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SIZE-SPECIFIC SENSITIVITY: APPLYING A NEW STRUCTURED POPULATION MODEL

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Abstract. Matrix population models require the population to be divided into discrete stage classes. In many cases, especially when classes are defined by a continuous variable, such as length or mass, there are no natural breakpoints, and the division is artificial. We introduce the "integral projection model," which eliminates the need for division into discrete classes, without requiring any additional biological assumptions. Like a traditional matrix model, the integral projection model provides estimates of the asymptotic growth rate, stable size distribution, reproductive values, and sensitivities of the growth rate to changes in vital rates. However, where the matrix model represents the size distributions, reproductive value, and sensitivities as step functions (constant within a stage class), the integral projection model yields smooth curves for each of these as a function of individual size. We describe a method for fitting the model to data, and we apply this method to data on an endangered plant species, northern monkshood (*Aconitum noveboracense*), with individuals classified by stem diameter. The matrix and integral models yield similar estimates of the asymptotic growth rate, but the reproductive values and sensitivities in the matrix model are sensitive to the choice of stage classes. The integral projection model avoids this problem and yields size-specific sensitivities that are not affected by stage duration. These general properties of the integral projection model will make it advantageous for other populations where there is no natural division of individuals into stage classes.

Key words: Aconitum noveboracense; continuous population structure; elasticity; integral projection model; matrix population models without the matrix; population growth rate; sensitivity analysis; size-specific sensitivity and elasticity; structured population model.

INTRODUCTION

A structured population model is a summary of rules specifying how the number and distribution of individuals within a population changes over time (Tuljapurkar and Caswell 1997, Gurney and Nisbet 1998). A population increases or decreases depending on the rates at which individuals are born, mature, reproduce, and die. A structured population model ties the population changes to the vital rates of the individuals comprising the population, under the assumption that a few state variables are adequate to describe the differences among individuals that affect vital rates. Within the class of structured population models there are many options, such as which vital rates might be density independent vs. density dependent; and whether external influences, such as environmental variability or other species, are incorporated into the model. However, most structured population models fall into one

of three categories: matrix models, ordinary differential equation (ODE) models, and partial differential equation (PDE) models. In this classification, model type is determined by whether time is discrete (matrix) or continuous (ODE, PDE), and whether the individual-level state is treated as a discrete (matrix, ODE) or a continuous (PDE) variable (Tuljapurkar and Caswell 1997).

Matrix projection models are popular, because they have relatively simple structure and provide useful information. The eigenvalues and eigenvectors of the projection matrix provide estimates of the population growth rate, the stable age or stage distribution, reproductive value, and the sensitivities of population growth rate to changes in life history parameters (Caswell 1989).

However, whenever a matrix projection or ODE model is applied to population characterized by a continuous state variable (e.g., age, mass, or leaf length), individuals must be divided into a discrete set of classes. In some cases, the division may be natural (for example, if there are discrete shifts in habitat or diet as an individual grows), but often the division is artificial. If the model has too few classes, biological realism is sacrificed, because highly dissimilar individuals are treated as if they were identical. Such models are also prone to misrepresent the transient dynam-

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ics of the population (Crouse et al. 1987, Cochran and Ellner 1992). Including too many classes can lead to parameter estimation problems, as each new class requires a new set of parameters to specify its mortality, fecundity, and state transition rates. Although Vandermeer (1978) and Moloney (1986) derived algorithms to determine optimal class boundaries, the errors related to class boundaries are only minimized, not eliminated. The stage classification also affects the interpretation of sensitivities and elasticities. Enright et al. (1995) found that in matrix models for perennial plants, decreasing the number of stage classes increased the apparent importance of survival rates relative to growth rates.

