hatching fraction in the density-dependent model[a]

Parameter	Change in parameter	Change in H^*
d	↑	↑
$\bar{c}$	↑	↓
s	↑	↓
$\bar{K}$	↑	↑
σ_K^2	↑	↓

[a] See Table 1 for parameter definitions.

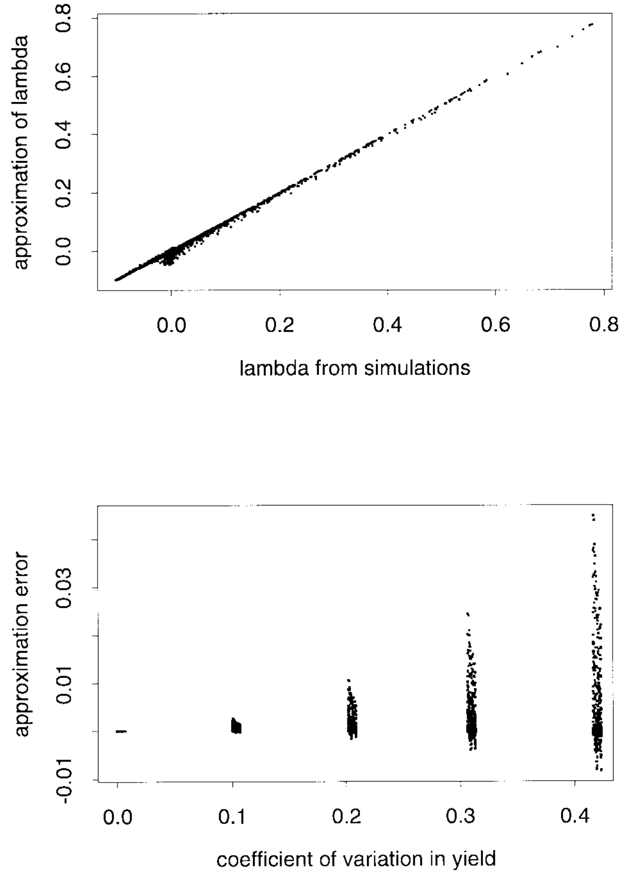


Fig. 4. Small-variance approximate growth rate for the density-dependent model versus the observed growth rate in simulations. Approximation errors (simulation – analytic) as a function of the variability in $K(t)$.

to hatching conditions. Large values of c correspond to a 'weak' deep bank and most of the eggs are exposed to hatching conditions. In this case, changing d has little effect on H^* because moving to the deep bank is essentially the same as staying in the shallow bank. Small values of c correspond to a 'strong' deep bank and, in this case, changing d can have a large effect on H^*. These qualitative relationships between c and d stay the same for all levels of environmental variability.

As in the density-independent model, for the case of small c and d, the return rate from the deep bank is negligible, and the structured model reduces to an unstructured model in which the effective seed survival is $s(1 - d)$. Consequently, the effect of an increase in d is equivalent to a decrease in s in an unstructured model, and the result is an increase in H^*.

For a fixed value of c, the ESS hatching fraction increases with d. However, the same cannot be said for a fixed value of d. When d is small (< 0.2), the largest ESS hatching fractions in all environments are for the extreme values of c. It should be noted that, at

