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Calculating effective growth rate from a random Leslie model: Application to incidental mortality analysis

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ABSTRACT

Demographic models are commonly used to study cetacean population dynamics and are characterized by a wide range of age classes. The primary building blocks are age-specific survival or mortality and birth rates, which can be combined using a Leslie matrix protocol to provide estimates of maximum possible rates of increase for population size. In this context, specific mortality data are valuable for modeling the viability of threatened species. Depletion of prey, pollution, and other anthropogenic disturbances are believed to have contributed to the decline of populations, but the evidence is less conclusive for these factors than for bycatch. In an attempt to estimate a population growth rate that incorporates uncertainties in vital parameters, we apply a random Leslie analysis to calculate effective growth rate for the time-dependent mean-value population. Here we provide the algorithm to implement it for a general 13×13 random survival model. An effective growth rate can be characterized by studying the time evolution of the mean-value population vector state (in an age-structured description). We show that the asymptotic behavior of the mean-value vector state, which characterizes the population growth rate when the model has random vital parameters, exhibits a value that is below previously expected potential estimations. We demonstrate the procedure using bibliographic revision data of the harbor porpoise (*Phocoena phocoena*) in Canadian waters, subjected to incidental mortality.

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1. Introduction

The assessment of growth rate in wildlife populations is a fundamental demographic parameter (Skalski et al., 2005). A number of studies have attempted to determine whether a population was declining by performing demographic analysis (Barlow, 1985; Wickens and York, 1997; Horvitz et al., 1997). These models can be used to evaluate the effects of the removal of animals from a population and are particularly useful in understanding the constraints on population growth imposed the life history parameters (Barlow and Boveng, 1991). Several methods have been used to estimate survival (or mortality) rates from age-frequency distributions.

For small odontocetes and other cetaceans, rates of increase have proven extremely difficult to measure in nature (Reilly and Barlow, 1986; Forney, 2001). Nonetheless, estimates of this intrinsic rate are sometimes necessary when considering incidental mortality quotas for populations under study (Smith, 1983; Lo and Smith, 1986; Wade, 1993). Hence, long-term monitoring of mortality is valuable in detecting unusual mortality events (Duignan

et al., 1996; Vidal and Gallo-Reynoso, 1996) and increases in mortality due to fisheries (Goodall et al., 1994; Nieri et al., 1999; Morizur et al., 1999; López et al., 2003; Archer et al., 2010), or other anthropogenic disturbances (Gaskin, 1982; Parsons and Jefferson, 2000; Weijs et al., 2010). Bycatch, the unintended mortality of non-target species, is widely recognized as one of the most serious environmental impacts of modern commercial fisheries (Alverson et al., 1994; Botsford et al., 1997). The most serious threat to the status of the harbor porpoise (*P. phocoena*) is the incidental mortality caused by entanglement in fishing gear (Gaskin, 1984; Woodley and Read, 1991; Read et al., 1993; Perrin et al., 1994; Trippel et al., 1996; Moore and Read, 2008). Decreases in relative abundance have been reported since the 1940s including recent studies throughout their range (Jefferson and Curry, 1994; Read and Gaskin, 1988; Tregenza et al., 1997; Trippel and Shepherd, 2004). Specific mortalities in the Canadian waters of Bay of Fundy/Gulf of Maine have occurred since the regular use of gillnets began in the 1960s (Gaskin, 1992; Read and Hohn, 1995). Concern has been expressed over the impact of these catches, since preliminary data indicate that the level of incidental mortality may be large relative to population size (Read and Gaskin, 1988; Palka et al., 1996).

With suitable survey data, survival and mortality can be estimated as age-specific. Unfortunately, there are no data on marked individuals for harbor porpoise and limited age distribution data

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comes from bycatch samples. Thus we are forced to accept uncertainties in vital parameters. It is widely accepted that many population analyses underscore the considerable uncertainty that exists regarding potential rate of increase (Caswell et al., 1998). In such situations, the range of variation of vital parameters in linear and non-linear models can contribute substantially to delineating management options and has important implications in conservation biology (Taylor et al., 2000; Parra et al., 2006; Slooten, 2007; Jenkins et al., 2009). These variations in vital parameters can frequently be considered to emulate stochastic dynamics in time (Tuljapurkar, 1982; Tuljapurkar et al., 2003), or have random values (Gerrodette et al., 1985; Caswell et al., 1998). In this sense, it is important to take into account the effect of random contributions when calculating rates of increase in age-structured models (Leslie, 1945). Interparameter relationships and the presence of correlations between vital parameters are also important items to be considered in the theory; for example: the correlated effect, induced by a reduction in survival rate, on the age-fertility parameter. Sensitivity analysis of linear models has shown that dominance of the same parameters is linked to survival rates rather than fecundity in terms of effects on increase in the population growth rate (Fifas et al., 1998). As a matter of fact, uncertainty in the estimation of the population growth rate has been largely limited to sensitivity analysis of the vital rates (Caswell, 1978; Goodman, 1971; Mills, 1999; Skalski, 2007). An important contribution to that analysis was the study of how much the variance in each vital rate contributes to overall variance in the growth rate λ (Brault and Caswell, 1993). On the other hand, by using Monte Carlo simulations an important piece of work (Caswell et al., 1998) has been reported in connection with the characterization of the uncertainty of the potential population growth rate λ, *i.e.*, these authors study the distribution of the dominant eigenvalue associated with a random Leslie matrix characterizing a given biological model. Therefore, great emphasis was put on the calculation of distribution of critical values defined by International Commissions for the purposes of demographic policy makers.

Our purpose in the present work is quite unlike previous studies. Here we also consider the situation where vital parameters may make random contributions (correlated or not). But in order to calculate an effective growth rate from the time-evolution of the mean population vector, the problem is mapped with a random Leslie matrix model characterized by an implicit joint probability for its entries. Then the effective growth rate λ_{eff} is defined in terms of the asymptotic long-time behavior of the mean-value population vector state (Cáceres and Cáceres-Saez, 2011). In fact, the dominant zero of the secular polynomial of a random Leslie matrix is the inverse of the effective growth rate. This value strongly depends on the probability distribution and the type of correlation between the elements of the Leslie projection matrix. In the present work, we exemplify our approach by modeling the rate of increase of a harbor porpoise population under random (disordered) incidental mortality. In addition, a general mathematical result for any type of distribution, considering only two-point correlations, is presented in Appendix A; this algorithm (for a 13×13 matrix model) could be applied to other similar biological systems.

This approach to uncertainty is fundamentally different from the approach described in Hilborn and Mangel (1997), where models are fitted to data using likelihood functions. In other words, parameters are estimated from data. In the present work, the parameters are assumed to be known, albeit with random perturbations. Thus, when we say that we "estimate" a population growth with uncertainties in the vital parameters, it should be understood that this is really a mathematical calculation using some complex mathematics. It is not an estimation in the statistical sense of estimating the values of parameters from data using some minimization or maximization criterion. For instance, this difference is starkly clear in our statement on Section 2.2.2, when we present the error bound in the

perturbative calculation of the effective growth rate λ_{eff}. This is why the confidence interval in the estimation of λ_{eff} is a small number. This is a statement on the mathematical error bound in the calculation by neglecting higher order cumulants in the perturbation theory, not the statistical confidence interval for the estimation of the growth rate.

2. Methods

2.1. The age-structured model

Population growth rate is calculated here by using the familiar Leslie matrix model: $\mathbf{X}(m+1) = \mathbf{M} \cdot \mathbf{X}(m)$, where $\mathbf{X}(m)$ is the age-structured population vector state at time m (Leslie, 1945; van Groenendael et al., 1988), *i.e.*: $\mathbf{X}(m)_j$ is the component j of the vector state at time m and will represent the population at the age j. In the present paper we will consider that parameters in Leslie' matrix $\mathbf{M}$, of dimension $N \times N$, may have a random contribution (time independent disorder) that varies the vital parameters around its mean values. These random deviations may have cross-correlations between them.

A simplified parameterization is used here, assuming a random survival Leslie matrix model (Cáceres and Cáceres-Saez, 2011). For the purposes of this assessment we use the vital parameters of the harbor porpoise derived from Read (1990), and schedules of natural mortality and several estimates of the proportion of the population subjected to incidental mortality presented by Woodley and Read (1991). In the Bay of Fundy/Gulf of Maine the harbor porpoises appear to form a discrete population unit (Gaskin, 1984; Palka et al., 1996). For the applicability of the Leslie matrix and based on our review of the empirical data, we use reproductive rates (m_j) and survival probabilities (p_j). Fecundity elements (f_j) for age classes are estimated as the product ($m_j p_j$). A summary of the compiled information is provided in Section 2.3. In previous life history studies of the harbor porpoise, a few older individuals were found but the vast majority were less than 10 years old (Read and Hohn, 1995). In accordance with the maximum age of 12 years and the estimation of the Age of First Reproduction (*AFR*) (Read, 1990), we use a 13×13 Leslie matrix $\mathbf{M}$ and classify calf from 0 to 2 years and non-calf from 3 to 12 years old (for the analysis concerning the life cycle of the harbor porpoises see Section 2.3).