In partial differential equation (PDE) models, the individual-level state variables are continuous, and individuals are not lumped into categories. Therefore, detailed information on vital rates can be part of the model, for example, vital rates can depend on size rather than size-class. Like the matrix models, PDE models can incorporate a variety of biological situations, including density dependence (Bell and Anderson 1967), and stage- or age-structured populations (Sinko and Streifer 1967, Metz and Diekmann 1986). The basic model structure is the same in all cases and can be expressed by an appropriate version of the McKendrick–von Foerster equation (e.g., Goodman 1967, Keyfitz 1967, Sinko and Streifer 1967, Roughgarden 1979). Wood (1994) has recently developed nonparametric methods for fitting a McKendrick–von Foerster equation to population census data, in a way that does not allow negative population sizes or death rates. However, in all of these continuous models, growth is strictly deterministic: two individuals that are the same size at birth remain the same size until one of them dies. Adding a diffusion term can accommodate variation in growth trajectories, but (as in diffusion models for spatial spread) this implicitly assumes a Gaussian distribution for the variations in growth increment among individuals of a given size. It is also difficult to include stochasticity (environmental or demographic) in a PDE model, or to use vital rates that are not in parametric form.

In this paper, we introduce a discrete-time structured population model, the "integral projection model," which retains the desirable properties of the matrix projection model, while avoiding entirely the need to group individuals into discrete stage classes. Using a data set on an endangered plant, with stem diameter as the individual-level state variable, we illustrate how the model can be fitted to field data. We then show how the model can be used for all the usual purposes of a matrix projection model, including sensitivity and elasticity analysis, and we then compare the results to those from a traditional model with stage classes. This case study illustrates how analysis of exactly the same data using the integral projection model can provide more detailed and accurate information than an analysis

using a matrix model. The mathematical properties of the model (Easterling 1998) are presented elsewhere. Here we present the model from the perspective of a user, data set in hand, who wants to compute sensitivities and elasticities for size-dependent vital rates.

INTEGRAL PROJECTION MODEL

The integral projection model describes how a population structured by a continuous individual-level state variable changes in discrete time. Although we consider a population described by size, the same model can apply to any continuous variable describing the state of an individual.

The state of the population is described by the size distribution $n(y, t)$. Intuitively, $n(y, t)$ is the number of size-y individuals at time t. Formally, $n(y, t)$ is the probability density of individual size y at time t, defined by the property that the number of individuals between sizes y and $y + dy$ at time t is given by $n(y, t)dy$, with relative error that goes to zero as dy decreases to zero. Typically, $n(y, t)$ would be a continuous function of y.

Individuals in the population may grow, survive, and produce new individuals in each time step. Let $p(x, y)dy$ be the probability that an individual size x at time t is alive and in the size interval $(y, y + dy)$ at time $t + 1$. Finally, define $f(x, y)dy$ as the number of newborns at time $t + 1$ in the size interval $(y, y + dy)$ per size-x individual alive at time t. The integral projection model for the number of individuals of size y at time $t + 1$ is then

$$n(y, t + 1) = \int_{\Omega} [p(x, y) + f(x, y)]n(x, t) \, dx$$

$$= \int_{\Omega} k(y, x)n(x, t) \, dx \qquad (1)$$

with the integration being over the set of all possible sizes Ω. The function $k(y, x) = p(x, y) + f(x, y)$ is called the *kernel*; this terminology comes from the theory of integral equations and has no biological connotations. The kernel is a nonnegative surface representing all possible transitions from size x to size y, and is analogous to the projection matrix containing nonzero entries for survival, growth, and fecundity.

The fecundity function $f(x, y)$ and the survival-growth function $p(x, y)$ are closely related to the corresponding entries in the matrix projection model. The fecundity entries in a matrix model are typically along the top row of the matrix, representing the contributions of each age class to the stage class containing newborns (e.g., the smallest size class). The analog for the integral model would be a function $f(x, y)$ that is positive for large x (parents) and small y (offspring), and is zero elsewhere. The function $p(x, y)$ incorporates both growth and mortality. It corresponds to the survival and growth entries in a Lefkovitch (1965) matrix, and it can account for individuals that grow larger or small-

er. It is important to point out that $\int p(x, y)dy$ will typically be <1, even though $p(x, y)$ is defined as a probability, because not all individuals survive from time t to time $t + 1$.

