Beyond survival estimation: mark–recapture, matrix population models, and population dynamics

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Abstract

Beyond survival estimation: mark–recapture, matrix population models, and population dynamics.— Survival probability is of interest primarily as a component of population dynamics. Only when survival estimates are included in a demographic model are their population implications apparent. Survival describes the transition between living and dead. Biologically important as this transition is, it is only one of many transitions in the life cycle. Others include transitions between immature and mature, unmated and mated, breeding and non–breeding, larva and adult, small and large, and location x and location y. The demographic consequences of these transitions can be captured by matrix population models, and such models provide a natural link connecting multi–stage mark–recapture methods and population dynamics. This paper explores some of those connections, with examples taken from an ongoing analysis of the endangered North Atlantic right whale (*Eubalaena glacialis*). Formulating problems in terms of a matrix population model provides an easy way to compute the likelihood of capture histories. It extends the list of demographic parameters for which maximum likelihood estimates can be obtained to include population growth rate, the sensitivity and elasticity of population growth rate, the net reproductive rate, generation time, measures of transient dynamics. In the future, multi–stage mark–recapture methods, linked to matrix population models, will become an increasingly important part of demography.

Key words: Matrix population models, Right whale, *Eubalaena glacialis*, Sensitivity, Elasticity.

Resumen

Más allá de la estimación de supervivencia: marcaje–recaptura, modelos matriciales de poblaciones y dinámica de poblaciones.— La probabilidad de supervivencia resulta especialmente interesante como componente de la dinámica poblacional. Sólo cuando las estimaciones de supervivencia se incluyen en un modelo demográfico, puede apreciarse su repercusión en la población. La supervivencia describe la transición entre la vida y la muerte. Pese a su importancia biológica, dicha transición sólo constituye una más de las que componen el ciclo vital, debiendo destacarse, entre otras, la que se produce entre la inmadurez y la madurez, la ausencia de apareamiento y el apareamiento, la reproducción y la ausencia de reproducción, el estado larval y el de adulto, pequeño y grande, y entre el emplazamiento x y el emplazamiento y. Las consecuencias demográficas de dichas transiciones pueden determinarse mediante modelos matriciales de poblaciones, que proporcionan un enlace natural capaz de vincular los métodos de marcaje–recaptura de fases multiestados con la dinámica poblacional. El presente estudio analiza algunas de dichas conexiones, incluyendo ejemplos extraídos de un análisis que sigue en marcha de la ballena franca (*Eubalaena glacialis*), en peligro de extinción. La formulación de problemas, considerados desde la perspectiva del modelo matricial de poblaciones, permite calcular fácilmente las probabilidades de las historias de captura, al tiempo que amplía la lista de parámetros demográficos con respecto a los que pueden obtenerse estimaciones por máxima verosimilitud, incluyendo la tasa de crecimiento poblacional, la sensibilidad y elasticidad de dicha tasa, la tasa neta de reproducción, el tiempo generacional y las mediciones de la dinámica transitoria. En el futuro, los métodos de marcaje–recaptura de multiestados, en combinación con los modelos matriciales de poblaciones, constituirán una parte cada vez más importante de la demografía.

Palabras clave: Modelos matriciales de poblaciones, Ballena franca, *Eubalaena glacialis, S*ensibilidad, Elasticidad.

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Introduction

Throughout its history, and certainly since the 1960s, the field of mark–recapture (MR) statistics has emphasized the estimation of survival probability. Lebreton et al. (1992) provided a state–of–the art review of the field, emphasizing tests of hypotheses about, and selection of models describing, survival probability. But survival probability is, in itself, of limited interest. After all, every individual dies eventually; why should we care about the short–term probability of this ultimately certain event? The answer, of course, is that survival is vitally important as a component of population growth. In the simple population growth model

$$N(t + 1) = [P \text{ (survival)} + E \text{ (reproduction)}] \ N(t) \quad (1)$$
$$= \lambda N(t)$$

the rate of increase λ is the sum of the survival probability and the birth rate.

A model like (2) makes the demographic analog of the homogeneity assumption of MR theory: that all individuals are identical. Since all individuals are obviously not identical, there is a long history (a century or more) of *demographic* population models —models that disaggregate individuals on the basis of age, physiological condition, size, developmental stage, spatial location, etc. (Lotka, 1907, 1924, 1934–1939; Kermack & McKendrick, 1927; Leslie, 1945; Keyfitz, 1968; Metz & Diekmann, 1986; Caswell, 1989, 2001; Tuljapurkar & Caswell, 1997).

Structured demographic models do two things. The most obvious but least important is to provide more accurate descriptions of population dynamics, by incorporating more biological differences among individuals and the way that those differences affect individuals' fates in a given environment. The more important thing has nothing to do with accuracy. Structured demographic models are valuable because they provide explanations of population dynamics in terms of the fates of individuals. Calculating the population growth rate from age– or stage–specific data may or may not produce more accurate predictions, but it shows how the life cycle influences population dynamics in ways that unstructured models cannot do.

Structured models can be written as partial differential equations, delay–differential equations, integrodifference equations, or matrix population models, depending whether individuals are divided into discrete classes or measured by a continuous variable, and whether time is discrete or continuous (Tuljapurkar & Caswell, 1997; Caswell, 2001):

	Discrete–state	Continuous–state
Discrete–time	Matrix population models	Integrodifference equations
Continuous–time	Delay–differential equations	Partial differential equations

Regardless of the mathematical framework, demographic models link the fates of individuals to the dynamics of populations. This individual–population link is the key to using MR methods to estimate the parameters in such models, because MR data are essentially individual data; putting a tag on an animal (or plant) distinguishes that individual from all others in the population. Repeated observations on that individual record its history, distinct from the history of any other individual.

Here, we will focus on matrix population models, because they correspond most closely to the structure of typical MR data, but it is worth noting that connecting MR methods and demographic models in the other frameworks is an important problem (e.g., Fujiwara, 2002).

We will describe, briefly, the structure of a matrix population model and some of the ways that such a model characterizes population dynamics (for a much more complete description, see Caswell, 2001). We will emphasize perturbation analysis as an integral part of demographic analysis. This will lead to a discussion of the link of such models to MR analysis, and to ways in which matrix population models naturally encapsulate the fundamental notion of the "likelihood of a capture history". Finally, we will illustrate some of these points with aspects of a demographic analysis of the North Atlantic right whale.

Matrix population models

A matrix population model requires, first, a choice of a projection interval, or time step, over which to project the population, and a set of life cycle stages into which to classify individuals. The stages are chosen by a homogeneity criterion: knowing the stage of an individual must suffice to predict, at least probabilistically, the response of an individual to the environment (Metz & Diekmann, 1986, Caswell, 2001). Choosing stages requires a knowledge of, and an ability to balance, the biology of the organism and the limitations of the available data.

Given the projection interval and the stages, the model can be written as

$$\mathbf{n}(t + 1) = \mathbf{A}_{t,\mathbf{n}(t)}\mathbf{n}(t) \quad (2)$$

Here $\mathbf{n}(t)$ is a vector whose entries give the numbers of individuals in each stage, and $\mathbf{A}$ is a square population projection matrix whose entries may depend on time, the environment, and/or population density.

Characterizing population dynamics

The dynamics induced by (2), and the quantities calculated to describe those dynamics, depend on the nature of the projection matrix. It is these quantities that a demographic analysis sets out to estimate.

Linear time–invariant models

The solution to (2) in this case can be written as a sum of exponentials of the eigenvalues of **A**. Because A is inherently non–negative, the Perron–Frobenius theorem guarantees that one of these eigenvalues is real, non–negative, and as great as or greater than the magnitude of any of the others. If **A** is also primitive, then this eigenvalue λ_1 (or, where the subscript is not needed for the context, λ) is strictly greater than any other, and the population eventually grows at this rate with a stable structure proportional to the corresponding right eigenvalue **w**. The left eigenvector **v** gives the distribution of reproductive values.

Before this asymptotic growth rate is realized, the population will exhibit transient fluctuations in both abundance and structure, which can be analyzed in terms of the subdominant eigenvalues and eigenvectors of **A**.

Periodic models

Periodic models are useful for describing effects of seasonal variation in the vital rates (e.g., Hunter, 2001; Hunter & Caswell, 2004a; Smith et al., 2004). They can also be used to describe inter–annual variation as an approximation to other kinds of variation.

Population growth over an annual cycle of p phases, starting at phase 1, is given by the product

$$\mathbf{A}_1 = \mathbf{B}_p \cdots \mathbf{B}_2 \mathbf{B}_1 \tag{3}$$

Note that the seasonal matrices are multiplied from right to left, in order. The population growth rate is given by the dominant eigenvalue λ of $\mathbf{A}_1$. The stable stage distribution (at phase 1) is given by the corresponding right eigenvector **w**. The reproductive value distribution is given by the left eigenvector **v**. The stable stage distribution and reproductive value at other phases of the cycle are given by the eigenvectors of the appropriate cyclic permutations of the $\mathbf{B}_i$; e.g., those at phase 2 would be obtained from

$$\mathbf{A}_2 = \mathbf{B}_1 \mathbf{B}_p \cdots \mathbf{B}_2 \tag{4}$$

Stochastic models

In a stochastic environment, population growth is described by the time–varying model

$$\mathbf{n}(t + 1) = \mathbf{A}_t \, \mathbf{n}(t) \tag{5}$$

where the matrices $\mathbf{A}_t$ are generated by a stochastic model for the environment. Given some reasonable assumptions about the environmental process and the matrices, asymptotic population growth is, with probability 1, characterized by the stochastic growth rate

$$\log \lambda_s = \lim_{T \to \infty} \frac{1}{T} \log \left\| \mathbf{A}_{T-1} \cdots \mathbf{A}_0 \mathbf{n}_0 \right\| \tag{6}$$

where $\|\mathbf{x}\| = \sum_i |x_i|$ is the 1–norm (Furstenberg & Kesten, 1960; Oseledec, 1968; Cohen, 1976, 1977a, 1977b; Tuljapurkar & Orzack, 1980; Tuljapurkar, 1989, 1990).