Due to lack of data, we adopt here, as in Woodley and Read's paper, two studies: Model A only two different natural survival probabilities for all life stages, and Model B a survivorship curve for Himalayan thar (*Hemitragus jemlahicus*) from Caughley (1966), is used as a model life table for estimating the harbor porpoise natural survival probability at different age stages. We consider that survival probabilities may be modified by (random) incidental mortality in addition to their natural dependence.

There are two sources of uncertainty in the estimates of incidental mortality: variability from year to year and sampling uncertainty within the year. By using a Monte Carlo procedure (Caswell et al., 1998) the authors reported a distribution for the mortality rate with a mean around 0.0495. This generated distribution is skewed to the right and contains considerable variability, but in principle this function could be fitted with a Gamma (Erlang) distribution (see Fig. 9 in Caswell et al., 1998). In order to exemplify our general method, we will adopt a much simpler characterization for the uncertainty, and then we shall assume a uniform distribution in the domain of values that were originally reported (Woodley and Read, 1991). The present example is a model to show the friendly applicability of our analytical procedure to tackle the complex problem of the time-evolution of a random recurrence relation of the Leslie type. However, the result of λ_{eff} strongly depends on the assumption of the type of distribution and correlations among the demographic

parameters in the random matrix, which is why the present algorithm is an important contribution in order to incorporate random variability from data.

Note that given a random Leslie matrix **M**, and if we knew the distribution of the dominant eigenvalue $\mathcal{P}(\lambda)$ (this has been an active topic of research in the last 10 years) this distribution could not be used to get the asymptotic long-time behavior of the mean-value of the population vector: $\langle \mathbf{X}(m \gg 1) \rangle$. In fact this calculation would also require knowledge of the dominant Perron–Frobenius eigenvector Ψ as a function of λ, in order to calculate the asymptotic limit:

$$\lim_{m \gg 1} \int \lambda^m \Psi(\lambda) \mathcal{P}(\lambda) d\lambda, \tag{1}$$

which is a formidable task!, see for example Bharucha-Reid (1970) and Frisch (1970).

Interestingly, we have recently reported (Cáceres and Cáceres-Saez, 2011) that the asymptotic behavior of the mean-value vector state $\langle \mathbf{X}(m \gg 1) \rangle$ can be calculated by rigorous perturbation expansion. From now on the mean-value $\langle \cdots \rangle$ indicates an average over all the random variables appearing in the Leslie matrix **M**. A detailed explanation of how to take a mean value on a random matrix is shown in Appendix A, see for example Eqs. (A.2)–(A.6). In general, we have proved that asymptotically the long-time behavior is:

$$\lim_{m \gg 1} \langle \mathbf{X}(m) \rangle \sim \lambda_{eff}^m \Phi, \tag{2}$$

where λ_{eff} is the "effective growth rate" of the age-structured population, which can be calculated by rigorous perturbation. Φ is the mean-value invariant population vector state which can be calculated from the residue of the mean-value Green function of Leslie' recurrence relation (see Eq. (A.12) in Appendix A).

Our task here will be to give an algorithm and mathematical results for modeling random survival cases in population dynamics. In addition, we will show how to calculate the effective growth rate λ_{eff} in a particular case, and compare it with the potential growth rate calculated for the four values of the incidental mortality reported in Woodley and Read's paper (1991). The extension of these calculations considering different distributions and correlations can also be implemented using the present algorithm. We are confident that our approach will help in the understanding of the age-structured time-dependent dynamic behavior associated with biological populations at risk.

2.2. Random Leslie' matrix model

2.2.1. The vital parameters

Vital parameters in a Leslie matrix are positive numbers, and the fact that these numbers may have uncertainties can frequently be handled by adopting a range for their values. In order to simplify the presentation of the paper, we introduce here the notation for a general 13×13 Leslie matrix **M**, where $f_j \geq 0$ are fecundity and $p_j \in [0, 1]$ are survival probabilities for each age class $j = 0, 1, 2, 3, \ldots$, i.e.,

$$\mathbf{M} = \begin{pmatrix} f_0 & f_1 & f_2 & f_3 & f_4 & \cdots & \cdots & f_{12} \\ p_0 & 0 & 0 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & p_1 & 0 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & p_2 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & 0 & p_3 & 0 & \cdots & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & 0 & 0 & \cdots & p_{11} & 0 \end{pmatrix}, \tag{3}$$

2.2.2. Working a random Leslie matrix

Assuming that the positive numbers in the Leslie matrix (3) may have random contribution we can rewrite **M** as the addition of two matrices: one is a bona fide mean-value Leslie' matrix **H**, and the other is a random matrix **B** characterized by a joint probability for its elements $P(\{\mathbf{B}_{qk}\})$. In general the statistical characterization must be done with care in order to preserve the fundamental property that for each realization of the disorder **M** is a non-negative matrix, then:

$$\mathbf{M} = \mathbf{H} + \mathbf{B}; \quad \langle \mathbf{B} \rangle = 0 \tag{4}$$

Considering that the survival parameters may have random contributions we can write:

$$\mathbf{H} = \begin{pmatrix} m_0 \langle p_0 \rangle & m_1 \langle p_1 \rangle & m_2 \langle p_2 \rangle & m_3 \langle p_3 \rangle & m_4 \langle p_4 \rangle & m_5 \langle p_5 \rangle & \cdots & m_{12} \langle p_{12} \rangle \\ \langle p_0 \rangle & 0 & 0 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & \langle p_1 \rangle & 0 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & \langle p_2 \rangle & 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & 0 & \langle p_3 \rangle & 0 & \cdots & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & 0 & 0 & \cdots & \langle p_{11} \rangle & 0 \end{pmatrix}, \tag{5}$$

and

$$\mathbf{B} = \begin{pmatrix} m_0 \beta_0 & m_1 \beta_1 & m_2 \beta_2 & m_3 \beta_3 & m_4 \beta_4 & m_5 \beta_5 & \cdots & m_{12} \beta_{12} \\ \beta_0 & 0 & 0 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & \beta_1 & 0 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & \beta_2 & 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & 0 & \beta_3 & 0 & \cdots & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & 0 & 0 & \cdots & \beta_{11} & 0 \end{pmatrix}. \tag{6}$$

Here we assume that we know the joint probability $P(\{\beta_j\})$ or the moments $\langle \beta_j \cdots \beta_{j'} \rangle$. If we put $\beta_j = \beta, \forall j$, i.e., we use only one random variable, it will mean that the survival parameters for all individuals are completely correlated with each other. It is more realistic to assume that they are not correlated. In any case, any plausible model can be worked out in the framework of our approach. In the present application we will assume that β_j are identically and independently distributed (see Appendix A.1).

The matrix **H** will reproduce the familiar result from a non-random Leslie' dynamics, i.e., the growth rate of the population is given by the positive eigenvalue of matrix **H** (the Perron–Frobenius eigenvalue $\lambda > 0$, Cáceres, 2003). In general this eigenvalue can be studied from the largest positive root of the characteristic polynomial:

$$\det |\mathbf{H} - \lambda \mathbf{1}| = 0, \tag{7}$$

here **1** is the identity matrix. Using the structure of the matrix (3), this polynomial can be written explicitly in the form:

$$P(\lambda) = 1 - \sum_{l=1}^{13} \frac{f_{l-1}}{p_{l-1}} \prod_{j=1}^{l} \frac{p_{j-1}}{\lambda} = 1 - \sum_{l=1}^{13} \frac{1}{\lambda^l} \frac{f_{l-1}}{p_{l-1}} (p_0 p_1 \cdots p_{l-1}). \tag{8}$$

Considering the correspondence $\lambda = e^r$, the age specific reproductive rate $m(x) = f(x)/p(x)$, and the survival probability

$l(x) = \prod_{j=1}^{x} p_{j-1}$ for an individual surviving the interval from birth to age x. Formula (8) gives the familiar Lotka's equation (Lotka, 1939) corresponding to the growth rate r in a time-continuous representation:

$$1 = \sum_{x=1}^{13} e^{-rx} m(x) l(x). \qquad (9)$$

The interesting point in Leslie' analysis is that our matrix approach allows us to tackle the random matrix problem in a perturbative way. In Cáceres and Cáceres-Saez (2011) we showed that the long-time behavior of the mean-value population vector state: $\lim_{m \gg 1} \langle \mathbf{X}(m) \rangle \sim \lambda_{eff}^m \Phi$, is dominated by the smallest strictly positive root $\tilde{z}_e (= 1/\lambda_{eff})$ of the secular polynomial $\mathbf{P}(z)$:

$$\det \left| \mathbf{1} - z \left(\mathbf{H} + \left\langle \sum_{k=0}^{\infty} [\mathbf{BG}^0 \mathcal{Q}]^k \mathbf{B} \right\rangle \right) \right| = 0. \qquad (10)$$

It is important to point out that the polynomial (10) is a rigorous perturbation expansion for small z (for any joint probability $P(\{\mathbf{B}_{nk}\})$). Here $\mathbf{G}^0$ is the deterministic Green function (corresponding to the mean-value Leslie matrix $\mathbf{H} = \langle \mathbf{M} \rangle$), see Appendix A.