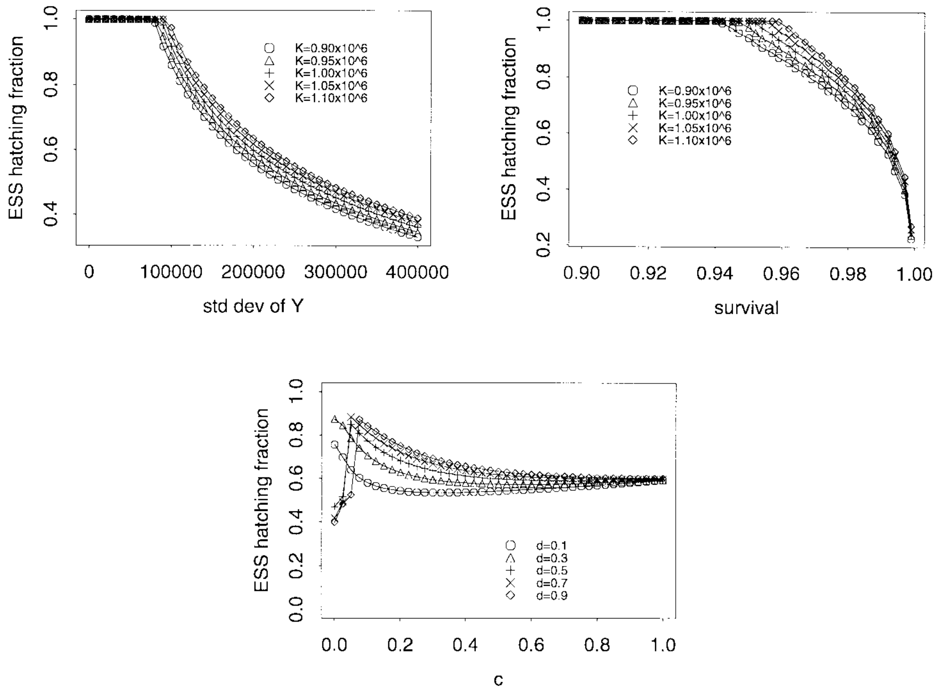


Fig. 5. ESS hatching fractions for the density-dependent model as functions of model parameters. Unless otherwise noted, the parameter values are $d = 0.5$, $\bar{K} = 1 \times 10^6$, $\sigma_K = 2 \times 10^5$, $s = 0.99$.

$d = 0.0$, the structured and unstructured models are the same and the value of c will not influence the ESS fraction (Fig. 5). For large d, the ESS hatching fraction decreases as c increases. The point or region where the behaviour changes has not been determined.

The effect of the other model parameters on H^* are the same as in the unstructured model (Ellner, 1985a,b). Increased egg survival favours increased dormancy (Fig. 5). In cases where survival is low, 100% hatching is favoured even if the variability of yield is high. Increasing $\bar{K}$ or decreasing σ_K has the effect of decreasing the coefficient of variation of $K(t)$ and increasing H^* (Fig. 5).

STRUCTURED VERSUS UNSTRUCTURED MODELS

Tuljapurkar and Istock (1993) modelled a structured population with variable diapause in a randomly varying environment. They compared a structured model to an unstructured model and analysed the effect of diapause and environmental variability on the population's growth rate in each model. Tuljapurkar and Istock (1993) concluded that the structured and unstructured models behave very differently when the diapause fraction f is large. They also suggested that a structured model leads to the prediction of a broad range of optimal diapause strategies. Tuljapurkar and Istock's structured model is

$$\begin{bmatrix} O_{t+1} \\ D_{t+1} \end{bmatrix} = \begin{bmatrix} R_t(1-f) & R_t s \\ f & 0 \end{bmatrix} \begin{bmatrix} O_t \\ D_t \end{bmatrix} \tag{19}$$

Following Cohen (1966), their unstructured model is

$$O_{t+1} = [R_t(1-f) + sf]O_t \tag{20}$$

where O_t is the number of offspring and D_t is the number of diapausers. R_t is the per capita reproductive rate, s is the fraction of diapause survivors, and f is the fraction of offspring that go into diapause.

However, we note that equation (19) does not just add structure to equation (20), it also changes the nature of diapause in the model. Diapause is for only one time step in their structured model (19). An individual that is in diapause at time t must reproduce at time $t+1$, and the offspring of that individual are in diapause at time $t+2$. The unstructured model allows an individual to spend several successive years in diapause because it does not distinguish whether an individual is from diapause or reproduction. Both models assume that mortality is 100% following reproduction.

Our models add structure to equation (20), without changing the nature of diapause. However, to compare our results with those of Tuljapurkar and Istock (1993), we first need to relax the assumption of equal hatching fractions in both egg banks. With h_s and h_d being the hatching fractions in the shallow and deep bank respectively, the density-independent model (2) becomes:

$$\begin{bmatrix} X_s(t+1) \\ X_d(t+1) \end{bmatrix} = \begin{bmatrix} h_s Y(t) + s(1-d)(1-h_s) & h_d c(t) Y(t) + (1-h_d) s c(t) \\ sd(1-h_s) & s(1-c(t)) \end{bmatrix} \begin{bmatrix} X_s(t) \\ X_d(t) \end{bmatrix} \tag{21}$$