Density–dependent models

The dynamics of a density–dependent population described by the nonlinear model

$$\mathbf{n}(t + 1) = \mathbf{A}_{\mathbf{n}(t)} \, \mathbf{n}(t) \tag{7}$$

are not characterized by exponential growth. Instead, trajectories typically converge to an attracting invariant set (equilibrium point, cycle, invariant loop, or strange attractor) on which the long–term average growth rate is 1. Often, these attracting invariant sets exhibit bifurcations as any parameter in the model is varied. Figure 1 shows an example from a simple two–stage model (juveniles and adults) with density–dependent fertility, in which

$$\mathbf{A}_\mathbf{n} = \begin{pmatrix} \sigma_1(1-\gamma) & f \exp\left(-\sum_i n_i\right) \\ \sigma_1 \gamma & \sigma_2 \end{pmatrix} \tag{8}$$

where σ_1 and σ_2 are juvenile and adult survival probabilities, γ is the maturation rate, and f is the fertility at low densities.

As f is increased, the equilibrium population increases from zero (at any value of f below the critical value at which the population is capable of growing at all at low densities) to higher and higher values. As f increases, a flip bifurcation occurs and the stable equilibrium is replaced by a stable 2–cycle. As f is increased further, the 2–cycle is replaced by a 4–cycle, which in turn is replaced by cycles of period 8, 16, etc. Eventually the dynamics become chaotic. For more details on such bifurcations, see Caswell (1997, 2001) and Neubert & Caswell (2000a). For an account of an outstanding experimental investigation of such bifurcations in laboratory populations of *Tribolium* flour beetles, see Cushing et al. (2003).

The point of this demonstration is not concern over whether a particular 2–stage population might exhibit chaotic dynamics, but to make the point that the characterization of a density–dependent model —the answer to the question "what are the implications of this set of parameters?"— is the entire bifurcation sequence. It is the result of the parameter values and the functional forms in the matrix $\mathbf{A}_\mathbf{n}$, which are exactly what would be estimated by a MR analysis using density as a covariate.

Because the long–term performance of a density–dependent population involves its attractor(s), two different measures of population performance have attracted attention. The first is the long–term population composition or some function of it. Choosing the function has not received much careful thought. There is a tendency to think of total density (for equilibria) or time–averaged total density (for cycles, etc.) without considering the bio-

logical justification for the choice. Since total density involves adding together individuals of very different properties (tiny seedlings and enormous trees, etc.), it is unlikely to capture much of relevance, but alternatives are not totally clear (for one, see (34) below)

The invasion exponent

An alternative measure of population performance is the invasion exponent. It can be motivated by comparing the growth rates of two density–independent populations, each with its own vital rates, and thus with population growth rates $\lambda^{(1)}$ and $\lambda^{(2)}$. If N_i is any measure of population size of type i, then asymptotically

$$\frac{1}{t} \log \frac{N_2(t)}{N_1(t)} \to \log \lambda^{(2)} - \log \lambda^{(1)} \qquad (9)$$

Type 2 will increase in frequency relative to type 1 if and only if $\log \lambda^{(2)} > \log \lambda^{(1)}$. Since $\log \lambda$ determines the ability of a type to invade, it is referred to as the *invasion exponent*. The sensitivity and elasticity of λ show the effect of parameter changes on the invasion exponent.

Invasion calculations can be applied to linear and nonlinear, deterministic and stochastic models (Metz et al., 1992; Ferriére & Gatto, 1995; Rand et al., 1994; Grant, 1997; Grant & Benton, 2000). Consider two types, each defined by vector θ_i of parameters; suppose that type 2 is trying to invade type 1. Its dynamics during this invasion will depend on its parameters, on the density of the resident, and on its own density. To make this dependence clear, we will write the projection matrix for type 2 as

$$\mathbf{A} = \mathbf{A}\big[\theta_2, \mathbf{n}_1(t), \mathbf{n}_2(t)\big] \qquad (10)$$

The invasion exponent describes the dynamics of type 2 when it invades at such a low density that $\mathbf{n}_2(t)$ is negligible for a very long time. It is given by the long–term average growth rate of type 2 while type 1 is on its attractor $\hat{\mathbf{n}}_1$:

$$\log \lambda_I^{(2 \to 1)} = \lim_{T \to \infty} \frac{1}{T} \log \big\| \mathbf{A}\big[\theta_2, \hat{\mathbf{n}}_1(T-1), 0\big] \cdots \qquad (11)$$
$$\cdots \mathbf{A}\big[\theta_2, \hat{\mathbf{n}}_1(0), 0\big] \mathbf{n}_2(0) \big\|$$

The notation λ_I (Caswell, 2001) emphasizes the relation between the invasion exponent and the growth rate in a constant environment (λ) or a stochastic environment (λ_s). The superscript $(2 \to 1)$ indicates that type 2 is invading type 1.

In the special case in which $\hat{\mathbf{n}}_1$ is an equilibrium point, the invasion exponent is just the log of the dominant eigenvalue of the constant projection matrix for type 2, evaluated at the equilibrium density of type 1:

$$\lambda_I^{(2 \to 1)} = \lambda\big(\mathbf{A}[\theta_2, \hat{\mathbf{n}}_1, \mathbf{0}]\big) \qquad (12)$$

For examples of the use of the invasion exponent in calculations regarding the evolution of dispersal, see Khaladi et al. (2000) and Lebreton et al. (2000).

Environment–dependent models

Suppose that the vital rates are functions of some environmental variable $\varepsilon(t)$; then we could write

$$\mathbf{n}(t+1) = \mathbf{A}_{\varepsilon(t)}\mathbf{n}(t) \qquad (13)$$

The dynamics of such a population depend on what the environment does, and there is surprisingly little to say in general about such models.

If $\varepsilon(t)$ represents a particular fixed environmental condition (habitat type, or level of pollution, say), interest might focus on potential population growth under different but fixed environmental conditions. Then life table response experiment (LTRE) analyses can be used to decompose the effects of the environment on λ into contributions from effects on each of the vital rates. For example, suppose that two environments (ε_1 and ε_2) are being compared. The matrices $\mathbf{A}_{\varepsilon_1}$ and $\mathbf{A}_{\varepsilon_2}$ yield population growth rates λ_{ε_1} and λ_{ε_2}. To first order

$$\lambda_{\varepsilon_1} - \lambda_{\varepsilon_2} \approx \sum_{i,j} (a_{ij}^{(\varepsilon_1)} - a_{ij}^{(\varepsilon_2)}) \frac{\partial \lambda}{\partial a_{ij}} \qquad (14)$$

where the derivative of λ is calculated according to (15) below. For details see Caswell (1989a, 2000, 2001); for examples see Levin et al. (1996), Cooch et al. (2001).

When $\varepsilon(t)$ represents an observed temporal trend, asymptotic dynamics may be of little relevance, and attention would focus on short–term population projections. Those projections will depend on the ability to forecast the trend accurately. In other cases, as when $\varepsilon(t)$ represents a climatic variable like rainfall, the asymptotic growth rate under a specified rainfall regime (characterized, say, by a time–series model or a stochastic model for disturbances like fire; Silva et al., 1991; Caswell & Kaye, 2001) would be of great interest.

In each of these cases, the environment–dependent model is reduced to a simpler model (short–term transient dynamics, long–term stochastic dynamics, or long–term linear dynamics in different environments). But this kind of model has received little general attention, perhaps because it has not been easy to estimate vital rates as functions of environmental variables in the field; that task becomes much easier with mark–recapture approaches.

Perturbation analyses

The demographic analyses in the preceding (non–exhaustive) list all take as given a set of demographic parameter values. But almost never are we interested in only one specific set of parameter values. There is always the possibility that the values could change, because of natural environmental change, human activity (including management actions), evolutionary change, or because the parameters are estimated with error. Perturbation analyses evaluate the effect of such changes. They are available for many of the demographic indices just described (Caswell, 2001).

Linear time–invariant models

The sensitivity of population growth rate λ of a change in a parameter θ is

$$\frac{\partial \lambda}{\partial \theta} = \mathbf{v}^{\mathsf{T}} \frac{\partial \mathbf{A}}{\partial \theta} \mathbf{w} \qquad (15)$$

where the eigenvectors are scaled so that their scalar product $\langle \mathbf{v}, \mathbf{w} \rangle = 1$ (Caswell, 1978, 2001) and $\mathbf{v}^{\mathsf{T}}$ is the trasposse of $\mathbf{v}$. In the important case where $\theta = a_{ij}$, this reduces to:

$$\frac{\partial \lambda}{\partial a_{ij}} = v_i w_j \qquad (16)$$

The proportional sensitivity, or elasticity, measures both changes and their effects on a logarithmic scale, and is given by:

$$\frac{\theta}{\lambda} \frac{\partial \lambda}{\partial \theta} \qquad (17)$$

See Link & Doherty (2002) for explorations of some interesting alternatives to considering the effect of proportional changes. Their paper is a response to concerns raised by the unfortunate tendency to think that elasticities (or sensitivities) measure the "importance" of a parameter, and then to be puzzled when the importance of survival, say, is not the same as the importance of mortality. The confusion can be alleviated by repeating, over and over, that sensitivities and elasticities are derivatives, nothing more. That the derivative of a quantity with respect to one variable is not the same as its derivative with respect to another variable is not particularly surprising. Because λ is generally a nonlinear function of the parameters, sensitivities and elasticities can only predict approximate results of large perturbations in θ. Experience has shown that, in most cases, they give usefully accurate predictions even for quite large changes.