Implicitly underlying the population-level model of Eq. 1 is a stochastic individual-based model, in which individuals follow Markovian growth trajectories, with an individual's chance of death, and the distribution of offspring number and size, depending on the individual's current size. Given the current population state, as summarized by $n(x, t)$, Eq. 1 gives the expected population state at time $t + 1$. Furthermore, because the operation of integration on the right-hand side of Eq. 1 is linear in $n(x, t)$, the same equation holds if $n(x, t)$ is the expected (rather than actual) population state at time t. Thus, given the population state at some initial time, Eq. 1 can be iterated to give the expected population state at all subsequent times. Eq. 1 can therefore be regarded as an analytic partial solution of a stochastic individual-based model that lets us compute expected trajectories without actually implementing and simulating the stochastic model. Of course, exactly the same is true of the matrix projection model, except that the Markov chain governing individual growth trajectories has a discrete, finite state space.

Comparison with other structured models

The integral projection model is similar to partial differential equation models in that the individual state is continuous, but it differs in having a discrete time step. The discrete time step allows the integral model to retain much of the structural and mathematical simplicity of the matrix model. The integral model also preserves the matrix model's close correspondence between the components of the model and the observable fates of individuals between successive censuses of the population, which makes it relatively simple to fit the model to repeat census data. An integral projection model can also be formulated in continuous time (Diekmann et al. 1998), but the model is mathematically much more complicated and corresponds less closely to the kinds of data usually used in constructing a matrix projection model (see *Discussion*). A discrete time model can be applied even if growth occurs continuously, as any continuous-time growth model implies a discrete-time model for the net growth between one sampling period and the next.

The integral model also has greater flexibility than partial differential equation (PDE) models in describing the distribution of size changes over a time step. Apart from some very mild technical assumptions (Easterling 1998), a user can select any distribution of growth rates that is necessary to fit the data at hand, any distribution of initial offspring size, and any functional form for the size dependence of mortality and fecundity. As in integral models for movement of organisms in space (Kot et al. 1996), going from an integral model to a PDE model requires some additional assumptions (see, e.g., Turchin [1998]: section 4.2 and Appendix A.1.2, for the steps involved). An unavoidable effect of these assumptions is to limit the possible shape for the distribution of size changes conditional on current size. The most common assumption (e.g., most of the models in Metz and Diekmann [1986] and Gurney and Nisbet [1998]) is that growth trajectories are deterministic. This would be analogous to a PDE model for spatial spread without a diffusion term, so that particles or individuals that start in the same place remain together for all time. The assumption of deterministic growth is necessary for the reduction of a PDE models to a delay differential equation (DDE) model for a structured population with discrete classes (Gurney and Nisbet 1998). The integral projection model, therefore, may be a more natural choice than a PDE or DDE model in situations where the stochastic nature of individual growth trajectories is an essential aspect of the population dynamics.

PROPERTIES OF THE INTEGRAL PROJECTION MODEL

The integral projection model shares many of the features that have made the matrix projection model popular: estimation of the exponential growth rate, eigenvectors representing reproductive value and the stable size distribution, and formulas for sensitivity and elasticity analysis (derived in Easterling 1998).

The integral model has a dominant eigenvalue λ that represents the population's asymptotic growth rate, under biological assumptions that are no more restrictive than those required in the matrix model. Corresponding to λ are dominant right and left eigenvectors $w(x)$ and $v(x)$, and, as in the matrix model, these give the stable size distribution and size-specific reproductive value, respectively. Note, however, that in the integral model these "eigenvectors" are functions of a continuous variable, individual size x. Methods for computing the dominant eigenvalue and corresponding eigenvectors are described in the Appendix, and are straightforward to code in matrix languages such as Matlab, S-Plus, GAUSS, or SAS IML.