For example, from (10) and neglecting all the random perturbations, *i.e.*, to $\mathcal{O}(\mathbf{B}^0)$, we get the secular polynomial:

$$\det |\mathbf{1} - z\mathbf{H}| = 0 \qquad (11)$$

which gives, with $z = 1/\lambda$, the same result as presented in (7) using a mean-value Leslie matrix.

The first perturbative contribution gives, up to $\mathcal{O}(\mathbf{B}^2)$, the secular polynomial $\mathbf{P}(z)$:

$$\det |\mathbf{1} - z(\mathbf{H} + \langle \mathbf{BG}^0 \mathcal{Q} \mathbf{B} \rangle)| = 0. \qquad (12)$$

A confidence interval (CI) to indicate the reliability of the estimate of z_e can rigorously be calculated from the neglected terms in (10); thus, an error bound for λ_{eff} can be calculated (Cáceres and Cáceres-Saez, 2011). A crude estimation of the confident number of digits in the effective growth rate λ_{eff} is given in terms of the size of the variance associated with the random variables that appear in the problem. Therefore the error in finding λ_{eff} from (12) is of order $\mathcal{O}(\mathbf{B}^4)$, see Appendix A.

To be able to estimate the effective growth rate $\lambda_{eff} = 1/z_e$ in terms of the smallest positive zero z_e of the secular polynomial (12), the first task is to calculate the matrix $\langle \mathbf{BG}^0 \mathcal{Q} \mathbf{B} \rangle$. This matrix can be calculated straightforwardly. In Appendix A we present this important result for Leslie' matrices of dimension 13×13, calculated from any cross-correlation of the form: $\langle \beta_j \beta_k \rangle = \delta_{jk} \langle \beta_j^2 \rangle$.

Higher order perturbations can also be analyzed in a similar way. As we mentioned before λ_{eff} will strongly depend on the type of correlations. For example we have shown in a 3×3 model that non-isotropic correlated models lead to an unusual prediction for λ_{eff} as a function of the correlation parameter, see Pool and Cáceres (2010) where we did calculations up to $\mathcal{O}(\mathbf{B}^6)$ to compare with the simulations.

In general, knowing $\mathbf{G}^0$ and noting that $\langle \mathbf{B} \rangle = 0$, from (6) the matrix $\langle \mathbf{BG}^0 \mathcal{Q} \mathbf{B} \rangle$ can be written (see Appendix A). Therefore, up to order $\mathcal{O}(\mathbf{B}^2)$, to estimate λ_{eff} from systematic data we have to calculate cross-moments of the associated random variables appearing in the Leslie matrix $\mathbf{M}$. These moments can be obtained from sampled data or from theoretical distributions.

In Fig. 1 we show the systematic procedure to eventually calculate the secular polynomial (12) from sample data. Nevertheless, in the next example we will work out, the calculation of the effective growth rate will be based on bibliographic revision data of the harbor porpoise in Canadian waters (Woodley and Read, 1991). In this paper the incidental mortality was a parameter ranged in a suitable
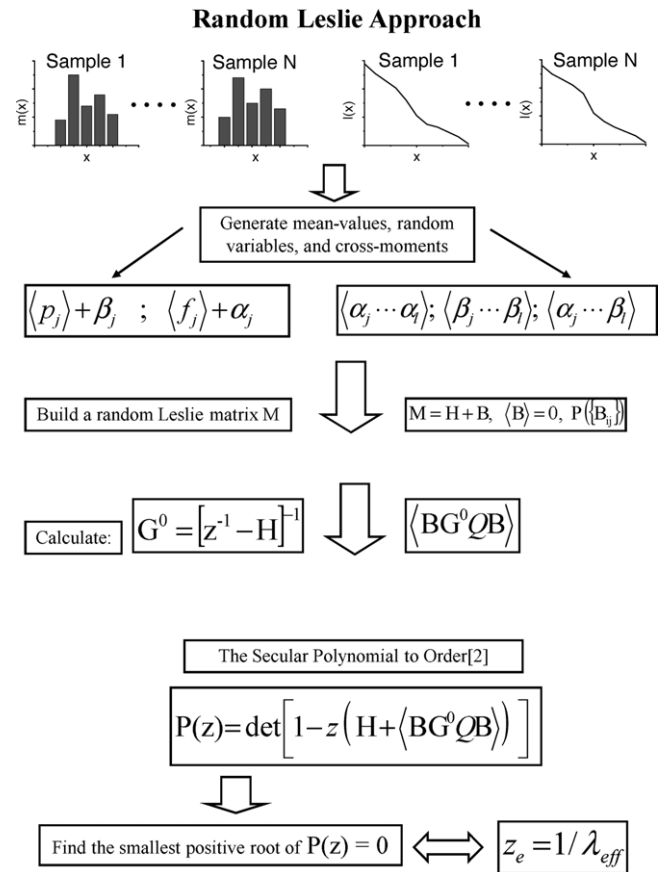

Fig. 1. The algorithm for calculating the effective growth rate λ_{eff} for a general random Leslie' model. From the sample data of age specific reproductive rates $m(x)$ and survival probabilities $l(x)$, for an individual surviving the interval from birth to age x, write the matrix $\mathbf{M}$ of dimension $(N \times N)$, where N represents the number of age-classifications in the model, thus the index $j \in (0, 1, 2, \ldots, N-1)$. Then split the Leslie matrix in the form: $\mathbf{M} = \mathbf{H} + \mathbf{B}$ where $\mathbf{B}$ is a random matrix. From the mean-value $\langle \mathbf{M} \rangle = \mathbf{H}$ calculate the deterministic Green matrix $\mathbf{G}^0$. From the random variables $\{\alpha_j, \beta_j\}$, $\forall j \in (0, 1, 2, \ldots, N-1)$ appearing in $\mathbf{B}$ any cross moment $\langle \alpha_j \cdots \alpha_l \beta_k \cdots \beta_m \rangle$ can be calculated. Then the cross moments $\langle \mathbf{B}_{iq} \cdots \mathbf{B}_{kl} \rangle$, $\forall \{i, q, k, l\} \in (1, 2, \ldots, N)$ can be specified. Note that the scalar $\mathbf{B}_{qk}$ is the element qk of the matrix $\mathbf{B}$ which can be written in terms of the random variables $\{\alpha_j, \beta_j\}$. From these moments any Terwiel's cumulant can be written as a suitable product of matrices, in particular the second cumulant: $\langle \mathbf{BG}^0 \mathcal{Q} \mathbf{B} \rangle$, see Appendix A for its general expression in the case $N=13$. Form $\langle \mathbf{BG}^0 \mathcal{Q} \mathbf{B} \rangle$ the secular polynomial $\mathbf{P}(z)$ (up to order $\mathcal{O}(\mathbf{B}^2)$) can be written. The effective growth rate is the strictly positive smallest root z_e of $\mathbf{P}(z) = 0$.

domain of values, therefore in order to exemplify our approach we can use these values, considering the incidental mortality to be a random variable.

The calculation of the Perron–Frobenius eigenvalue $\lambda(\mathbf{H})$ corresponding to Leslie' matrix $\mathbf{H} = \langle \mathbf{M} \rangle$, and the smallest positive zero of the secular polynomial (12) were calculated using the Mathematica 5.2 Software assuring up to 10^{-10} digits.

2.3. A life history example

2.3.1. Woodley & Read's life table history parameters

Following criterion for sexually reproducing species, both p_j, and m_j, are expressed in terms of females only. For the harbor porpoise population we follow the suggestion from Woodley and Read (1991) using an *AFR* = 3, the data of $\{m_j\}$, and the fact that the incidental mortality for calf (0, 1, 2-ages) would be greater than non-calf by a factor of 43/30, we can write Table 1:

In this table h is the incidental mortality, and n_j the natural mortality variable for age $j \geq 0$. In Woodley and Read (1991) four probability values for the incidental mortality were used:

Table 1
Harbor porpoise life history parameters from the prescription given in Woodley and Read's paper.