Since the elasticities of λ to changes in the a_{ij} sum to 1, they can (with care) be interpreted as showing the proportional contribution of the a_{ij} to population growth rate. In evolutionary contexts, the sensitivities of λ measure the selection gradients on the a_{ij}. (The elasticities, in contrast, do not measure selection gradients, and are of only limited use in evolutionary calculations; see Caswell 2001, Section 11.2)

Periodic models

In a periodic model, we want to compute the sensitivities and elasticities of λ to changes in the entries of each of the seasonal matrices $\mathbf{B}_i$, using the approach of (Caswell & Trevisan, 1994; Lesnoff et al., 2003). Let $\mathbf{S_A}$ be the sensitivity matrix for $\mathbf{A}$ (i.e., the matrix whose (i,j) entry is $\partial \lambda / \partial a_{ij}$). In general, suppose that there are p matrices in a seasonal cycle, $\mathbf{B}_1, ..., \mathbf{B}_p$. To calculate the sensitivity of λ to the entries of $\mathbf{B}_m$, let

$$\mathbf{A} = \mathbf{F}^{(m)} \mathbf{B}_m \mathbf{G}^{(m)} \qquad m = 1, ..., p \qquad (18)$$
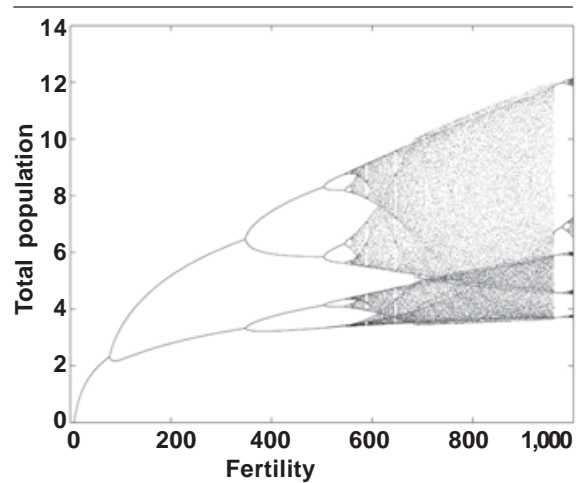

Fig. 1. A bifurcation diagram for the density-dependent model (8). For each value of fertility *f*, the asymptotic attractor is plotted. Equilibria appear as single lines, cycles as multiple lines, and chaotic dynamics as a cloud of points.

Fig. 1. Diagrama de bifurcación para el modelo dependiente de densidades (8). Para cada valor de fertilidad f*, se representa gráficamente el atractor asintótico. Los equilibrios se muestran como líneas simples, los ciclos mediante líneas múltiples y la dinámica caótica como una nube de puntos.*

where

$$\mathbf{F}^{(m)} = \begin{cases} \mathbf{B}_p \cdots \mathbf{B}_{m+1} & m \neq p \\ \mathbf{I} & m = 1 \end{cases} \qquad (19)$$

$$\mathbf{G}^{(m)} = \begin{cases} \mathbf{B}_{m-1} \cdots \mathbf{B}_1 & m \neq 1 \\ \mathbf{I} & m = p \end{cases}$$

The sensitivity matrix $\mathbf{S}_{\mathbf{B}_m}$ whose entries are the sensitivities of λ to $b_{ij}^{(m)}$ is

$$\mathbf{S}_{\mathbf{B}_m} = \mathbf{F}^{(m)\mathsf{T}} \mathbf{S_A} \mathbf{G}^{(m)\mathsf{T}} \qquad (20)$$

The elasticity matrix $\mathbf{E}_{\mathbf{B}_m}$ is

$$\mathbf{E}_{\mathbf{B}_m} = \frac{1}{\lambda} \mathbf{B}_m \circ \mathbf{S}_{\mathbf{B}_m} \qquad (21)$$

where $\circ$ denotes the Hadamard, or element–by–element, matrix product.

The elasticities $e_{ij}^{(m)}$ sum to 1 for each m. Thus they can be interpreted as proportional contribution of the vital rates $b_{ij}^{(m)}$ to population growth, exactly is done for non–seasonal models.

Stochastic models

Tuljapurkar (1990) derived the sensitivity of log λ_s and the elasticity of λ_s to changes in $a_{ij}(t)$. The

matrices $\mathbf{A}_t$ are generated by the stochastic environment. Assume that $\mathbf{A}_t$ is subject to a small perturbation, so that

$$\mathbf{A}_t \rightarrow \mathbf{A}_t + \varepsilon \mathbf{C}_t \qquad (22)$$

The entries of $\mathbf{C}_t$ determine which elements of $\mathbf{A}_t$ are perturbed, and the relative magnitudes of those perturbations.

To calculate the effect of the perturbation on $\log \lambda_s$, the stochastic model for the environment is used to generate a sequence of matrices $\mathbf{A}_0, ..., \mathbf{A}_{T-1}$, where T is a large number. Starting from an arbitrary nonnegative initial vector $\mathbf{w}(0)$, with $\|\mathbf{w}(0)\| = 1$, use the sequence of matrices to generate a sequence of stage distribution vectors

$$\mathbf{w}(t+1) = \frac{\mathbf{A}_t \mathbf{w}(t)}{\|\mathbf{A}_t \mathbf{w}(t)\|} \qquad (23)$$

and one–step growth rates

$$R(t) = \frac{\|\mathbf{A}_t \mathbf{w}(t)\|}{\|\mathbf{w}(t)\|} \qquad (24)$$

where $\|\cdot\|$ denotes the 1–norm. Similarly, starting with an arbitrary nonnegative terminal vector $\mathbf{v}(T)$ with $\|\mathbf{v}(T)\| = 1$, generate a backwards sequence of reproductive value vectors

$$\mathbf{v}^\mathsf{T}(t-1) = \frac{\mathbf{v}^\mathsf{T}(t)\mathbf{A}_{t-1}}{\|\mathbf{v}^\mathsf{T}(t)\mathbf{A}_{t-1}\|} \qquad (25)$$

In terms of these quantities, Tuljapurkar (1990) showed that the stochastic growth rate after the perturbation, $\log \lambda_s(\varepsilon)$, is:

$$\log \lambda_s(\varepsilon) = \log \lambda_s + \varepsilon \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{\mathbf{v}^\mathsf{T}(t+1)\,\mathbf{C}_t\,\mathbf{w}(t)}{R_t \mathbf{v}^\mathsf{T}(t+1)\,\mathbf{w}(t+1)} \quad (26)$$

The coefficient of ε on the right hand side of (26) is the sensitivity of the stochastic growth rate to the perturbations imposed by the sequence of perturbation matrices $\mathbf{C}_t$.

If only a single element of $\mathbf{A}_t$ is perturbed (say, $a_{ij}(t)$) and the perturbation is the same at each time, $\mathbf{C}_t$ is a constant matrix with a 1 in the (i,j) position and zeros elsewhere;

$$\mathbf{C}_t = \mathbf{e}_i \, \mathbf{e}_j^\mathsf{T} \qquad (27)$$

where $\mathbf{e}_i$ is a vector with a 1 in the ith entry and zeros elsewhere. Substituting (27) into (26) leads to Tuljapurkar's formula for the sensitivity of $\log \lambda_s$ to a_{ij}:

$$\frac{\partial \log \lambda_s}{\partial a_{ij}} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{v_i(t+1)\,w_j(t)}{R_t \mathbf{v}^\mathsf{T}(t+1)\,\mathbf{w}(t+1)} \qquad (28)$$

The elasticity of λ_s to a_{ij} is calculated by assuming that the perturbation $c_{ij}(t)$ is proportional to $a_{ij}(t)$, so that $\mathbf{C}_t$ is a matrix with $a_{ij}(t)$ in the (i,j) position and zeros elsewhere:

$$\mathbf{C}_t = \mathbf{e}_i \, \mathbf{e}_i^\mathsf{T} \mathbf{A}_t \, \mathbf{e}_j \, \mathbf{e}_j^\mathsf{T} \qquad (29)$$

Substituting (29) into (26) gives the elasticity of λ_s to a_{ij}:

$$\frac{\partial \log \lambda_s}{\partial \log a_{ij}} = \lim_{t \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{v_i(t+1)\,a_{ij}\,w_j(t)}{R_t \mathbf{v}^\mathsf{T}(t+1)\mathbf{w}(t+1)} \qquad (30)$$

Density–dependent models

The perturbation analysis of a density–dependent model can be carried out in terms of the invasion exponent λ_I or the equilibrium density $\hat{\mathbf{n}}$. There are intimate connections between the two measures of performance (Takada & Nakajima, 1992, 1998; Caswell et al., 2004). Let us write the projection matrix as:

$$\mathbf{A} = \mathbf{A}\left[\theta, f_1(\mathbf{n}), ..., f_r(\mathbf{n})\right] \qquad (31)$$

where θ is a parameter and the f_i are functions of density that appear in the model. There will be more than one such function if different vital rates are affected by different sets of stages in the life cycle.