Because the fecundities and survivorships in the integral projection model are represented by a surface rather than a matrix, sensitivity analysis for the model involves determining the sensitivity of the dominant eigenvalue to changes in the survivorship/fecundity surface $k(y, x)$ over a small region centered over each point (y, x). Technically, "small" is defined as the limit as the small region is shrunk to a point at (y, x), with the sensitivity of λ scaled by the "area" of the small region around (y, x). The definition of sensitivity (and hence of elasticity) in the integral model thus differs in an essential way from that in the matrix model. In the integral model, sensitivity describes the change in λ resulting from a change in demographic parameters affecting only individuals at a particular size. This only affects an individual once (except for the rare event that an individual stays exactly the same size). In the

matrix model, sensitivity describes the total effect of a parameter change applied to all individuals in a size class. Because an individual may remain in the same size class more than one year, individuals may "see" the parameter change more than once.

With this definition, the sensitivity and elasticity formulas for the integral model are very similar to those for a matrix model (Caswell 1978). The sensitivity of the growth rate λ to changes in survivorships and fecundities is

$$s(z_1, z_2) = \frac{\partial \lambda}{\partial k(z_1, z_2)} = \frac{v(z_1)w(z_2)}{\langle w, v \rangle} \qquad (2)$$

where $s(z_1, z_2)$ is the sensitivity of λ to a small change in the $k(y, x)$ values near (z_1, z_2) and $\langle w, v \rangle = \int w(x)v(x)\ dx$ (Easterling 1998). The corresponding elasticity estimates are therefore given by

$$e(z_1, z_2) = \frac{k(z_1, z_2)}{\lambda} \cdot \frac{v(z_1)w(z_2)}{\langle w, v \rangle}. \qquad (3)$$

The elasticity function integrates to unity (i.e., $\int \int e(z_1, z_2)\ dz_1\ dz_2 = 1$), corresponding to the elasticities summing to unity in the matrix projection model (Easterling 1998). However, the interpretation of the sensitivity (Eq. 2) is slightly different here than in the matrix model. The sensitivity defined in Eq. 2 gives the rate of increase in λ as the kernel k is increased in a small disk centered at (z_1, z_2), scaled relative to the size of the disk. This corresponds roughly to scaling a matrix model's sensitivities relative to the widths of the stages involved in the transition rate being perturbed. Alternatively, the fact that the scaling cancels out, when two sensitivities are compared, means that values obtained directly from Eq. 2 can be interpreted as the relative sensitivity of λ to changes in different size-specific transition rates. Sensitivities and elasticities corresponding to those obtained from a matrix model can be computed by integrating the "pointwise" sensitivities and elasticities, defined in Eqs. 2 and 3, over the size ranges affected by the change in transition rates.

AN INTEGRAL PROJECTION MODEL FOR NORTHERN MONKSHOOD

Our case study species is northern monkshood, *Aconitum noveboracense,* an herbaceous perennial plant listed as threatened under the U.S. Endangered Species Act (Dixon and Cook 1990). Northern monkshood reproduces by flowering and by vegetative propagation. Plants may be reduced in size by deer grazing. Dixon and Cook (1990) conducted annual censuses of marked individuals at 14 sites in New York, USA, for five years. Pooled across years, nine of the 14 sites have estimated growth rates $\lambda < 1$, while the other five have growth rates $\lambda > 1$. Each site has significant year-to-year variation in growth rate. Plant size, specifically stem diameter, was used to describe the population, because size is often better than age when predicting

plant growth, seed production, and survival (Silvertown and Lovett Doust 1993).

Typically, this kind of population data would be analyzed with a matrix model, and this has been done by Dixon and Cook (1990) and Dixon et al. (1997). In order to do so, individuals were grouped into discrete size-classes, and the matrix entries represent mean vital rates for individuals within the class. Even if size class boundaries represent natural biological delimiters (such as size at first reproduction), information is lost when individuals of different sizes are grouped into a class and treated as if they were identical. Monkshood, however, is size structured without any clear divisions into size classes. By analyzing the data using the integral projection model, we can produce a complete sensitivity analysis without having to select class boundaries.