This model contains both our density-independent model (2) and Tuljapurkar and Istock's (1993) model as special cases. With $d = c = h_d = 1$, (21) simplifies to

$$\begin{bmatrix} X_s(t+1) \\ X_d(t+1) \end{bmatrix} = \begin{bmatrix} h_s Y_t & Y_t \\ s(1-h_s) & 0 \end{bmatrix} \begin{bmatrix} X_s(t) \\ X_d(t) \end{bmatrix} \tag{22}$$

Note that (22) has the same dynamics as (19) when $h_s = 1 - f$; our hatching fraction is one minus their diapause fraction. The variable O_t is the same as X_s, while $D_t = X_d/s$. The difference between D_t and X_d emerges when mortality of diapausers is accounted for in the models and does not change the behaviour of the models. The unstructured model can be expressed in terms of the structured density-independent model parameters as

$$X(t+1) = [(1-h)s + hY(t)]X(t) \tag{23}$$

with the same assumptions on s, h and $Y(t)$ as the structured model. The growth rate of (23) is given by

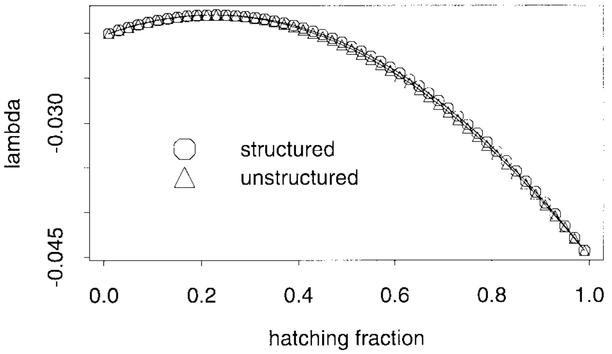
$$\lambda_u = E \ln[(1-h)s + hY(t)] \tag{24}$$

Tuljapurkar and Istock's (1993) claim that structured and unstructured models are very different for large diapause fractions is not true in our model (21). There is a difference in the growth rates λ and λ_u but the difference is for intermediate values of the diapausing fraction (Fig. 6). When the diapausing fraction is high (hatching fraction is low), the unstructured and structured models give very similar predictions of the growth rate, and the growth rates for the structured and unstructured population are identical when diapause is 100%. Total diapause corresponds to no hatching. In this case $h = 0$ and (24) shows that the unstructured model population decreases at a rate of $\ln(s)$. When $h_s = h_d = 0$ in our structured model, we have

$$\begin{bmatrix} X_s(t+1) \\ X_d(t+1) \end{bmatrix} = \begin{bmatrix} s(1-d) & sc \\ sd & s(1-c) \end{bmatrix} \begin{bmatrix} X_s(t) \\ X_d(t) \end{bmatrix} \tag{25}$$

Note that $X_s(t+1) + X_d(t+1) = s(X_s(t) + X_d(t))$; this population also decays at a rate of $\ln(s)$. So the structured and unstructured models have very similar growth rates for small hatching fractions (large diapause fraction) and identical growth rates for no hatching (Fig. 6).

In our models, structure is added to the egg bank without changing the nature of diapause. In both the structured and unstructured versions of our model, individuals are allowed to diapause multiple times. Thus, it is possible to see the effect of adding structure in our models, while Tuljapurkar and Istock's (1993) comparison between structured and unstructured models is confounded by their change in the nature of diapause. As noted above, our structured and unstructured models make identical predictions $h = 0$ and 1. Between these end-points, the differences between the models change as the nature of the egg bank structure changes. The models predict almost identical growth rates for a 'weak' structured deep egg bank (Fig. 6). In this case, most of the eggs in the deep bank are exposed to favourable hatching conditions. The difference in predicted growth rates grows



strong deep bank

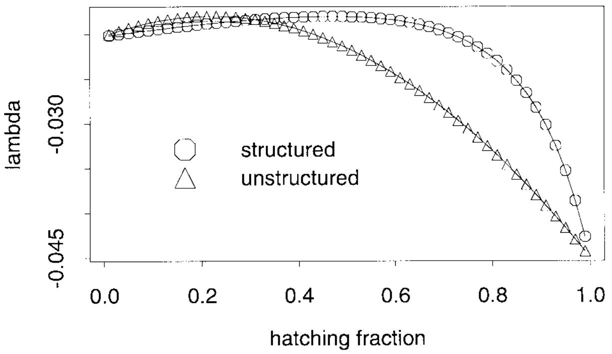


Fig. 6. Comparison of the growth rates for structured and unstructured models. Comparisons are made for a 'weak' deep bank ($d = 0.2$, $c = 0.8$) and a 'strong' deep bank ($d = 0.8$, $c = 0.2$). Other parameters are $s = 0.98$, $\bar{Y} = 1.0$, $\sigma_Y = 0.3$.