Let

$$\lambda = \lambda \left(\mathbf{A}\left[\theta, f_1(\hat{\mathbf{n}}), ..., f_r(\hat{\mathbf{n}})\right]\right) \qquad (32)$$

be the population growth rate calculated from the matrix at equilibrium ($\lambda = 1$). Then it can be shown (Caswell et al., 2004) that

$$\left. \frac{\partial \lambda}{\partial \theta}\right|_{\hat{\mathbf{n}}} = \frac{\partial \tilde{N}}{\partial \theta} \qquad (33)$$

where $\tilde{N}$ is an effective equilibrium density, which is a linear combination of stage densities

$$\tilde{N} = \mathbf{g}^\mathsf{T} \hat{\mathbf{n}} \qquad (34)$$

with the weight on stage i given by

$$g_i = \sum_{h=1}^{r} \frac{\partial \lambda}{\partial f_h} \left. \frac{\partial f_h}{\partial n_i}\right|_{\hat{\mathbf{n}}} \qquad (35)$$

The biologically effective density $\tilde{N}$ weights the density of the stages by their importance to density–dependent effects ($\partial f_h / \partial n_i$) and the importance of those effects to demography ($\partial \lambda / \partial f_h$). This combination of density–dependence and demography is exactly the content of the nonlinear model, so $\tilde{N}$ has ample biological justification as an interesting quantity. This result provides a valuable link between λ (and thus all kinds of evolutionary invasion questions) and equilibrium population (and thus all kinds of questions related to population management); see Grant & Benton (2003) for a discussion of the need for such relationships.

Estimation: beyond survival

The point of this quick tour through the types of matrix population models is to emphasize that the construction of such a model creates a whole suite of population parameters, particularly those describing perturbations, that can be estimated.

Estimation with mark–recapture analyses

The population projection matrix and its dependence on time or the environment is the central entity in population dynamics. Mark–recapture methods–in particular, the multi–state versions–are an extraordinarily powerful tool for constructing such models. Demographers have been slow to realize this fact. For example, Caswell (1989) wrote an entire book on matrix population models without mentioning multistate MR methods, although they date back to Arnason (1973). He knew better by 2001, partly because Nichols et al. (1992) presented the first explicit application of multistate MR methods to matrix population models. The link is simple. A matrix population model contains a complete description of the probabilities of transition among all the identified stages *plus death*. The history of any individual consists of a sequence of such transitions, beginning with birth and ending with death. MR data consists of observations of such sequences, with the possible extra complication of failing to observe or capture the individual at each time; in other words, of capture histories. The key to estimating parameters (survival or more complex patterns of transition), is to use the probability of a set of capture histories as the likelihood of the parameters generating the probability. A matrix population model makes it possible to do this in a remarkably straightforward way.

Decomposing the projection matrix

In most (all?) cases, the projection matrix can be decomposed into a part $\mathbf{T}$ that represents transitions of individuals already present in the population and a part $\mathbf{F}$ that represents the creation of new individuals by reproduction:

$$\mathbf{A} = \mathbf{T} + \mathbf{F} \qquad (36)$$

(Feichtinger, 1971; Cochran & Ellner, 1992; Cushing & Yicang, 1994). We will focus on $\mathbf{T}$, and return to $\mathbf{F}$ later.

Let s be the number of stages in the model. Create the $(s+1) \times (s+1)$ matrix $\mathbf{\Phi}$ by adding death as a stage

$$\Phi = \left(\begin{array}{c|c} \mathbf{T} & 0 \\ \hline \mathbf{m} & 1 \end{array} \right) \qquad (37)$$

where $\mathbf{m}$ is a row vector of stage–specific probabilities of death, $m_j = 1 - \sum_i t_{ij}$. The matrix $\mathbf{\Phi}$ is the transition matrix of an absorbing Markov chain, and can be used to calculate many demographically useful quantities, including the distribution of ages at death (even though age may not appear in the model), the net reproductive rate, the generation time, age–specific survivorship, the stable age distribution within each stage, and the probability of any event that can be expressed in terms of stages (Caswell, 2001). Because $\mathbf{\Phi}$ is derived from A, it may vary with time, density, or environmental factors.

The probability of capture histories

For our present purposes, the most important use of $\mathbf{\Phi}$ is that it makes it easy to write down the probability of a multi–state capture history. Let

$$\mathbf{P} = \left(\begin{array}{ccc|c} p_1 & \cdots & 0 & 0 \\ 0 & p_2 & \cdots & 0 \\ 0 & 0 & \ddots & \vdots \\ \hline 0 & \cdots & 0 & p_{s+1} \end{array} \right) \qquad (38)$$

be a diagonal matrix of capture probabilities. If $p_{s+1} = 0$, recoveries of dead individuals are not considered, but the life cycle graph can be extended to include categories representing newly dead and dead–and–gone, and both recaptures and recoveries considered together.

For what follows, it will be useful to define $\mathbf{e}_i$ as a column vector with a 1 in the ith entry and zeros elsewhere, $\mathbf{e}$ as a column vector of ones, and $\mathbf{E}_i = \mathbf{e}_i \mathbf{e}_i^T$ as a matrix with a 1 in the (i,i) position and zeros elsewhere. The columns of a matrix can be summed by multiplying on the left by $\mathbf{e}^T$.

An individual is first marked at time $t = 1$ and then recaptured (or not) at times $t = 2,...,T$. The capture history consists of a sequence of numbers,

$$h = X_1, X_2, ..., X_T \qquad (39)$$

where X_t indicates the stage of the individual or the fact that it was not seen at time t. If the individual is not seen, let $X_t = 0$.

Suppose an individual was marked in state X_1 at $t = 1$. Then the vector $\mathbf{e}_{X_1}$ gives the probability distribution of its state at $t = 1$. The probability distribution of its state after the transition from $t = 1$ to $t = 2$ is the vector $\Phi_1 \mathbf{e}_{X_1}$ including the probability of death. The entries of the vector $\mathbf{P}_2 \Phi_1 \mathbf{e}_{X_1}$ give the probability of capturing the individual in each of the stages at $t = 2$. Similarly, the entries of the vector $(\mathbf{I} - \mathbf{P}_2) \Phi \mathbf{e}_{X_1}$ give the probabilities of failing to capture the individual in each of the stages at $t = 2$. Continuing this process leads to the following simple formula for the probability of any capture history (Caswell, 2001; Fujiwara & Caswell, 2002).

$$P\left[X_1,...,X_T \mid \Phi, \mathbf{P} \right] = \ell\left(\Phi, \mathbf{P} \mid X_1,...,X_T \right) \qquad (40)$$

$$= \mathbf{e}^T \mathbf{Q}_{T-1} \cdots \mathbf{Q}_1 \mathbf{e}_{X_1} \qquad (41)$$

where

$$\mathbf{Q}_t = \begin{cases} \mathbf{E}_{X_t} \mathbf{P}_{t+1} \Phi_t & \text{if } X_{t+1} \neq 0 \\ \\ (\mathbf{I} - \mathbf{P}_{t+1}) \Phi_t & \text{if } X_{t+1} = 0 \end{cases} \qquad (42)$$

This provides a simple matrix extension of the familiar formula for the probability of a capture history in the CJS model; it is possible because $\mathbf{\Phi}$ includes death as a state.

For example, suppose that an individual is marked in stage 1, captured in stage 3, captured in stage 5, and then not captured for two time intervals, so that

$$h = 1,3,5,0,0$$

Applying (42) gives (43)

$$P[h] = \mathbf{e}^T[(\mathbf{I} - \mathbf{P}_5)\mathbf{\Phi}_4][(\mathbf{I} - \mathbf{P}_4)\mathbf{\Phi}_3][\mathbf{E}_5\mathbf{P}_3\mathbf{\Phi}_2][\mathbf{E}_3\mathbf{P}_2\mathbf{\Phi}_1]\mathbf{e}_1$$

Because death is included as an absorbing state in $\mathbf{\Phi}$, this formula automatically accounts for all the possibilities of survival and state transition during the terminal string of (two) zeros in this sighting history. To see how this works, consider a simple example with only two stages and time–invariant transitions

$$\Phi = \left(\begin{array}{cc|c} t_{11} & t_{12} & 0 \\ t_{21} & t_{22} & 0 \\ \hline m_1 & m_2 & 1 \end{array} \right) \qquad (44)$$

and sighting probabilities. Consider the capture history $h = 2,1,0$. The individual is known to be in stage 2 at $t = 1$, so the probability distribution of its initial state is $\mathbf{Z} = (0\ \ 1\ \ 0)^T$. At $t = 2$ the probability distribution of its state is

$$\Phi z = \left(\begin{array}{c} t_{12} \\ t_{22} \\ m_2 \end{array} \right) \qquad (45)$$

The probability of being captured in each of those stages is

$$\mathbf{P}\Phi z = \left(\begin{array}{c} p_1 t_{12} \\ p_2 t_{22} \\ p_3 m_2 \end{array} \right) \qquad (46)$$

But we know it was captured in state 1, so only the first entry in this vector is relevant:

$$\mathbf{E}_1\mathbf{P}\Phi z = \left(\begin{array}{c} p_1 t_{12} \\ 0 \\ 0 \end{array} \right) \qquad (47)$$