Vital parameters	Age classification
$m_0 = m_1 = m_2 = 0$	Null birth rate for age classes: 0, 1, 2
$m_3 = 0.10$	Age-specific birth rate class: 3
$m_4 = 0.36$	Age-specific birth rate class: 4
$m_j = m = 0.5$	Age-specific birth rate classes: $5 \leq j \leq 12$
$p_0 = \left(1 - \frac{43}{30} h\right)(1 - n_j)$	Calf survival probability
$p_j = (1 - h)(1 - n_j)$	Non-calf survival probability
$f_j = m_j p_j$	Age-specific fertility

$h = \{0.0183 ; 0.0352, 0.0523, 0.1006\}$. The natural mortality rate of *phocoenid* calves is still not known, and for non-calf individuals this parameter was assumed to be the same for all age classes ranging from 0.1 to 0.29 in Model A. In Model B, non-calf $n'_j s$ were calculated for each age class from a smoothed age-frequency formula (Caughley, 1966). The combination of natural mortality and substantial incidental mortality reduces the likelihood that an individual will achieve its maximum potential lifespan (Read and Hohn, 1995).

2.3.2. Incidental mortality

As we have commented before, we are going to exemplify our approach by studying the effective growth rates of the harbor porpoise population as a function of natural mortality n_j, but considering that the incidental mortality h is a random variable uniformly distributed in the interval [$h_{min} = 0.0183$ to $h_{max} = 0.1006$], for the present purpose it is enough to consider this simplest distribution for h.

In the present example, we are going to obtain an effective growth rate λ_{eff} in accordance with the time-evolution of the mean-value population vector state $\langle \mathbf{X}(m) \rangle$ associated with the analysis presented in Woodley and Read (1991). Similar analyses using different distributions for h, such as those reported in Caswell et al. (1998), can also be tackled within our framework, but this interesting study is left for future contributions. Thus, the present result is not universal in the sense that λ_{eff} strongly depends on the distribution and correlations used in the model. An interesting example was presented using a non-trivial 3×3 correlated model in Pool and Cáceres (2010) where the agreement between theory and simulation has also been shown.

2.3.3. Model A with constant non-calf survival probability p_j

It is questionable that harbor porpoise demography can be adequately described using a model that assumes equal non-calf mortality rates for all age classes. Nevertheless, this model is rich enough to offer the possibility of analyzing the effects of disorder on the vital parameters in a straightforward way. Assuming that there is a range of uncertainty for the incidental mortality h, the parameters p_0 and p_j will have random interference through the random variable h. Using the usual notation for the mean-values of scalar random numbers $\langle \cdots \rangle$ (see Eq. (A.6), *etc.*, in Appendix A) and the set of random variables with mean-values zero $\{\beta_j\}$, we can write Table 2:

Table 2
Random survival model for any distribution of the incidental mortality h inside the domain of values proposed by Woodley and Read.

Random survival probability	Random variables, $\{\beta_j\}$	h is distributed in:
$p_0 = \langle p_0 \rangle + \beta_0$	$\beta_0 = \frac{43}{30}(1 - n_j)(\langle h \rangle - h)$	$h \in [h_{min}, h_{max}]$
$p_j = \langle p_j \rangle + \beta_j$	$\beta_j = (1 - n_j)(\langle h \rangle - h)$	$h \in [h_{min}, h_{max}]$

Table 3
Random fertility inference from the random survival model.

Random fertility	Random variables $\{\beta_j\}$	h is distributed in:
$f_3 = m_3(\langle p_3 \rangle + \beta_3)$	$\beta_3 = (1 - n_j)(\langle h \rangle - h)$	$h \in [h_{min}, h_{max}]$
$f_4 = m_4(\langle p_4 \rangle + \beta_4)$	$\beta_4 = (1 - n_j)(\langle h \rangle - h)$	$h \in [h_{min}, h_{max}]$
$f_j = m(\langle p_j \rangle + \beta_j)$	$\beta_j = (1 - n_j)(\langle h \rangle - h)$	$h \in [h_{min}, h_{max}]$

Note that in Model A $n_j = n$ is a natural mortality parameter, then the mean values are:

$$\langle p_0 \rangle = (1 - n)\left(1 - \frac{43}{30}\langle h \rangle\right),$$

$$\langle p_j \rangle = (1 - n)(1 - \langle h \rangle).$$

From Table 1 it is simple to see the dependence of fecundity on survival probabilities, thus if we introduce uncertainty into the survival parameters these dependences will also appear in the corresponding fecundity parameters f_j. To clarify this point, we explicitly express age-specific fertility (see Table 3) in terms of the set of random variables $\{\beta_j\}$, *i.e.*:

In Model A it is assumed that natural mortality n_j is the same for all age classes, therefore $\langle p_j \rangle = \langle p \rangle$, $\forall 3 \leq j \leq 12$, and we get that the mean fertilities depend on $\langle p \rangle$ and m_j only.

2.3.4. Model B with Caughley's smoothed survival variation

As in Woodley and Read (1991) we assume that the harbor porpoise has a life history comparable to that of the Himalayan thar: litter size of one, annual reproduction, with few individuals living past age class 12. Up to an age of 12 years, the Himalayan thar frequencies were smoothed according to the formula:

$$\log_{10}(y) \simeq 1.9673 + 0.0246x - 0.01036x^2; \quad x \geq 1, \tag{13}$$

where y is the frequency and x the age. Therefore, we can use Caughley's estimates for the age-structure of natural mortality: $n_j \equiv n(x=j) = 1 - y_{x+1}/y_x$ (Caughley, 1966). Incorporating this age-structure into survival probabilities gives more reasonable results for the stable proportion of the harbor porpoise population (Woodley and Read, 1991).

By introducing smoothed function (13) into the vital parameters of our random Leslie matrix, we retain the same separation as before: a random part and a mean-value part as in Tables 2 and 3. Now the only difference is that $\langle p_j \rangle$ is different for each $j \geq 1$. In this way, we can improve the analysis of the cetacean population by introducing Caughley's smoothed survival variation into our random model.

2.4. Example of application: uncertainty in the incidental mortality

As previously mentioned, we now present the application of an approach considering random incidental mortality quotas for the porpoises inhabiting Canadian waters. Vital parameters in the Leslie matrix were separated into two contributions (5) and (6): a mean-value matrix **H** and a random matrix **B**. The random fertilities and survival probabilities follow from Table 2 and 3, and the explicit values for the range of parameters follows from Woodley and Read (1991); thus, thus, using a uniform distribution in this range we get (Table 4):

with $j = 1, 2, 3, \ldots 12$. In Model A the natural mortality variable n_j was chosen to be the same for each age class $j > 0$. In Model B $n_{j>0}$ was selected from the smoothed Caughley's function, thus the natural calf mortality n_0 is the model-parameter. The matrix $\mathbf{G}^0$ can easily be calculated using the mean-values from (5). The matrix $\langle \mathbf{BG}^0 \mathcal{Q} \mathbf{B} \rangle$ can be calculated knowing $\mathbf{G}^0$ and the values $\langle \beta_0^2 \rangle$, $\langle \beta_j^2 \rangle$, see Appendix A.

Table 4
Moments of the random variables β_j using random incidental mortality h with uniform distribution inside the domain of values proposed by Woodley and Read.

Uniform random variable	$h \in [h_{\min} ; h_{\max}]$	$\{h_{\min} = 0.0183 ; h_{\max} = 0.1006\}$
Mean value	$\langle h \rangle$	$= 5.9449 \times 10^{-2}$
2nd-moment	$\langle h^2 \rangle$	$= 0.4098 \times 10^{-2}$
Square dispersion	σ_h^2	$= 0.0564 \times 10^{-2}$
2nd-moment of β_0	$\langle \beta_0^2 \rangle$	$= \left(\frac{43}{30}(1 - n_j) \right)^2 \sigma_h^2$
2nd-moment of β_j	$\langle \beta_j^2 \rangle$	$= (1 - n_j)^2 \sigma_h^2$

Table 5
Random vital parameters corresponding to Model A with constant natural mortality n_j for any age $j > 0$.