as the deep egg becomes 'stronger' (Fig. 6). The differences are for $0 < h < 1$, and the nature of the deep egg bank does not change the fact that the models produce identical predictions at $h = 0$ and 1.

Adding structure to the egg bank makes a significant difference in the population growth rate and the optimal hatching fraction. The structure increases the optimal hatching fraction regardless of the nature of the egg bank structure. This may indicate long-term storage favours reduced dormancy and that the rare opportunities to 'escape' long-term storage should be taken. The optimal hatching fraction can be significantly higher in the structured model. No parameter combinations have been found where the structured model has a lower optimal hatching fraction than the unstructured model. As with the predicted growth rates, the difference in the optimal hatching fraction grows as the 'strength' of the deep egg bank grows. The deep egg bank effectively increases mortality and this favours a higher optimal hatching fraction (Cohen, 1966).

Tuljapurkar and Istock (1993) state that adding population structure produces a much broader range of hatching fractions with growth rates very close to the optimum. In some examples of their model, the optimum is almost attained for more than half the parameter space. To determine if this result remains valid in our generalization of Tuljapurkar and Istock's model, we compared the second derivative with respect to the hatching fraction of λ, evaluated at the optimal hatching fraction, in the structured and unstructured versions of the model. The same parameter combinations used to test the approximation of λ were used. The structured model generally does produce a broader optimum (second derivative smaller by a factor of 10, on average). However, plots of λ typically do not have values near the optimum for many or most of the values of h, even in the structured model. Adding structure definitely broadens the optimum, but the effect is not as dramatic as in Tuljapurkar and Istock's model. They suggest a broad optimum could account for the maintenance of multiple diapause phenotypes in a population. Our results indicate that an optimum broad enough to support this argument would only occur in one-year-only diapause models like that of Tuljapurkar and Istock's; our small-variance approximation of Tuljapurkar and Istock's model also has a broad optimum.

DISCUSSION

Many organisms possess a dormant life-stage and dormancy can be a strategy of survival in an unpredictable environment. The results presented here continue the work of Cohen and Ellner by adding structure to the seed or egg bank. The central feature of the analysis is the reduction of the matrix-difference equation to a one-dimensional equation so that the moments of the population vector can be derived. The ratio method suggested by Tuljapurkar (1984) failed when the parameters are such that the bank in the denominator of this ratio can become empty. This problem was possibly avoided in previous work because it was used in age-structured models where neither age class could disappear. With a structured egg bank, it is entirely possible that one component is empty while the total population continues to persist.

Adding structure to the egg bank can make significant changes to the optimal hatching strategies. While it adds biological reality, adding structure to the egg bank also makes the approximation of the growth rate such an involved calculation that symbolic software is the only reasonable way to handle the algebra. The accuracy of the approximation suggests that the extra complexity and computer time are worth the effort. Rees (1994) modelled a structured plant population with seeds and adults. Because an analytic determination of the dominant Lyapunov exponent was not possible for his random environment model, Rees (1994) used simulation to determine the ESS germination strategy. This paper shows that a very accurate approximation of the Lyapunov exponent can be determined and the approximation provides a way to thoroughly examine the model predictions.