For this case study, we used Dixon and Cook's (1990) data from one site that was pooled over three years to estimate the kernel of the integral projection model. The stem diameter and number of leaves were recorded for each marked plant. We used stem diameter as our measure of plant size. The stem diameter of very small plants could not be measured without damaging the plants; for those plants, only the number of leaves was recorded. We therefore defined the size of small plants by regressing stem diameter against number of leaves for all plants, where both could be measured, with the result that the stem diameter for small plants was approximated as 0.2 mm $\times$ no. leaves. This approximation simplifies the fitting process, but it is not a necessary step for the integral projection model.

Estimating the kernel from the fate of marked individuals

The kernel $k(y, x)$ represents all possible size transitions, including births of new individuals. For estimating the kernel from data, it is necessary to estimate separately the survival transitions $p(x, y)$ and the fecundity $f(x, y)$. We now describe a method for estimating these functions from observations of the fate of individuals, such as our data on northern monkshood. The information used to estimate the kernel are as follows: the size of each individual at time t; whether or not the individual survived to time $t + 1$; the size of surviving individuals at time $t + 1$; and the number of offspring produced by each individual at time t, along with the size of each offspring.

As a general approach to selecting functional forms for components of the kernel, we first fitted a linear model and then tested the linear model against nonlinear alternatives: addition of quadratic and cubic terms, and B-splines with 3, 4, and 5 degrees of freedom. Models were fitted using the S-plus Generalized Linear Model function (MathSoft, Seattle, Washington, USA), and the significance of nonlinear terms was tested using the S-plus function *anova*( ) with χ^2 test statistic (Hastie
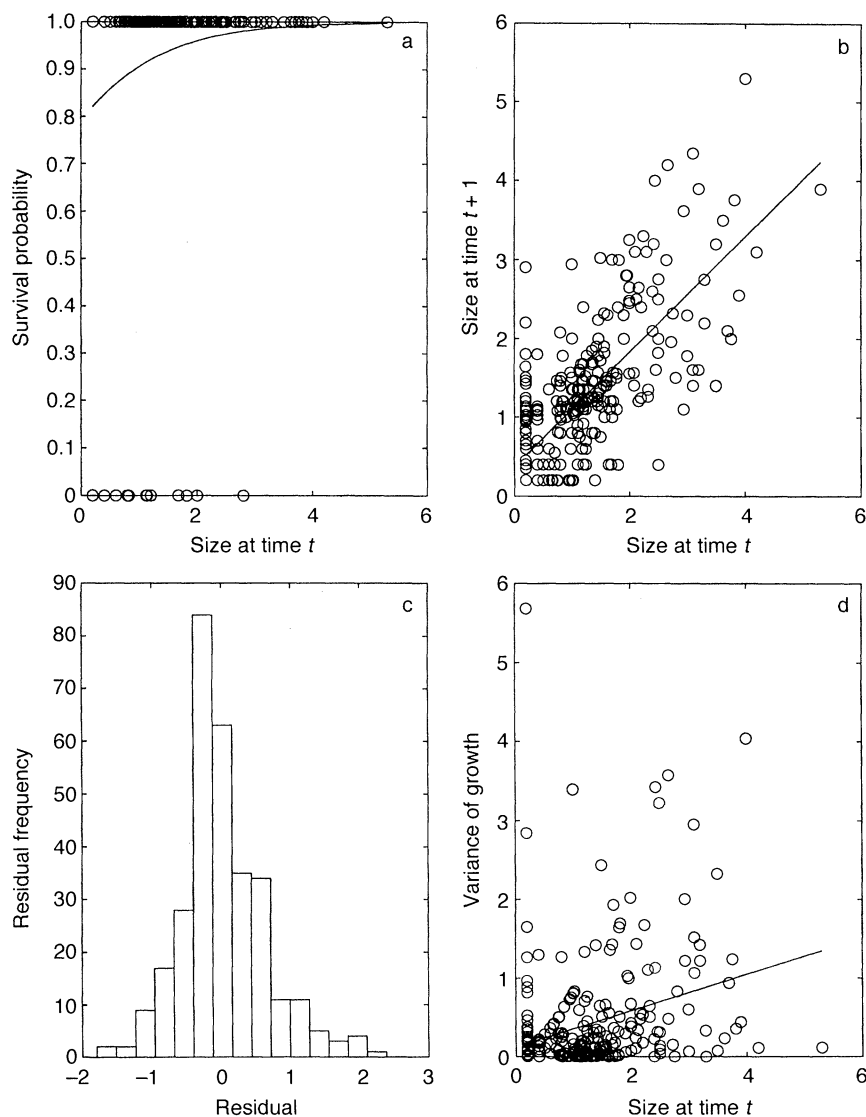
FIG. 1. Fitting a survival and growth function to the monkshood data. (a) The survival data are plotted (0, death; 1, survival), as a function of individual size x (stem diameter in millimeters), along with the logistic regression fitted to the data. The fitted curve is $\log(s/(1-s)) = 1.34 + 0.92x$ ($P < 0.001$). (b) The data on year-to-year changes in size, along with the linear regression fit for mean size in year $t + 1$, as a function of size in year t. The fitted line is $y = 0.37 + 0.73x$ ($P < 0.001$). (c) Histogram of residuals from the linear model in panel (b). (d) Squared growth residuals as a function of individual size, along with the linear regression fit for the mean squared residual, which is the variance of size in year $t + 1$, given the size in year t. The fitted line is $y = 0.127 + 0.23x$ ($P < 0.001$).