Random vital parameters in Model A	Age classification
$p_0 = \langle p_0 \rangle + \beta_j$	For calf age classes: $0 \leq j \leq 2$
$p_j = \langle p \rangle + \beta_j$	For non-calf age classes: $3 \leq j \leq 12$
$f_j = m_j(\langle p \rangle + \beta_j)$	For non-calf age classes: $3 \leq j \leq 4$
$f_j = m(\langle p \rangle + \beta_j)$	For non-calf age classes: $5 \leq j \leq 12$
$\beta_j = \frac{43}{30}(1 - n_j)(\langle h \rangle - h)$	Random variables for $0 \leq j \leq 2$
$\beta_j = (1 - n_j)(\langle h \rangle - h)$	Random variables for, $3 \leq j \leq 12$
$n_j = n \in [0.1-0.29]$	Natural mortality parameter $1 \leq j \leq 12$

2.4.1. Analysis of Model A

In this case we use a random Leslie matrix **M** with the following parameters (see Table 5):

Where $\langle p_0 \rangle$ and $\langle p \rangle$ are characterized for any value of the variable $n_{j>0}$, see Tables 2 and 4.

2.4.2. Analysis of Model B

In this case, using (13) we can write the random Leslie matrix **M** with the following parameters (see Table 6):

Now $\langle p_j \rangle$ is characterized for any value of the smoothed function using $n_j \equiv n(x = j)$, see Eq. (13).

3. Results

3.1. Random incidental mortality analysis

In Fig. 2(a) and (b) we have plotted λ_{eff} as a function of the non-calf natural mortality $n_{j>0}$ and of the calf natural mortality variable n_0 respectively, considering that the incidental mortality

Table 6
Random vital parameters corresponding to Model B; natural mortality is age-dependent using the smoothed Caughley parameterization for natural mortality $n_{j>0}$, from Eq. (13).

Random vital parameters in Model B	Age classification
$n_j = 1 - 10^{[0.0246 - 0.01036(2j-1)]}$	Age specific natural mortality $1 \leq j \leq 12$
$p_0 = \langle p_0 \rangle + \beta_0$	Calf survival for $j = 0$
$p_j = \langle p_j \rangle + \beta_j$	Survival for $1 \leq j \leq 12$
$f_j = m_j(\langle p_j \rangle + \beta_j)$	Fertility for $3 \leq j \leq 4$
$f_j = m(\langle p_j \rangle + \beta_j)$	Fertility for $5 \leq j \leq 12$
$\beta_0 = \frac{43}{30}(1 - n_0)(\langle h \rangle - h)$	Random variable for $j = 0$
$\beta_j = (1 - n_j)(\langle h \rangle - h)$	Random variable for $1 \leq j \leq 12$
$\langle p_0 \rangle = (1 - n_0)\left(1 - \frac{43}{30}\langle h \rangle\right)$	Survival mean value for $j = 0$
$\langle p_j \rangle = (1 - n_j)(1 - \langle h \rangle)$	Survival mean value for $1 \leq j \leq 12$
$n_0 \in [0.19-0.53]$,	Calf natural mortality parameter

h is a random variable uniformly distributed in the range reported in Woodley and Read (1991). The present calculation λ_{eff} is located around the middle of the four values of h used by Woodley and Read. As mentioned earlier, the effective growth rate could also be calculated by using a different distribution, for instance the one generated by Monte Carlo calculations (Caswell et al., 1998). In fact, the response (*i.e.*, the rate λ_{eff}) will strongly depend on the type of distribution used for the calculation of the secular polynomial. By taking the $\ln \lambda$, this function would correspond to a continuous-time generalization of the growth rate and is in accordance with the analysis made in Figs. 1 and 2 in Woodley and Read's paper. The behavior of $\lambda_{eff} = \lambda_{eff}(n_j)$ is linear because of the lack of an age-structure in Model A. In Model B, this linearity is lost as a consequence of the incorporation of Caughley's estimates for the survival age-structure. On the other hand, the range of the random variables $\{\beta_j\}$ is so small that the corrections to $\mathcal{O}(\mathbf{B}^2)$ are almost undetectable from our plots in Fig. 2(a) and (b) when it is compared with the contribution to $\mathcal{O}(\mathbf{B}^0)$.

In Table 7 we show, for Model A and Model B a numerical comparison between $\ln \lambda(\mathbf{H})$ and $\ln \lambda_{eff}$ as a function of $n_{j>0} = n$ and n_0 respectively. Note that always $\ln \lambda(\mathbf{H}) < \ln \lambda_{eff}$ indicating that $\langle \mathbf{X}(m) \rangle$ is partially dominated by the largest eigenvalue for any realization of the disorder when the distribution is uniform, but for other distributions and/or much more complex cross-correlations between vital parameters the response would be non-trivial; see, for example Pool and Cáceres (2010).
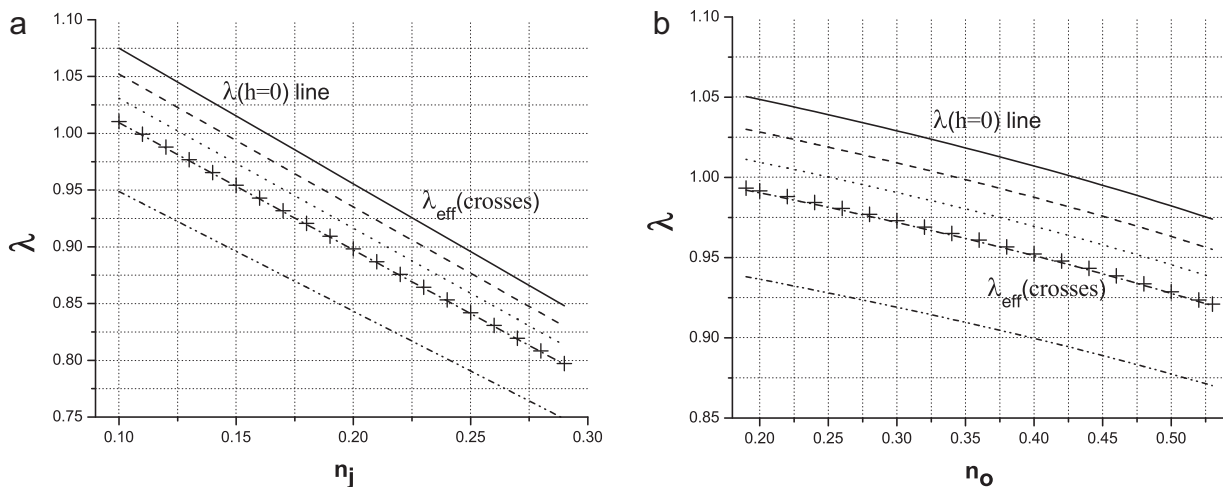

Fig. 2. Potential growth rate λ (line ($h = 0$), dashes, dotted, dashes-dotted, *etc.*) for five values of h. From the top to the bottom: $h = \{0; 0.0183; 0.0352; 0.0532; 0.1006\}$, against the predicted effective growth rate λ_{eff} (crosses), considering h to be a uniformly distributed random variable with support: $h \in [h_{\min} = 0.0183, h_{\max} = 0.1006]$. (a) as a function of n_j for the Model A (here natural mortality $n_{j>0}$ is an age-independent model-parameter so $n_j = n \in [0.1-0.29]$); and (b) as a function of n_0 for Model B (here natural mortality $n_{j>0}$ is age-dependent, so calf mortality is the model-parameter $n_0 \in [0.19-0.53]$). The CI (error bound) for λ_{eff} can be estimated as $\sim 10^{-8}$.

Table 7

Numerical evaluation of the continuous-time growth rate $\ln \lambda(\mathbf{H})$ calculated using the mean value Leslie' matrix $\mathbf{H} = \langle \mathbf{M} \rangle$ and the corresponding effective growth rate $\ln \lambda_{eff}$ calculated up to order $\mathcal{O}(\mathbf{B}^2)$ using the secular polynomial (12), as a function of natural mortalities n and n_0 for Models A and B; respectively. In Model A natural mortality $n_{j>0}$ is an age-independent model-parameter, so $n_j = n \in [0.1–0.29]$. In Model B we use Caughley's age-structured natural mortality $n_{j>0}$ proposed from the Himalayan thar life history, using the calf mortality as the model-parameter $n_0 \in [0.19–0.53]$. The CI for λ_{eff} can be estimated as $\sim 10^{-8}$.