One motivation for the structured egg bank model was the *Diaptomus sanguineus* population in Bullhead Pond. An obvious application of the models is to predict what the optimal hatching strategy should be for these copepods. Model parameters for the density-independent and density-dependent models can be estimated using information from DeStasio (1989), Hairston *et al.* (1995, 1996) and unpublished field and experimental data (see Ellner *et al.*, 1999, for a summary of the available data). Egg survivorship and movement of eggs between egg banks are the same for both models (parameters c, d and s). There is little upward mixing in the sediment of Bullhead Pond (Kearns *et al.*, 1996), so the parameter c is assumed to be small ($0.04 < c < 0.2$); based on Ellner *et al.* (1999, table 2), we can roughly estimate $c = 0.1$. For Bullhead Pond, the 'shallow' bank is the leaves of submerged macrophytes and the sediment surface. Eggs are in this 'shallow' bank for a short time before becoming covered by fresh sediments. Therefore, the sinking rate parameter d is large ($0.9 < d < 0.99$). Hairston *et al.* (1995) report egg survival rates (s) of 98–99%.

The density-dependent model requires an estimate of the yield $K(t)$, which is simply the total number of eggs produced in year t. From 7 years of data, the total number of eggs produced (estimated as in Ellner *et al.*, 1999) has a mean of 9.1×10^9 with a standard deviation of 4.6×10^9. The yield $K(t)$, therefore, has a coefficient of variation of 0.51. Using the small-variance approximation, the predicted ESS hatching fractions in the density-dependent model were between 0.41 and 0.74 for the parameter ranges given above. In simulations with log-normally distributed $K(t)$, the ESS hatching fractions were just slightly higher (0.55–0.8); once again, the 'small-variance' approximation works even at high variance. The density-independent model requires an estimate of per capita yield. The average emergence from the egg bank over 3 years was 1.47×10^9 nauplii (DeStasio, 1989). Based on this emergence rate and total egg production, a very rough estimate of mean per capita yield is $E[Y_t] \approx 6$. A mean per capita yield this high always resulted in an optimal hatching fraction of $H = 1$, since there are no catastrophe years with zero yield.

Which of these predictions is best supported by the data? The large number of eggs in long-term diapause in this population (Hairston *et al.*, 1995) is not necessarily evidence that H is below 1, because the large value of d and small value of c would allow the egg bank to build up even if H is very close to 1. However, there is indirect experimental evidence that H is fairly small. Most eggs require more than 12 months of incubation in the laboratory before they hatch (Hairston *et al.*, 1996) and, therefore, would not hatch in the fall after they were produced. Based on the distribution of egg incubation times in the laboratory (Hairston *et al.*, 1996), $H \approx 0.25$ would be a reasonable estimate. This estimate assumes that all eggs spend their first year in the 'shallow' bank, and corresponds to the fraction of eggs (derived from females sampled from the water column) that hatch within 12 months of incubation. This is not too far from the predictions of the density-dependent model. Several factors may account for the difference. First, the experimental conditions (Hairston *et al.*, 1996) did not include a rewarming 'spring' period following the simulated 'winter' conditions, so the laboratory hatching rate may be an underestimate of what occurs in the field.

Second, in the actual population there is phenotypic and presumably genetic variance for hatching rate (Hairston *et al.*, 1996), and this is not accounted for in the model considered here. Finally, the ESS hatching fraction is very sensitive to small changes in s when s is near 1 (Ellner, 1985a,b); in particular, increasing s from 0.99 to 1.0 will bring the ESS H down to 0. Given that 50% hatching was obtained on eggs estimated to be about 300 years old (Hairston *et al.*, 1995), $s = 0.997$ might be a reasonable estimate, and this produces predicted ESS values as low as 0.32 within our bounds on the other parameters.

For many plant populations, a reasonable assumption is that the seed burial rate d and the emergence rate c are both small. The optimal or ESS hatching strategy will then be close to that of an unstructured model in which burial is counted as mortality (so that the effective seed survival is $s(1 - d)$). We also found that variability in c has little effect on model predictions: even if seeds only emerge from burial during rare years when a large disturbance occurs, the population behaves in the long run as if the emergence rate were constant. Our results in the preceding section call into question Tuljapurkar and Istock's (1993) argument that population structure *per se* can explain observations of co-existence diapause types in a population, because it causes selection to be weak in the neighbourhood of the optimum diapause strategy. Although weak selection does occur in their model, we found that it does not occur if long-term persistence in diapause is possible. Consequently, our results support adaptive explanations (developed for example by Geritz, 1995; Hairston *et al.*, 1996; Geritz *et al.*, 1999) for diversity of seed or egg types within a single population.