Applying the transition matrix to this vector gives the probability, at $t = 3$, of the three states

$$\mathbf{\Phi}\mathbf{E}_1\mathbf{P}\Phi z = \left(\begin{array}{c} t_{11} p_1 t_{12} \\ t_{21} p_1 t_{12} \\ m_1 p_1 t_{12} \end{array} \right) \qquad (48)$$

The individual was not captured at $t = 3$, the probability of which is

$$(\mathbf{I} - \mathbf{P})\mathbf{\Phi}\mathbf{E}_1\mathbf{P}\Phi z = \left(\begin{array}{c} (1\text{-} p_1)\, t_{11} p_1 t_{12} \\ (1\text{-} p_2)\, t_{21} p_1 t_{12} \\ (1\text{-} p_3)\, m_1 p_1 t_{12} \end{array} \right) \qquad (49)$$

Finally, we add all these probabilities to obtain the probability of all possible transition and sighting sequences compatible with the capture history.

$$
\begin{aligned}
\mathbf{e}^T(\mathbf{I} - \mathbf{P})\mathbf{\Phi}\mathbf{E}_1\mathbf{P}\Phi z\ &=\ (1 - p_1)\,t_{11}p_1 t_{12} & (50) \\
&+\ (1 - p_2)\,t_{21}p_1 t_{12} & (51) \\
&+\ (1 - p_3)\,m_1 p_1 t_{12} & (52)
\end{aligned}
$$

The first term in this sum corresponds to (reading from right to left) transition from 2 to 1, capture in 1, transition from 1 to 1 and failure to capture in 1. The second term corresponds to transition from 2 to 1, capture in 1, transition from 1 to 2, and failure to capture in 2. The third term corresponds to transition from 2 to 1, capture in 1, death fro stage 1, and failure to recover as dead. Adding yet another zero to the capture history and multiplying (49) by $(\mathbf{I} - \mathbf{P})\mathbf{\Phi}$ will give the somewhat larger set of possibilities at $t = 4$.

Making the customary assumption of independent and identical individuals, the log likelihood for the entire collection of capture histories is

$$\log L(\mathbf{\Phi}, \mathbf{P}) = \sum_k \log \ell_k (\mathbf{\Phi}, \mathbf{P}) \qquad (53)$$

Maximum likelihood estimates of the parameters can be found by maximizing log L (e.g., using Matlab optimization routines). Nested models can be compared using log–likelihood tests, and model selection using information–theoretic methods (Akiake's Information Criterion, or AIC; see Burnham & Anderson, 1998) can be carried out directly using log L.

Models in which $\mathbf{\Phi}$ and $\mathbf{P}$ depend on time, external covariates, or individual covariates can be defined by making the appropriate matrix entries functions of the covariates and maximizing the likelihood with respect to the resulting parameters.

The *m*–array

We note that it is also possible to construct the multi–state version of the *m*–array from $\mathbf{\Phi}$ and $\mathbf{P}$, in calculations essentially identical to those of Brownie et al. (1993), and to use it to derive the likelihood function.

More things to estimate

Fertility

The estimate of $\mathbf{\Phi}$ provides estimates of the entries in $\mathbf{T}$, the transition portion of the projection matrix $\mathbf{A}$. Fertility, however, appaears in $\mathbf{F}$, and estimation of $\mathbf{F}$ requires extra information on reproduction. One way to obtain some of this information is to include a state in the life cycle corresponding to reproduction or breeding. Every time an individual enters this state, she produces some number of offspring. If the expectation of that number is known, or can be estimated, then the estimate of $\mathbf{\Phi}$ also provides an estimate of $\mathbf{F}$, which will contain positive values only in entries corresponding to transitions to the reproductive state. The fertilities in $\mathbf{F}$ will depend on the reproductive biology of the species, with care taken to account for when in the

annual cycle censuses occur (Caswell, 2001). In the example we consider here, the right whale produces only a single calf in a reproductive event, so construction of **F** is relatively easy.

Demographic indices

If the parameters defining the model are estimated by maximizing the likelihood log L, then any invertible function of those parameters is also a maximum likelihood estimate. That means that the matrix population model provides maximum likelihood estimates of, *inter alia*, the population growth rate, stable stage distribution, reproductive value distribution, damping ratio, period of oscillation, and the sensitivity and elasticity of population growth rate to all parameters. And that's just for the linear time invariant case. If a stochastic model is estimated, then the analysis provides maximum likelihood estimates of the stochastic growth rate and its sensitivity and elasticity. And a density–dependent model yields maximum likelihood estimates of the attractor(s) to which the population will converge (equilibria, cycles, invariant loops, or strange attractors) and the sensitivity of the invasion exponent and the effective equilibrium population to changes in the parameters.

Standard errors for all these parameters can be obtained from the results of maximizing the likelihood, either by the Taylor series expansion method for those quantities (like λ) whose sensitivity to parameters can be written down, or by a parametric bootstrap approach using the information matrix. For example, if **C** is the covariance matrix of the parameter vector θ, then to first order

$$V(\lambda) = \frac{\partial \lambda^{\mathsf{T}}}{\partial \theta} \mathbf{C} \frac{\partial \lambda}{\partial \theta} \qquad (54)$$

where the vector of derivatives $\partial \lambda / \partial \theta$ is obtained from (15). In addition, model uncertainty can be analyzed using information–theoretic methods (Burnham & Anderson, 1998).

It is hard to overstate the potential of this for demographic studies.

An example: the North Atlantic right whale

The North Atlantic right whale (*Eubalaena glacialis*) was once abundant in the northwestern Atlantic, but as an early preferred target of commercial whalers by 1900 it had been hunted to near extinction. The remaining population (only about 300 individuals) is distributed along the Atlantic coast of North America, from summer feeding grounds in the Gulf of Maine and Bay of Fundy to winter calving grounds off the Southeastern U.S. In the more than 50 years since the end of commercial whaling, the population has recovered only slowly. Right whales are killed by ship collisions and entanglement in fishing gear, and may be affected by pollution of coastal waters. .

Individual right whales are photographically identifiable by scars and callosity patterns. Since 1980, the New England Aquarium has surveyed the population, accumulating a database of over 10,000 sightings. Treating the first year of identification of an individual as marking, and each year of resighting as a recapture, we have used MR statistics to estimate demographic parameters of this endangered population (Caswell et al., 1999; Fujiwara & Caswell, 2001, 2002; Fujiwara, 2002). From a conservation point of view, the most alarming finding has been a declining trend in the survival of reproducing females, which in turn has driven a decline in population growth rate so that λ is now less than 1.

Life cycle structure

Figure 2 shows a transition graph for the right whale. It distinguishes males and females, and divides each sex into developmental stages. Females are classified as calves, immature, mature, mothers (reproducing females), and post–mothers (i.e., mature females in an interbirth interval). This graph differs from that in Fujiwara and Caswell (2001) by incorporating the post–mother stage, which enforces a 2–year minimum for the interbirth interval, which is supported by the data.

The inclusion of a stage representing breeding females captures the biologically important act of breeding as an explicit transition in the life cycle, which is particularly critical when mature females do not breed every year. It permits calculation of the fertility part of the projection matrix, because in this case we know that only a single calf is produced by a reproducing female.

Modelling transitions

A model in which all transition and sighting probabilities were free to vary independently would, for this data set, have about 300 parameters. We chose a much more parsimonious universe of models to investigate. Because previous analyses (Fujiwara & Caswell, 2001) had shown that variation in calf survival, mother survival, and reproductive rate were the most variable, we permitted variation only in ϕ_{21}, ϕ_{54}, and the birth probability conditional on survival, γ_{43}, defined by

$$\phi_{43} = \sigma_3 \, \gamma_{43} \qquad (55)$$

where σ_3 is the survival probability of stage 3. We examined models in which each of these three parameters was constant or a logistic function of time and/or of the North Atlantic Oscillation (NAO). The NAO is a major climatic and oceanographic oscillation, defined in terms of the barometric pressure difference between Iceland and the Azores (e.g., Hurrell, 1995); the NAO is know to have effects on a variety of ecological systems (Ottersen et al., 2001), including plankton in the western North Atlantic, where right whales feed.
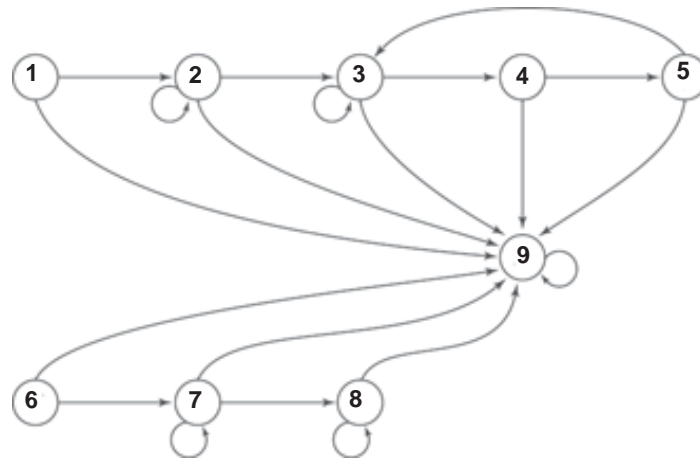
Fig. 2. Transition graph for the right whale (Fujiwara, 2002). Stages N_1–N_5 are females: N_1. Calf; N_2. Immature; N_3. Mature; N_4. Mother; N_5. Post–breeding. Stages N_6–N_8 are males: N_6.Calf; N_7. Immature; N_8. Mature; N_9. Dead.