Model A			Model B		
n	$\ln \lambda(\mathbf{H})$	$\ln \lambda_{eff}$	n_0	$\ln \lambda(\mathbf{H})$	$\ln \lambda_{eff}$
0.10	0.0003899	0.0102869	0.19	−0.0160236	−0.0066621
0.11	−0.0107798	−0.0008873	0.20	−0.0177852	−0.0084354
0.12	−0.0220789	−0.0121839	0.22	−0.0213686	−0.0120320
0.13	−0.0335081	−0.0236166	0.24	−0.0250378	−0.0157128
0.14	−0.0450684	−0.0351713	0.26	−0.0287956	−0.0194784
0.15	−0.0567650	−0.0468715	0.28	−0.0326471	−0.0233505
0.16	−0.068599	−0.0587102	0.30	−0.0365975	−0.0273095
0.17	−0.0805757	−0.0706800	0.32	−0.0406532	−0.0313874
0.18	−0.0926965	−0.0828056	0.34	−0.0448185	−0.0355650
0.19	−0.104967	−0.0950692	0.36	−0.0491009	−0.0398641
0.20	−0.1173892	−0.1074961	0.38	−0.0535073	−0.0442863
0.21	−0.1299686	−0.1200794	0.40	−0.0580444	−0.0488436
0.22	−0.1427070	−0.1328459	0.42	−0.0627225	−0.0535379
0.23	−0.1556110	−0.1457196	0.44	−0.0675499	−0.0583815
0.24	−0.1686825	−0.1587847	0.46	−0.0725384	−0.0633871
0.25	−0.1819284	−0.1720346	0.48	−0.0776967	−0.0685679
0.26	−0.1953508	−0.1854865	0.50	−0.0830403	−0.0739265
0.27	−0.2089571	−0.1991829	0.52	−0.0885820	−0.0794870
0.28	−0.2227498	−0.2128591	0.53	−0.0914324	−0.0823495
0.29	−0.2367367	−0.2268378			

One of our tasks was to show how to calculate the effective growth rate λ_{eff} (crosses) and compare it with the potential growth rate calculated from different values of incidental mortality h, *i.e.*, $\lambda(h)$, see Fig. 2(a) and (b) (the line corresponds to the case $h = 0$). In the present calculations we have used a uniform distribution in accordance with data published by Woodley and Read (1991). Model A shows, for the mean-value population vector, that the effective growth rate: $\lambda_{eff} = \lambda_{eff}(n_j)$ is lower than 1 for any value of natural mortality rates $n_j = n \geq 0.11$. Model B, which incorporates Caughley's estimates for survival probability does not produce a stable mean-value population vector. The effective growth rate: $\lambda_{eff} = \lambda_{eff}(n_0)$ is lower than 1 for any value of natural mortality rates of calves $n_0 \geq 0.19$. A reminder that such (low) rates $n_0 < 0.19$ are unlikely to occur in nature.

4. Discussion

4.1. General considerations

The asymptotic behavior of the mean-value population vector state $\langle \mathbf{X}(m) \rangle$ has been characterized by an effective growth rate λ_{eff}, which is an important result that cannot be calculated knowing the distribution of the dominant Perron–Frobenius eigenvalue $\mathcal{P}(\lambda)$. As noted in Eq. (1) the asymptotic behavior of $\langle \mathbf{X}(m \gg 1) \rangle$ would require knowledge of all the moments of λ, which is a formidable numerical task using $\mathcal{P}(\lambda)$. Our effective growth rate can be calculated using any joint distribution, and in general the response λ_{eff} depends on the type of correlation used to characterize the random elements appearing in the matrix $\mathbf{B}$. The interesting point of calculating the mean-value invariant vector state Φ can also be done within the present framework, see Appendix A, Eq. (A.12). The secular polynomial (up to order $\mathcal{O}(\mathbf{B}^2)$) is characterized by the cumulant $\langle \mathbf{B} \mathbf{G}^0 \mathbf{B} \rangle$, thus if the structure of $\mathbf{B}$ is of the random-survival type (as presented in Eq. (6)) we have explicitly calculated the matrix $\langle \mathbf{B} \mathbf{G}^0 \mathbf{B} \rangle$ which can be used in many similar biological problems. Thus, knowing the cross-correlations $\langle \beta_i \beta_j \rangle$ from specific data or from some realistic statistical assumptions, the value of λ_{eff} is reduced to the calculation of the smallest zero

of the secular polynomial $\mathbf{P}(z)$, see Eq. (12). In this case the error bound in the estimation of λ_{eff} would be $\mathcal{O}(\mathbf{B}^4)$, see Appendix A.1.

4.2. Concerning random incidental mortality analysis

As we pointed out in the introduction, λ_{eff} is the relevant rate that has to be considered when there are uncertainties in the vital parameters. The naive approximation of using $\lambda(\mathbf{H})$ corresponds to $\mathcal{O}(\mathbf{B}^0)$ and we have reported that $\lambda(\mathbf{H})$ does not contain any correlation with the habitat of the population (Cáceres and Cáceres-Saez, 2011). Any cumulant of order k in the polynomial (10) represents a particular structure of correlation that we need to evaluate carefully. The response to $\mathcal{O}(\mathbf{B}^2)$ depends on the size of fluctuations and on the correlation structure in the elements of $\mathbf{M}$. As we have noted, our analytical approach can be used to consider any distribution for the random variables appearing in $\mathbf{B}$, the only restriction on these random variables being to preserve the positivity of the Leslie matrix $\mathbf{M}$ for any realization of the disorder. In the present study, we have shown an application using a uniform probability distribution for the incidental mortality h. Other probability characterizations will be reported elsewhere. The important point of our approach is that the estimation of the effective rate takes into account the vector state, and it is also possible to calculate the mean-value invariant population vector state Φ with the same accuracy. Similar calculations have already been reported showing excellent agreement with numerical simulations (Pool and Cáceres, 2010).

We see from Table 7 that even when large potential growth rates are plausible for small values of calf natural mortality variable n_0 (if the incidental mortality is small), the overall result is very drastic, in the sense that $\langle \mathbf{X}(m) \rangle$ will not be stable because $\lambda_{eff} < 1$. Here a uniform range of uncertainty in the vital parameters has been taken into account to predict an effective growth rate for the time-evolution of the mean-value vector state. Considering random incidental mortality quotas for the study of harbor porpoise demography from the Bay of Fundy/Gulf of Maine, the present analysis shows that this population cannot sustain even such moderate levels of random incidental mortality.

The important conclusion of our rigorous perturbation analysis is that the effective growth rate λ_{eff} [crosses in Fig. 2(a) and (b)] is

below values predicting a stable population. This means that using a uniform distribution the asymptotic behavior of $\langle \mathbf{X}(m) \rangle$ is controlled by an effective growth rate that is below values associated with small indices of incident mortality h [dashes ($h_{min}=0.0183$), dotted ($h=0.0352$) curves].

We agree with Woodley and Read's conclusions, and in fact our results are even more critical in the sense that the dynamics of the mean-value vector state indicates that only a dramatic decline in calf natural mortality would allow the population to withstand random incidental mortality quotas. To our knowledge, this is the first time that the time-evolution of the mean-value vector state has been used to define an effective growth rate.

We have followed the estimates of the *phocoenid* population proportions affected by fishery bycatch, but in particular the lower and upper limits may be questionable values as used in Woodley and Read's paper. Nevertheless, we have shown that considering a mean-value of incidental mortality quotas such as: $\langle h \rangle \simeq 10^{-2}$ with a small dispersion $\sigma_h^2 \simeq 10^{-4}$, leads to dramatic conclusions concerning the effective growth rate.

Currently, the major conservation issue on small cetacean populations is the adverse effect of incidental mortality (Read et al., 2006; Moore et al., 2010; Wade, 1998). Progress has been made in reducing bycatch (Hall, 2000; Hall et al., 2000), but much work still remains to be done worldwide. We are confident that the present analysis will contribute to management options (Dawson et al., 1998; Trippel et al., 1999; Barlow and Cameron, 2003). The evidence of decline of the harbor porpoise population, like that of other dolphins, should remind us of the vulnerability of this species in the oceans.

4.3. Concerning random time-dependent perturbations

It is worth noting here that many other growth rates have been reported in connection with a random time-dependent environment (Tuljapurkar et al., 2003). For example, the stochastic growth rate λ_s is defined in terms of a "cumulative population quantity", *i.e.*, assuming a random time-dependent Leslie recurrence relation of the form: $\mathbf{X}(m+1)=\mathbf{M}(m) \cdot \mathbf{X}(m)$ (note that in this case $\mathbf{M}(m)$ depends on m) a stochastic growth rate is defined using a scalar population instead of the age-structured vector state:

$$\log \lambda_s = \lim_{m \to \infty} \left(\frac{1}{m} \right) \log \left[\frac{\sum_j \mathbf{X}(m)_j}{\sum_j \mathbf{X}(0)_j} \right], \tag{14}$$

where $\sum_j$ indicates summing over the age-structure of the vector state.

We recall that only the case of a strong serial correlation between habitat states corresponds to the random Leslie' problem we have solved. On the other hand, a megamatrix growth rate λ_M has been reported in connection with the model of a Markov transition between habitat states (Pascarella and Horvitz, 1998), but its definition is also given in terms of the time-average of a "cumulative growth quantity" rather than using a vector state as in our approach. In any case both quantity λ_s and λ_M are used in modeling the stochastic change (in time) of the habitat. Nevertheless, Tuljapurkar *et al.* have recently reported that even when both definitions are related to the same stochastic problem neither of the growth rates λ_s or λ_M are completely equivalent (Tuljapurkar et al., 2003).