More generally, this paper makes two important points for modelling dormancy. First, a structured model is needed when some portion of the population is unavailable for hatching in a given year. There are many cases where the biology suggests this type of model and we have presented a convenient method for analysing such models. One needs to consider if part of the population under consideration is not part of the current active population. Second, the nature of dormancy assumed in a structured model should be carefully noted. Comparing our results with those of Tuljapurkar and Istock (1993) reveals that two reasonable but different dormancy models can give very different predictions.

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APPENDIX: APPROXIMATION OF λ

The first step in deriving an approximation for λ is using Bartlett's method to derive the stationary moments of (3). The right-hand side of (3) is expanded in a Taylor series in $\Phi(t)$, $c(t)$ and $Y(t)$ about the stationary point $(\Phi_0, \bar{c}, \bar{Y})$, where $\Phi_0 = F(\Phi_0, \bar{c}, \bar{Y})$. This results in

$$\Phi(t+1) = \Phi_0 + \frac{\partial \tilde{F}}{\partial \Phi}(\Phi(t) - \Phi_0) + \frac{\partial \tilde{F}}{\partial c}(c(t)) - \bar{c}) + \frac{\partial \tilde{F}}{\partial Y}(Y(t) - \bar{Y}) + \cdots \tag{A1}$$

$\tilde{F}$ means that the expression is evaluated at $(\Phi_0, \bar{c}, \bar{Y})$. It is assumed that $c(t) = \bar{c} + O(\varepsilon)$ and $Y(t) = \bar{Y} + O(\varepsilon)$. The stationary point Φ_0 is subtracted from both sides and equation (A1) is squared. $\Phi(t)$, $c(t)$ and $Y(t)$ are independent (i.e. $E[c(t)Y(t)] = 0$) by assumption and $E[\Phi(t)] = E[\Phi(t+1)]$ by stationarity. All terms of $O(\varepsilon^3)$ or higher are dropped and the expectation is taken. This produces the second moment equation,

$$E[\Psi(t)^2] = \frac{\left(\frac{\partial \tilde{F}}{\partial c}\right)^2 \operatorname{var}(c(t)) + \left(\frac{\partial \tilde{F}}{\partial Y}\right)^2 \operatorname{var}(Y(t))}{1 - \left(\frac{\partial \tilde{F}}{\partial \Phi}\right)^2} \tag{A2}$$

where $\Psi(t) = \Phi(t) - \Phi_0$. An approximation to the first moment is obtained by taking the expected value of the Taylor expansion (A1) without squaring, but including all second-order terms. This gives

$$E[\Psi(t)] = \frac{\frac{1}{2}\left\{\frac{\partial^2 \tilde{F}}{\partial \Phi^2} E[\Psi(t)^2] + \frac{\partial^2 \tilde{F}}{\partial c^2} \operatorname{var}(c(t)) + \frac{\partial^2 \tilde{F}}{\partial Y^2} \operatorname{var}(Y(t))\right\}}{1 - \frac{\partial \tilde{F}}{\partial \Phi}} \tag{A3}$$

These moments are used in the expansion of (4) described in the text to complete the second-order approximation of λ.

In the density-dependent model, the variances and covariance of $X_{s,\mathrm{est}}(t)$ and $X_{d,\mathrm{est}}(t)$ are needed and are derived from (17). To derive the expressions for the established population, write (17) as

$$X_{t+1} = AX_t + V_t \tag{A4}$$

where

$$X_t = \begin{bmatrix} X_{s,\mathrm{est}}(t) \\ X_{d,\mathrm{est}}(t) \end{bmatrix} \quad \text{and} \quad V_t = \begin{bmatrix} K(t) \\ 0 \end{bmatrix} \tag{A5}$$

Let $\bar{V} = E[V_t]$ and let $\bar{X}$ solve $\bar{X} = A\bar{X} + \bar{V}$. Subtract $\bar{X} = A\bar{X} + \bar{V}$ from (A4) and write the result in terms of $Y_t = X_t - \bar{X}$ and $W_t = V_t - \bar{V}$. This gives $Y_{t+1} = AY_t + W_t$, with solution

$$Y_{t+1} = \sum_{0}^{\infty} A^k W_{t-k} \tag{A6}$$

The variance–covariance matrix for X_t can be expressed as

$$E\{Y_{t+1}Y'_{t+1}\} = E\left\{\left(\sum_{k=0}^{\infty} A^k W_{t-k}\right)\left(\sum_{j=0}^{\infty} W'_{t-j} A^{j'}\right)\right\} \tag{A7}$$