Fig. 2. Gráfico de transición correspondiente a la ballena franca (Fujiwara, 2002). Las fases N_1–N_5 *son hembras:* N_1. *Ballenato;* N_2. *Inmadura;* N_3. *Madura;* N_4. *Madre;* N_5. *Post reproducción. Las fases* N_6–N_8 *son machos:* N_6. *Ballenato;* N_7. *Inmaduro;* N_8. *Maduro;* N_9. *Muerto.*

$$\phi_{21}(t) = f \text{ (time, NAO)} \tag{56}$$

$$= \frac{\exp [\, \alpha_1 + \beta_1\, t + \gamma_1\, \text{NAO}(t-2)]}{1 + \exp [\, \alpha_1 + \beta_1\, t + \gamma_1\, \text{NAO}(t-2)]} \tag{57}$$

$$\phi_{54}(t) = f \text{ (time, NAO)} \tag{58}$$

$$= \frac{\exp [\, \alpha_2 + \beta_2\, t + \gamma_2\, \text{NAO}(t-2)]}{1 + \exp [\, \alpha_2 + \beta_2\, t + \gamma_2\, \text{NAO}(t-2)]} \tag{59}$$

$$\phi_{43}(t) = f \text{ (time, NAO)} \tag{60}$$

$$= \frac{\exp [\, \alpha_3 + \beta_3\, t + \gamma_3\, \text{NAO}(t-1)]}{1 + \exp [\, \alpha_3 + \beta_3\, t + \gamma_3\, \text{NAO}(t-1)]} \tag{61}$$

This yields $4^3 = 64$ different models for the transition probabilities, with 37–42 parameters.

Previous analyses had shown that sighting probability varied greatly over time, but with considerable correlation among stages. Thus we modelled sighting by letting p_3 (sighting probability of mature females) vary freely over time, and setting

$$p_i(t) = \frac{\exp [\, a_i + b_i\, \text{logit} \, (p_3\, (t))]}{1 + \exp [\, a_i + b_i\, \text{logit} \, (p_3\, (t))]} \quad i \neq 3 \tag{62}$$

Each model was fit by maximizing the likelihood L in (53). AIC values were calculated as $2 \log L - 2\, n_p$, where n_p is the number of parameters.

The spectrum of ΔAIC values (AIC relative to the minimum) is shown in figure 3. The time–invariant model has the highest ΔAIC value; the data clearly do not support constant vital rates.

Models including only a temporal trend or only NAO dependence are also not supported. The best model has time dependence of mother's survival and birth probability, and NAO dependence of all three parameters.

The F matrix

Each female that becomes a mother (which happens with probability $\phi_{43}(t)$) produces a single calf which, is female with probability 0.5. To be counted as reproduction, the calf must survive long enough to be catalogued. We assume that this requires 6 months, and that the calf will die during this time if its mother dies (which happens with probability $\phi_{54}(t+1)$). Thus

$$F_{13}(t) = 0.5 \; \phi_{43}(t) \; (\; \phi_{54}(t+1) \;)^{0.5} \tag{63}$$

Some demographic results

Combining $\mathbf{T}_t$ and $\mathbf{F}_t$ gives us a series of population projection matrices $\mathbf{A}_t$ for each model. As an example of the kind of results available, consider the following.

A time–invariant model

Even though the data do not support a time–invariant model, it is worth examining the resulting projection matrix as the best single image of the overall demography of the right whale during the 1980s and 1990s (64):
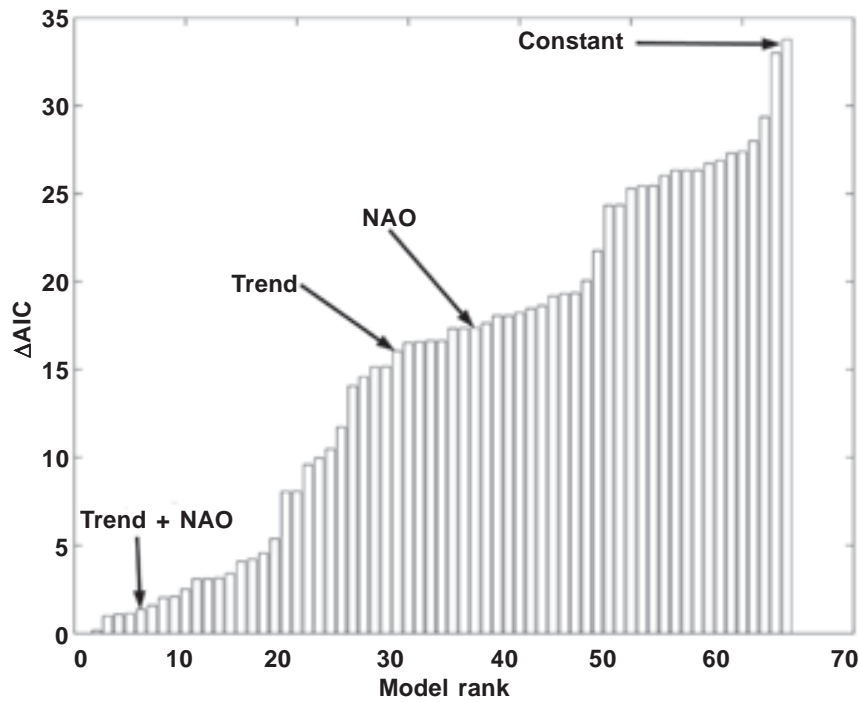
Fig. 3. ΔAIC values for 64 models fit to the demographic transitions of the right whale.

Fig. 3. Los valores ΔAIC correspondientes a 64 modelos se ajustan a las transiciones demográficas de la ballena franca.

$$
\mathbf{A} = \begin{pmatrix}
0 & 0 & \mathbf{0.13} & 0 & 0 & 0 & 0 & 0 \\
0.90 & 0.85 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.12 & 0.71 & 0 & 1.00 & 0 & 0 & 0 \\
0 & 0 & 0.29 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.85 & 0 & 0 & 0 & 0 \\
\hline
0 & 0 & \mathbf{0.13} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.90 & 0.82 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.13 & 0.95
\end{pmatrix}
$$

The fertility elements of **A** are in bold face; the transition matrix **T** has zeros in those entries and the fertility matrix **F** is zero except for those entries. The upper left submatrix describes production of females by females, the lower right submatrix the production of males by males, the lower left submatrix the production of males by females, and the upper right submatrix the production of females by males.

T is the transient portion of an absorbing Markov chain, with eventual absorbtion by death. Thus, the (i,j) entry of the fundamental matrix

$$\mathbf{N} = (\mathbf{I} - \mathbf{T})^{-1} \tag{65}$$

gives the expected number of time intervals spent in stage j before absorbtion (i.e., death) by an individual starting in stage i. Thus the column sums of **N** give the life expectancies of individuals in different stages (66):

$$
\mathbf{N} = \begin{pmatrix}
1.00 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
5.88 & 6.52 & 0 & 0 & 0 & 0 & 0 & 0 \\
16.35 & 18.11 & 22.94 & 19.49 & 22.93 & 0 & 0 & 0 \\
4.74 & 5.25 & 6.65 & 6.65 & 6.65 & 0 & 0 & 0 \\
4.02 & 4.46 & 5.65 & 5.65 & 6.65 & 0 & 0 & 0 \\
\hline
0 & 0 & 0 & 0 & 0 & 1.00 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 4.88 & 5.41 & 0 \\
0 & 0 & 0 & 0 & 0 & 12.56 & 13.91 & 19.54
\end{pmatrix}
$$

Thus the life expectancy for a female calf is 32 years (the sum of column 1); that for male calf is 18.4 years (the sum of column 6). This pattern, with male life expectancy shorter than that of females, appears to be not unusual in cetaceans.

A female in stage 4 has just reproduced. The inter–birth interval is the time before she reproduces again. This interval is infinite if she dies before reproducing, so a meaningful average can be calculated only from the distribution of interval lengths conditional on reproducing again. The conditional distribution is calculated from **T** by creating a new absorbing state ("reproduced before dying"), calculating the probability of absorbtion in this state rather than its competitor ("died before
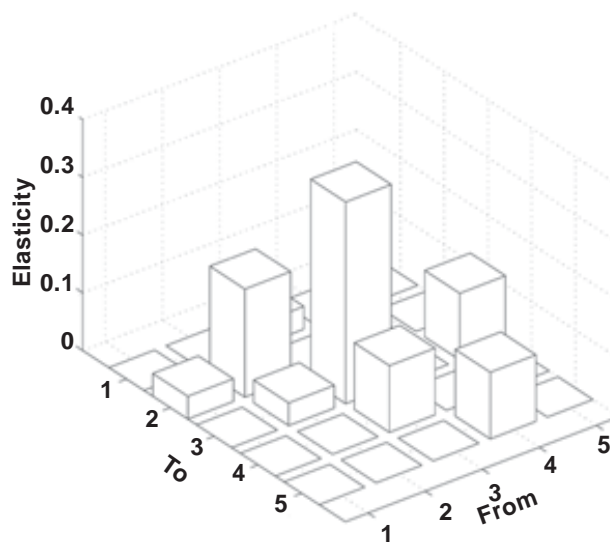
Fig. 4. The elasticity of λ to changes in the elements of **A** for the time–invariant right whale model.

*Fig. 4. La elasticidad de λ frente a la presencia de cambios en los elementos de **A** para el modelo de ballena franca invariable con el tiempo.*

reproducing"), and creating a conditional transition matrix $\mathbf{T}^{(c)}$, conditional on absorbtion in this state (Caswell, 2001, Chapter 5). This estimate of **T** yields a median inter–birth interval of 4.0 years.