We want to emphasize that our approach to solving a random Leslie model is related to the uncertainties of the vital parameters (*i.e.*, a disordered environment), and the definition of the effective growth rate λ_{eff} is a rigorous result related to the asymptotic behavior of the mean value vector state. Furthermore, we note here that a random time-dependent environment naturally introduces a "stochastic" variable into the problem. This

last mathematical problem is quite different from the inclusion of random variables in a Leslie matrix. In fact mathematically speaking, the "disordered" case corresponds to the "stochastic" one when considering an infinitely long-time correlation in the stochastic variable (Brissaud and Frisch, 1974; Budde and Cáceres, 1988). We note that using experience from solid-state physics, a random time-dependent perturbation, *i.e.*, the "stochastic case", can be solved in a self-consistent approximation (Harrison and Zwanzig, 1985).

Discrete population models can also be applied to populations classified by multiple criteria. For example, Rogers (1966) describes the growth of the human population of California and the rest of the United States, and age-specific migration between the two regions. The analysis could also be extended to populations in several regions, the result being large partitioned-growth Leslie' matrices. The self-consistent approximation we mentioned previously, is a good technique to tackle enlarged Leslie' matrices with transition rates between spatial locations. This kind of work will be the subject of future contributions.

Acknowledgements

Appendix A. Random Leslie matrix review

Consider the linear recurrence relation:

$$\mathbf{X}(m+1)_j = (\mathbf{M} \cdot \mathbf{X}(m))_j, \quad m = 0, 1, 2, \ldots$$
$$= \sum_i \mathbf{M}_{ji} \mathbf{X}(m)_i \tag{A.1}$$

where the $N \times N$ Leslie matrix $\mathbf{M}$ can be split into two contributions: $\mathbf{M} = \mathbf{H} + \mathbf{B}$. As noted earlier, $\mathbf{H}$ represents the non-random part (it has a Leslie form), and the random part $\mathbf{B}$ also has the Leslie form but for each sample of disorder it does not need to fulfill the condition $\mathbf{B}_{ij} \geq 0$. This is so because for any realization of the disorder the general condition is $\mathbf{M}_{ij} \geq 0$. Thus, the joint probability $P(\{\mathbf{B}_{ij}\})$ should be chosen with care in order to fulfill the general condition $\mathbf{M}_{ij} \geq 0$. A different situation occurs when we extract the scalar moments $\langle \mathbf{B}_{ij} \cdots \mathbf{B}_{lk} \rangle$ from suitable experimental data; in this case we do not need to assume any distribution but we should be able to compute the moments up to a given order $\mathcal{O}(\mathbf{B}^k)$ from the data, see Fig. 1.

From now on any functional average will be written, in short notation, in the form:

$$\langle F(\mathbf{B}) \rangle = \sum_{ij} P(\{\mathbf{B}_{ij}\}) F(\mathbf{B}). \tag{A.2}$$

If a random variable were continuous we should understand: $\sum \to \int d\mathbf{B}_{ij}$. There is a great simplification in the algebra if we introduce a Projection Operator acting on any functional of the random matrix $\mathbf{B}$. So from now on, we will use the notation:

$$\mathcal{P} F(\mathbf{B}) \equiv \langle F(\mathbf{B}) \rangle, \tag{A.3}$$

and for its complementary Projection Operator we get:

$$\mathcal{Q}F(\mathbf{B}) \equiv (1 - \mathcal{P})F(\mathbf{B}) = F(\mathbf{B}) - \langle F(\mathbf{B}) \rangle. \tag{A.4}$$

The Projection Operators $\mathcal{Q} \equiv (\mathbf{1} - \mathcal{P})$ and $\mathcal{P}$ only work on the right hand side of any random matrix $\mathbf{B}$. For example we can consider the objects:

$$\mathcal{Q}\mathbf{B}\mathbf{B} = (\mathbf{1} - \mathcal{P})\mathbf{B}\mathbf{B} = \mathbf{B}\mathbf{B} - \langle \mathbf{B}\mathbf{B} \rangle,$$
$$\mathcal{P}\mathbf{B}\mathcal{Q}\mathbf{B} = \langle \mathbf{B}\mathbf{B} \rangle - \langle \mathbf{B} \rangle^2, \tag{A.5}$$

where $\mathbf{B}\mathbf{B}$ is understood as the matrix multiplication operation, *i.e.*:

$$\mathcal{P}(\mathbf{B}^2)_{lm} = \langle \mathbf{B}^2 \rangle_{lm} \equiv \langle \mathbf{B}\mathbf{B} \rangle_{lm} = \left\langle \sum_p \mathbf{B}_{lp}\mathbf{B}_{pm} \right\rangle$$

$$= \sum_{ij} P(\{\mathbf{B}_{ij}\}) \sum_p \mathbf{B}_{lp}\mathbf{B}_{pm} = \sum_p \langle \mathbf{B}_{lp}\mathbf{B}_{pm} \rangle \tag{A.6}$$

etc.

Leslie' recurrence relation (A.1) can be solved using the *z*-transform in vector notation. The Green function of this problem is $\mathbf{G}(z) = [\mathbf{1} - z\mathbf{M}]^{-1}$. In order to consider the random problem, we split Leslie' recurrence relation into two contributions in the form:

$$\mathbf{X}(m + 1) = \mathbf{H} \cdot \mathbf{X}(m) + \mathbf{B} \cdot \mathbf{X}(m), \tag{A.7}$$

where the joint probability $P(\{\mathbf{B}_{ij}\})$ or the moments $\langle \mathbf{B}_{ij} \cdots \mathbf{B}_{lk} \rangle$ are supposed to be known. The associated Green function of this new problem is a functional of the random variables appearing in the matrix $\mathbf{B}$. To calculate the mean-value Green function we use the Projection Operators $\mathcal{P}$ and $\mathcal{Q}$. We showed (Cáceres and Cáceres-Saez, 2011) that the mean-value Green function is:

$$\langle \mathbf{G}(z) \rangle = \left[\mathbf{1} - z \left(\mathbf{H} + \left\langle \sum_{k=0}^{\infty} [\mathbf{B}\mathbf{G}^0 \mathcal{Q}]^k \mathbf{B} \right\rangle \right) \right]^{-1}, \tag{A.8}$$

where $\mathbf{G}^0$ is the deterministic Green function:

$$\mathbf{G}^0 \equiv \left[\frac{1}{z}\mathbf{1} - \mathbf{H} \right]^{-1}. \tag{A.9}$$

From (A.8) the secular polynomial $\mathbf{P}(z)$, see Section 2 (Eq. (10)), follows immediately.

To calculate the dominant zero z_e from $\mathbf{P}(z)$ we need to specify the random matrix model $\mathbf{B}$ and give the joint probability $P(\{\mathbf{B}_{ij}\})$ or know the scalar moments $\langle \mathbf{B}_{ij} \cdots \mathbf{B}_{lk} \rangle$. In this way we can analyze the stability of the mean-value population vector state for any statistical model. We choose here a particular model of disorder as presented in Section 2 (Eq. (6)) (a correlated survival-fertility model). Then considering the Terwiel cumulant structure given in Section 2 (Eq. (10)), the first non-null contribution, up to $\mathcal{O}(\mathbf{B}^2)$, gives in the form:

$$\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q}\mathbf{B} \rangle = \langle \mathbf{B}\mathbf{G}^0 \mathbf{B} \rangle - \langle \mathbf{B}\mathbf{G}^0 \langle \mathbf{B} \rangle \rangle = \langle \mathbf{B}\mathbf{G}^0 \mathbf{B} \rangle, \tag{A.10}$$

where we used $\langle \mathbf{B} \rangle = 0$, this is a general result for any joint distribution $P(\{\mathbf{B}_{ij}\})$.

Using a uniform distribution for $h \in [h_{\min}, h_{\max}]$, we find that all the product of elements $\langle \mathbf{B}_{ij}\mathbf{B}_{lk} \rangle$ are multiplied by the small dispersion: $\langle h^2 \rangle - \langle h \rangle^2 \sim 5 \times 10^{-4}$. Thus calculating the dominant zero z_e from $\mathbf{P}(z)$ will introduce an error estimated by $\mathcal{O}(\mathbf{B}^4) \sim (\sigma_h^2)^2 \sim 10^{-8}$. This is so because in this case all cumulants of order $\mathcal{O}(\mathbf{B}^3)$ are null. In fact an error bound of this order can be rigorously introduced from the neglected terms in (10), see Cáceres and Cáceres-Saez (2011).