Expand (A7) and take the expected value of each term. The yield each year is assumed to be independent of any other year, so $E\{W_i W'_j\} = 0$ if $i \neq j$. The result is

$$E\{Y_{t+1}Y'_{t+1}\} = \sum_{k=0}^{\infty} E\{A^k W_{t-k} W'_{t-k} A^{k'}\} = \sum_{k=0}^{\infty} PD^k P^{-1} \textstyle\sum_w^2 P^{-1'} D^k P' \tag{A8}$$

where $A = PDP^{-1}$ with D diagonal and $\Sigma_w{}^2 = \begin{bmatrix} \sigma_K{}^2 & 0 \\ 0 & 0 \end{bmatrix}$.

The elements of (A8) are the variance and covariance terms used in the approximation of the invader growth rate.

In the density-dependent model, the matrix equation describing the invader population (13) is reduced to a one-dimensional difference equation in terms of the fraction P in one bank,

$$P(t+1) = F(P(t), X_{s,\mathrm{est}}(t), X_{d,\mathrm{est}}(t), K(t)) \tag{A9}$$

Using the same technique as above for the density-independent model, the first and second moments of $P(t)$ are

$$E[P(t) - \bar{P}] = \\ \frac{\frac{1}{2}(\partial^2 p\, \sigma_p^2 + \partial^2 s \sigma_s^2 + \partial^2 d \sigma_d^2 + \partial^2 K \sigma_K^2) + (\partial p)(\partial s)\sigma_{ps} + (\partial p)(\partial d)\sigma_{pd} + (\partial s)(\partial d)\sigma_{sd}}{1 - \partial p} \tag{A10}$$

and

$$E[(P(t) - \bar{P})^2] = \frac{(\partial s)^2\sigma_s^2 + (\partial d)^2\sigma_d^2 + (\partial K)^2\sigma_K^2 + (\partial p)(\partial s)\sigma_{ps} + (\partial p)(\partial d)\sigma_{pd} + (\partial s)(\partial d)\sigma_{sd}}{1 - (\partial p)^2} \tag{A11}$$

where $\partial x = (\partial F/\partial x)|_{(\bar{P},\bar{X}_{s,\mathrm{est}},\bar{X}_{d,\mathrm{est}},\bar{K})}$, $\partial^2 x = (\partial^2 F/\partial x^2)|_{(\bar{P},\bar{X}_{s,\mathrm{est}},\bar{X}_{d,\mathrm{est}},\bar{K})}$, and $\sigma_{xy} = E[(X - \bar{X})(Y - \bar{Y})]$.

σ_s^2, σ_d^2 and σ_{sd} are from (17) but σ_{ps} and σ_{pd} are still needed. These two additional covariances are results of the change to density-dependent yield. The yield at each time step is split between the invader population and the established population, so the number of eggs of each type are not independent. The covariances between the fraction of invaders in the shallow egg bank and the numbers of established eggs in the shallow and deep banks are necessary. (13) is reduced to an equation in terms of the variable fraction of eggs in the deep bank $P(t)$ and (17) is written as two equations, one for the established shallow bank and one for the established deep bank. These can be written as:

$$X_{s,\mathrm{est}}(t+1) = f_1(X_{s,\mathrm{est}}(t), X_{d,\mathrm{est}}(t), K(t)) \tag{A12}$$

$$X_{d,\mathrm{est}}(t+1) = f_2(X_{s,\mathrm{est}}(t), X_{d,\mathrm{est}}(t)) \tag{A13}$$

$$P(t+1) = f_3(X_{s,\mathrm{est}}(t), X_{d,\mathrm{est}}(t), P(t), K(t)) \tag{A14}$$

The right-hand sides of (A12), (A13) and (A14) are expanded in a second-order Taylor series. The expanded versions of (A12) and (A14) are multiplied and the expectation is taken. Similarly, expanded (A13) and (A14) are multiplied and the expectation is taken. It is assumed the covariances between the number of established eggs and the fraction of invader eggs are stationary. The result is a linear system of equations for the covariance terms σ_{ps} and σ_{pd}.