Combining **F** and **T**, we calculate the net reproductive rate (the expected lifetime reproductive output of a newborn female) as

$$R_0 = \text{dominant eigenvalue of } \mathbf{FN} \qquad (67)$$
$$= 2.18 \qquad (68)$$

The population growth rate, calculated from the dominant eigenvalue of **A**, is

$$\lambda = 1.025 \qquad (69)$$

that is, a growth of about 2.5% per year.

The elasticity of λ to changes in the a_{ij} is shown in figure 4. λ is most elastic to changes in the transitions representing survival and growth of mature females, mothers, and inter–birth females. Changes in fertility would have little effect on λ.

Beyond time–invariance

The matrix **A** gives the best possible time–invariant model, given the mark–recapture data from 1980–1997. But the AIC values show it placing a dismal last among all 64 models examined. Clearly the data do not support a time–invariant model. A detailed analysis of the whole family of models is not possible here (Fujiwara et al., in prep.), but it is worth considering the implications of some of the models.

Given a time–varying model, it is possible to calculate λ at each time, as a measure of the quality of the environment at that time. This is a hypothetical calculation, giving the rate at which the population would be capable of growing *if* the environment was fixed in the state it was in when the vital rates were measured.

As in previous analyses (Fujiwara & Caswell, 2001), a model with a temporal trend in survival and breeding probability was a great improvement over the time–invariant model. The best model (ΔAIC = 0) included the temporal trend in mother's survival and breeding probability, and NAO effects on calf survival, mother's survival, and breeding probability. Figure 5 shows calf survival, mother's survival, and breeding probability as functions of time for these two models. There has been a slight decline in the first, and a dramatic decline in the second and third of these quantities. The two models agree in the rate and amount of decline; the best model adds some NAO–driven fluctuations around the smooth trend of the time model.

These survival and transition estimates are only the beginning. Figures 6 and 7 translate them into trajectories of female life expectancy and net reproductive rate, both of which have declined. The birth interval has increased; figure 8 shows the mean inter–birth interval implied by the two models; it has increased from about 4 to about 7 years. Similar patterns are shown by the median interval and others measures of the time between births.

Figure 9 shows the population growth rates cal-

culated from these two models, compared with the value from the time–invariant model. Conditions for the right whale appear have deteriorated since 1980. If conditions typical of the late 1990s were to be maintained the population would be doomed to extinction, since $\lambda < 1$. It can be shown that the decline in λ is due mainly to the reduction in survival of mothers. The best model, which includes NAO effects, creates variability around this trend, but does not obscure it. The time–invariant model, unsupported though it may be, yields a value of λ comfortably in the middle of the range spanned by the time–varying models.

Although the vital rates and population growth rates have changed dramatically, the results of perturbation analysis have not. Figure 10 shows one way of looking at this, presenting the elasticity of λ to changes in the survival probability of each stage. While there has been a gradual decline in all of them, the elasticity to survival of mature females is consistently highest, followed by that to immature survival and survival of mothers or post–mothers. The elasticity to λ to calf survival is consistently the lowest. It is encouraging that the all these models point to the same target —improvement in survival— for management actions.

Conclusion

These fragments of right whale demography only begin to suggest the power of combining multi–state mark–recapture analysis and matrix population models. All that is needed to take advantage of this power is a model that includes a description of the life cycle. We say "a" description advisedly, many such descriptions are possible. Demographers may be more accustomed to flexibility in defining stages and structuring life cycles than are mark–recapture practitioners. Given such a description of the entire life cycle, all becomes possible. For example, in the simplest case of a constant matrix:

1. From an estimate of the matrix Φ, one can estimate life expectancy, age–specific survival (even if the model is stage– rather than age–classified), and the distribution of inter–event times (e.g., inter–breeding intervals).

2. The fertility matrix F, combined with Φ, can provide an estimate of the parameters in a multi–type branching process, which permits a detailed analysis of demographic stochasticity, including variability in population growth and probability of extinction (Caswell, 2001, Chapter 15).

3. In another direction, F and Φ together provide estimates of the net reproductive rate R_0, age–specific fertility (even though model is stage–classified), generation time, and the stable age–within–stage distribution.

4. Extracting the transition matrix T from Φ and combining it with F gives an estimate of the population projection matrix A from which both transient and asymptotic dynamics can be estimated, including population growth rate, stable stage distribu-
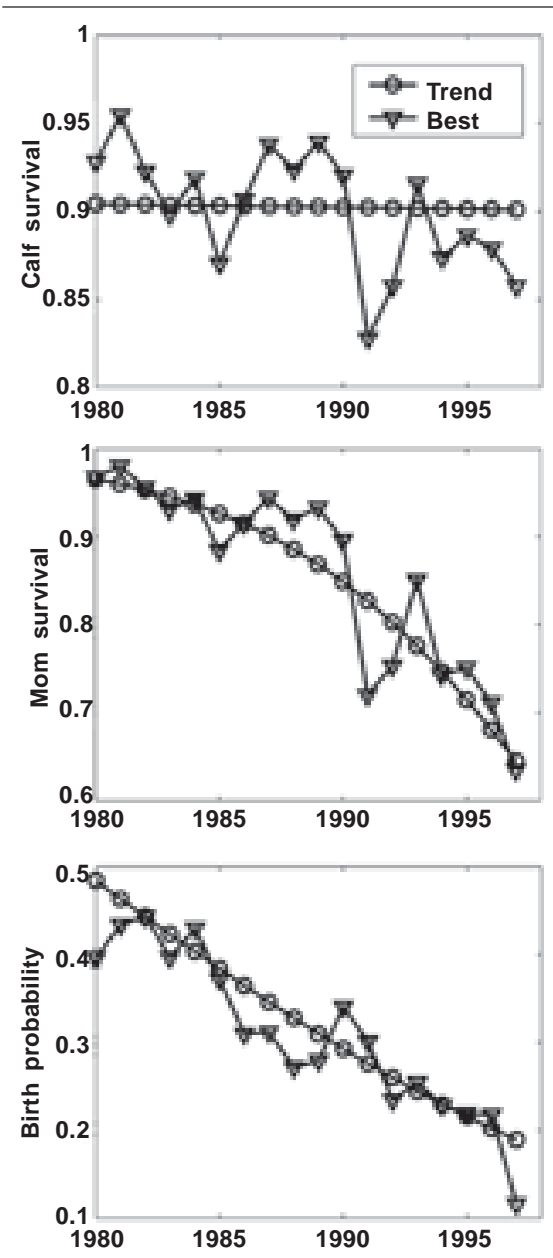

Fig. 5. Temporal variation in calf survival, mother survival, and birth probability in the temporal trend model and the best model.

Fig. 5. Variación temporal en la supervivencia de los ballenatos, de las madres y de la probabilidad de nacimiento en el modelo de tendencias temporales y en el mejor modelo.

tion, reproductive value, and the sensitivity and elasticity of those quantities.

5. If the model is density–dependent, the projection matrix provides the machinery for a complete nonlinear analysis, including estimates of equilibria, stability, resilience, reactivity, bifurcations, invasion
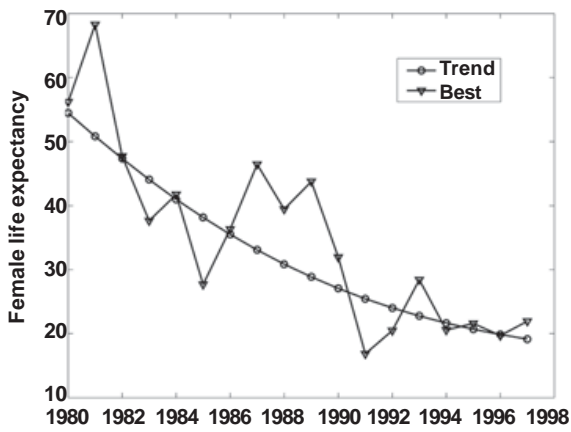
Fig. 6. Temporal variation in female life expectancy at birth in the temporal trend model and the best model.

Fig. 6. Variación temporal en la esperanza de vida al nacer en las hembras en el modelo de tendencias temporales y en el mejor modelo.
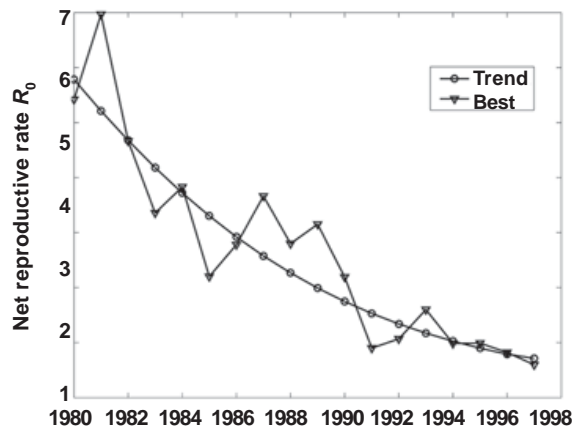

Fig. 7. Temporal variation in net reproductive rate R_0 in the temporal trend model and the best model.