The particular cumulant $\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q}\mathbf{B} \rangle$ is the simplest one that comes from the time-evolution (*z*-transform structure) of the perturbed

Green function. In general any cumulant can be calculated knowing the statistical properties that we chose for the set of random variables (Cáceres and Cáceres-Saez, 2011).

In total analogy, if we want to study a perturbation up to $\mathcal{O}(\mathbf{B}^4)$ we have to calculate the next non-null Terwiel cumulant (Terwiel, 1974; Cáceres, 2003, 2004), *i.e.*,:

$$\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q}\mathbf{B}\mathbf{G}^0 \mathcal{Q}\mathbf{B}\mathbf{G}^0 \mathcal{Q}\mathbf{B} \rangle. \tag{A.11}$$

This object looks much more complex, but it can also be handled analytically with little effort.

The mean value invariant vector Φ can be calculated in the same order of approximation as we used for the effective growth rate λ_{eff} in the following form. If the Leslie matrix is irreducible the mean value of the Green matrix: $\langle \mathbf{G}(z) \rangle$, will have a simple pole of the form $(z_e - z)^{-1}$. This means that in the limit $z \to z_e$ the dominant diverging form will be: $\langle \mathbf{G}(z) \rangle \simeq (z_e - z)^{-1}\mathcal{G}$, where $(-)\mathcal{G}$ is the residue of $\langle \mathbf{G}(z) \rangle$ at z_e. Therefore, from Tauberian's theorem for any initial condition $\mathbf{X}(0)$ we get at the limit $m \gg 1$ that: $\mathbf{X}(m \gg 1) \sim (1/z_e)^{n+1}\mathcal{G} \cdot \mathbf{X}(0)$. Here $z_e = 1/\lambda_{eff}$ and the matrix $\mathcal{G}$ has all its columns equal, thus the invariant vector Φ can be read from any column in the form (Cáceres and Cáceres-Saez, 2011):

$$\Phi = \mathcal{G} \cdot \mathbf{X}(0) \tag{A.12}$$

A.1. Random correlated survival-fertility model: calculation of $\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q}\mathbf{B} \rangle$

Here we want to present a general result (for Leslie' matrices of dimension 13×13) that can be used to calculate any second cumulant such as: $\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q}\mathbf{B} \rangle$. Thus, up to $\mathcal{O}(\mathbf{B}^2)$ and using the statistical independence assumption for the set of random variables $\{\beta_j\}$, $\forall j = 0, 1, 2, \ldots, 12$, the cumulant $\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q}\mathbf{B} \rangle$ is characterized by the elements $\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{lk}$, where the indices $\{l, k\}$ run as 1, 2, 3, ..., 13; *i.e.*, using the random survival-fertility structure of $\mathbf{B}$, see Section 2 (Eq. (6)), we get the general results:

$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{1,l} = 0, \quad \forall l = 1, 2, 3.$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{1,l} = \langle \beta_{l-1}^2 \rangle (g_{l,l+1}m_{l-1} + g_{l,1}m_{l-1}^2), \quad \forall l = 4, 5$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{1,l} = \langle \beta_{l-1}^2 \rangle (g_{l,l+1}m + g_{l,1}m^2), \quad 6 \leq l \leq 12$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{1,13} = \langle \beta_{12}^2 \rangle g_{13,1}m^2$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{2,1} = \langle \beta_0^2 \rangle g_{1,2}$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{2,l} = 0, \quad 2 \leq l \leq 13$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{3,1} = 0$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{3,2} = \langle \beta_1^2 \rangle g_{2,3}$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{3,l} = 0, \quad 3 \leq l \leq 13$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{4,l} = 0, \quad \forall l = 1, 2$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{4,3} = \langle \beta_2^2 \rangle g_{3,4}$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{4,l} = 0, \quad 4 \leq l \leq 13$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{5,l} = 0, \quad \forall l = 1, 2, 3$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{5,4} = \langle \beta_3^2 \rangle (g_{4,5} + g_{4,1}m_3)$$
$$\langle \mathbf{B}\mathbf{G}^0\mathbf{B} \rangle_{5,l} = 0, \quad 5 \leq l \leq 13 \tag{A.13}$$

$\langle \mathbf{BG^0B} \rangle_{6,l} = 0, \quad \forall l = 1, 2, 3, 4$

$\langle \mathbf{BG^0B} \rangle_{6,5} = \langle \beta_4^2 \rangle (g_{5,6} + g_{5,1} m_4)$

$\langle \mathbf{BG^0B} \rangle_{6,l} = 0, \quad 6 \le l \le 13$

$\langle \mathbf{BG^0B} \rangle_{7,l} = 0, \quad 1 \le l \le 5$

$\langle \mathbf{BG^0B} \rangle_{7,6} = \langle \beta_5^2 \rangle (g_{6,7} + g_{6,1} m)$

$\langle \mathbf{BG^0B} \rangle_{7,l} = 0, \quad 7 \le l \le 13$

$\langle \mathbf{BG^0B} \rangle_{8,l} = 0, \quad 1 \le l \le 6$

$\langle \mathbf{BG^0B} \rangle_{8,7} = \langle \beta_6^2 \rangle (g_{7,8} + g_{7,1} m)$

$\langle \mathbf{BG^0B} \rangle_{8,l} = 0, \quad 8 \le l \le 13$

$\langle \mathbf{BG^0B} \rangle_{9,l} = 0, \quad 1 \le l \le 7$

$\langle \mathbf{BG^0B} \rangle_{9,8} = \langle \beta_7^2 \rangle (g_{8,9} + g_{8,1} m)$

$\langle \mathbf{BG^0B} \rangle_{9,l} = 0, \quad 9 \le l \le 13$

$\langle \mathbf{BG^0B} \rangle_{10,l} = 0, \quad 1 \le l \le 8$

$\langle \mathbf{BG^0B} \rangle_{10,9} = \langle \beta_8^2 \rangle (g_{9,10} + g_{9,1} m)$

$\langle \mathbf{BG^0B} \rangle_{10,l} = 0, \quad 10 \le l \le 13$

$\langle \mathbf{BG^0B} \rangle_{11,l} = 0, \quad 1 \le l \le 9$

$\langle \mathbf{BG^0B} \rangle_{11,10} = \langle \beta_9^2 \rangle (g_{10,11} + g_{10,1} m)$

$\langle \mathbf{BG^0B} \rangle_{11,l} = 0, \quad 11 \le l \le 13$

$\langle \mathbf{BG^0B} \rangle_{12,l} = 0, \quad 1 \le l \le 10$

$\langle \mathbf{BG^0B} \rangle_{12,11} = \langle \beta_{10}^2 \rangle (g_{11,12} + g_{11,1} m)$

$\langle \mathbf{BG^0B} \rangle_{12,l} = 0, \quad 12 \le l \le 13$

$\langle \mathbf{BG^0B} \rangle_{13,l} = 0, \quad 1 \le l \le 11$

$\langle \mathbf{BG^0B} \rangle_{13,12} = \langle \beta_{11}^2 \rangle (g_{12,13} + g_{12,1} m)$

$\langle \mathbf{BG^0B} \rangle_{13,13} = 0,$

where we have introduced the simplified notation for the elements of the deterministic Green matrix (A.9): $\mathbf{G}_{lk}^0 \equiv g_{l,k}, \forall \{l, k\} = 1, 2, 3, \ldots, 13$. We note that these expressions can be used for any distribution characterizing the moments $\langle \beta_j \beta_l \rangle = \delta_{jl} \langle \beta_j^2 \rangle$. The case when the set $\{\beta_j\}$ is not statistically independent can also be handled in a similar way.

Any statistics are incorporated by evaluating $\langle \beta_j^2 \rangle, \forall j = 0, 1, 2, 3, \ldots, 12$. In the present case, using a uniform distribution for h we get

$$\langle h \rangle = \frac{(h_{\max} + h_{\min})}{2},$$
$$\langle h^2 \rangle = \frac{(h_{\max}^3 - h_{\min}^3)}{3(h_{\max} - h_{\min})},$$

then:

$$\langle \beta_0^2 \rangle = \left(\frac{43}{30}(1 - n_j) \right)^2 \sigma_h^2,$$
$$\langle \beta_j^2 \rangle = (1 - n_j)^2 \sigma_h^2,$$

with $\sigma_h^2 \equiv \langle h^2 \rangle - \langle h \rangle^2$. Note that because in Model A there are only two values of survival probabilities we finally get $\langle \beta_0^2 \rangle \ne \langle \beta_j^2 \rangle = \langle \beta^2 \rangle$ for $1 \le j \le 12$. In Model B each $\langle \beta_j^2 \rangle$ will be different because in that case we are using Caughley's smoothed function n_j to characterize p_j.

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