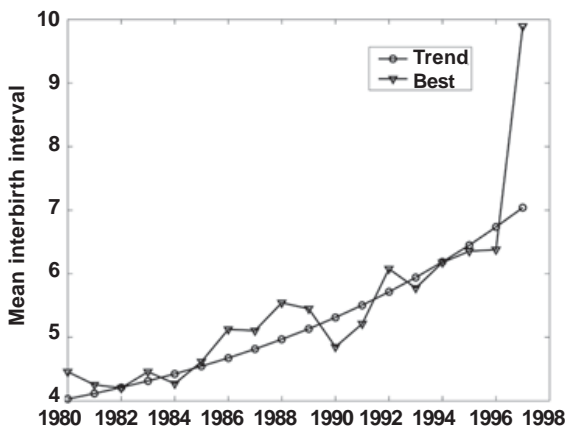*Fig. 7. Variación temporal en la tasa neta de reproducción R$_0$ en el modelo de tendencias temporales y en el mejor modelo.*

Fig. 8. Temporal variation in the mean interbirth interval, conditional on survival, in the temporal trend model and the best model.

Fig. 8. Variación temporal en el intervalo medio entre nacimientos, condicionada a la supervivencia, en el modelo de tendencias temporales y en el mejor modelo.
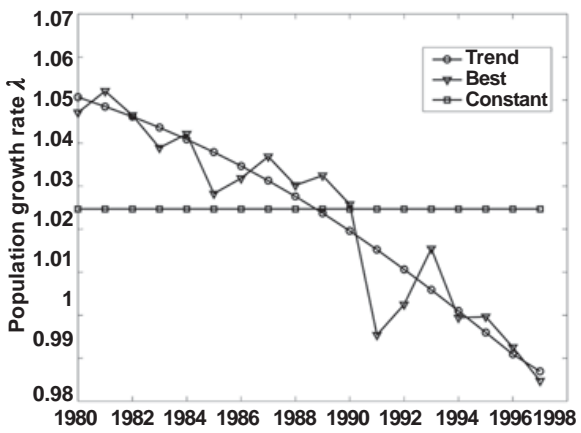
Fig. 9. The population growth rate λ produced by three models for the right whale.

Fig. 9. Tasa de crecimiento poblacional λ generada por tres modelos para la ballena franca.

exponents, and the sensitivity and elasticity analysis of both equilibria and invasion exponents.

6. We have not emphasized spatial models, but there are two directions in which matrix models

provide powerful analyses of demography and dispersal. If a population projection matrix (linear or nonlinear) is combined with a distribution of dispersal distances, it is possible to estimate the invasion wave speed as a measure of the ability of the population to expand into previously unoccupied
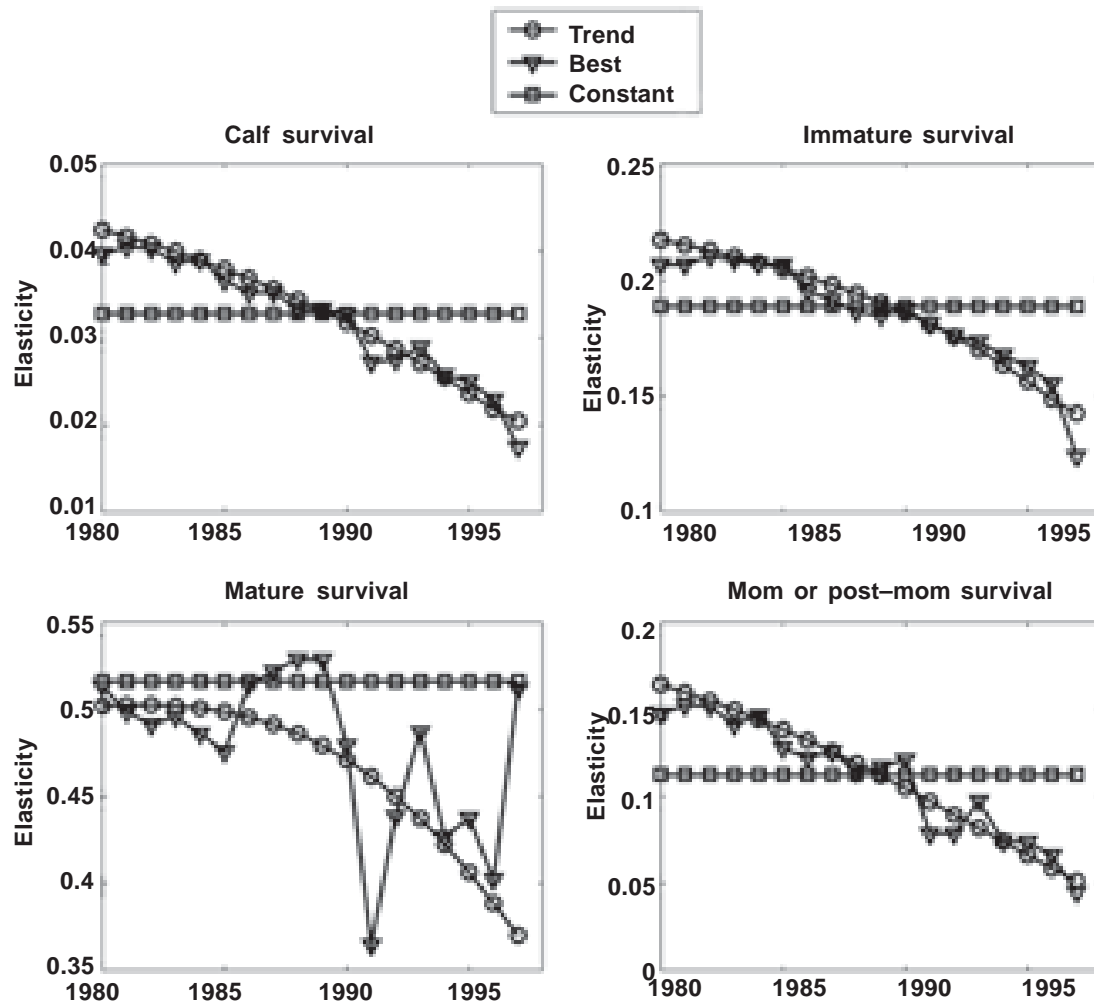
Fig. 10. The elasticity of population growth rate λ to changes in survival of each stage, in the constant, time trend, and best models. Elasticities to changes in mother survival and post–mother survival are identical.

Fig. 10. Elasticidad de la tasa de crecimiento poblacional λ frente a la presencia de cambios en la supervivencia de cada fase, en el modelo de efectos fijos, en el de tendencias temporales y en el mejor modelo. Las elasticidades frente a la presencia de cambios en la supervivencia de las madres y en la supervivencia tras haber sido madres son idénticas.

territory (Neubert & Caswell, 2002b). If matrices are available for several sites and location is considered as a state along with life cycle stage, then the resulting multiregional model will describe both population growth and distribution, including sensitivity and elasticity of population growth rate to both demographic and dispersal parameters (e.g., Rogers, 1995; Lebreton, 1996; Hunter & Caswell, 2003b).

Although some of these methods can be applied to Φ even if it does not include the entire life cycle, doing so provides only a small fraction of the information that a complete demographic analysis can provide. There is much to gain in our understanding of population dynamics by making the

estimation of demographic models a goal at the outset of a mark–recapture study.

Open problems

We close by pointing out some unsolved problems. We anticipate that this section will rapidly become obsolete.

Because MR methods make it so natural to estimate projection matrices as functions of environmental covariates, it would be good to have a more coherent theory for environment–dependent models. The lack of theory is as much a problem of not knowing the questions to ask as of not knowing how

to answer them, especially when the the environmental dependence cannot be reduced to either time–invariance or a stationary stochastic process.

Pradel's (1996) approach to estimating the observed rate of growth of a population (he originally used ρ for this quantity, but it has since regrettably been denoted by λ) is an important advance. Understanding the relation between a fully stage–specific version of ρ and the demographic λ, both obtained from multi–state mark–recapture analysis, would be extremely useful (Nichols et al., 2000 have made a start). There are many reasons why a population might fail to grow at its potential rate λ (e.g., a non–stable stage–distribution), but there are few documented cases to generalize about (e.g. Sandercock & Beissinger, 2002).

The task of estimating **F** deserves more attention. Including reproductive states in the life cycle graph (as in the right whale) helps, but requires information on fecundity to go with it. Perhaps reverse–time mark–recapture analyses (Pradel, 1996) can help. Integrated modelling approaches, in which mark–recapture and census data are combined (Besbeas et al., 2002, 2003) could also provide estimates of **F**.

The estimation of density dependence is another important problem. In principle, density should be no different from any other external covariate. We know of only one statistical analysis of bifurcation patterns (in the flour beetle *Tribolium* (Cushing et al., 2003), and it used inverse methods rather than MR). There should be more.

Stochastic models are essential for understanding the effect of environmental fluctuations on population dynamics and persistence, but the estimation of stochastic models by MR is in its infancy. Bayesian methods for hierarchical random effects models may contribute to solving this problem. One challenge will be to identify appropriate distributions for the necessary matrix–valued random variates.

Finally, methods that integrate mark–recapture and count information open up exciting possibilities. Taken by itself, the inverse problem of determining a model from a time–series of population estimates is usually poorly conditioned (because there are many sets of parameters that can generate the same or nearly the same time–series). Methods include transforming the matrix population model into a nonlinear autoregressive model with lognormally distributed errors (Dennis et al., 1995), quadratic programming methods that minimize the squared deviations between observed and predicted time–series (Wood, 1997), methods based on the Kalman filter and other state–space approaches (Besbeas et al., 2002, 2003; De Valpine & Hastings, 2002), and Bayesian methods (Gross et al., 2002). Although in this venue we view count data as strengthening the analysis of mark–recapture data, it is just as legitimate to think of the problem the other way around: mark–recapture data can render an ill–conditioned inverse problem soluble.

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