and Pregibon 1992). Parameter estimates are given in the legends to Figs. 1 and 2.

The growth and survival function $p(x, y)$ was estimated by breaking it into separate growth and survival components. Survival and growth are separated by writing $p(x, y)$ in the form $p(x, y) = s(x)g(x, y)$, where $s(x)$ is the survival probability of a size-x individual and $g(x, y)$ is the probability of a size-x individual growing to be size y. Because any individual that survives must be some size in the next year, we must have $\int g(x, y) \, dy = 1$.

The survival function $s(x)$ was estimated by logistic regression of survival (one or zero, corresponding to survival or death, respectively) on size x, as illustrated in Fig. 1a. The fitted linear model is of the form $\log(s(x)/(1-s(x))) = a + bx$. The addition of nonlinear terms was not significant ($P > 0.2$ in all cases), so this linear model was retained.

To fit the growth function $g(x, y)$, we first plotted the relationship between individual sizes at times t and $t + 1$ (Fig. 1b). A linear model appears to be adequate for describing the relationship between size at time t,
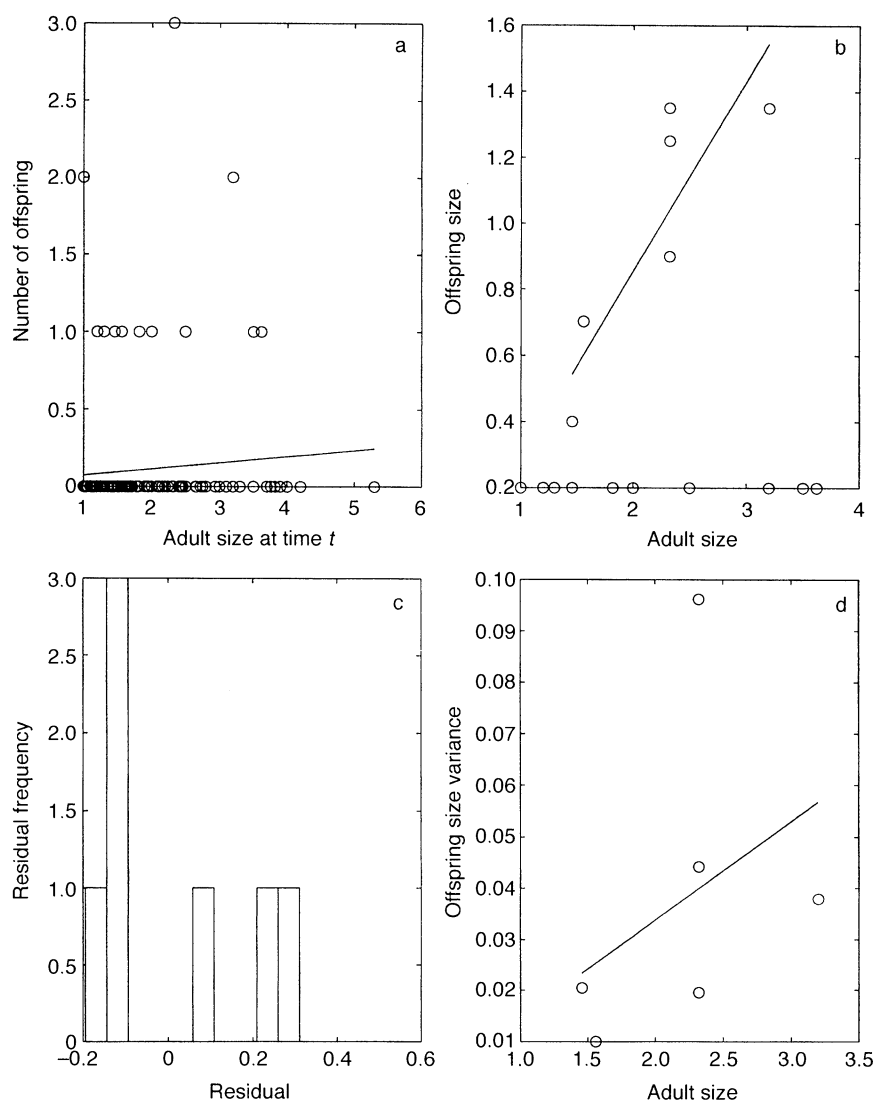
FIG. 2. Fitting a fecundity function to the monkshood data. (a) Number of offspring as a function of individual size x (stem diameter in millimeters), along with the linear regression for mean number of offspring. The fitted line is $y = 0.034 + 0.038x$ ($P < 0.001$). (b) Offspring size, as a function of adult size. The linear regression fit (solid line) is for the relationship between adult size and the mean size of "larger" offspring (size > 0.2 mm). The fitted line is $y = -0.30 + 0.57x$. (c) Residuals from the linear model in panel (b). (d) Squared offspring size residuals, as a function of adult size, along with the linear regression fit for the mean squared residual, which is the variance of offspring size as a function of adult size. The fitted line is $y = -0.0046 + 0.192x$.

and mean size at time $t + 1$; as with $s(x)$, the linear model was not rejected against the nonlinear alternatives ($P > 0.5$ in all cases). The residuals from this linear model, which represent the random component of individual growth trajectories, conform reasonably well to a normal distribution (Fig. 1c). However, the variance in size at time $t + 1$ may also be affected by size at time t. Residual variance is equal to the mean square of residuals, so we can estimate the size-dependence of the variance by plotting the squared residuals (from Fig. 1b) vs. size (Fig. 1d). Again, a linear

model appears to be adequate and was not rejected against the nonlinear alternatives ($P > 0.1$ in all cases). Combining these pieces, the fitted growth function $g(x, y)$ says that the new size y of an individual that is currently size x is distributed as $y = \sigma(x)Z + \mu(x)$, where Z is normally distributed with mean of zero, variance of unity, and the mean size $\mu(x)$ and the variability $\sigma(x)$ are linear functions of x. That is,

$$g(x, y) = \frac{1}{\sqrt{2\pi}\sigma(x)} e^{-(y-\mu(x))^2/2\sigma(x)^2}$$

and the growth and survival component of the kernel is then represented as follows:

$$p(x, y) = s(x)\frac{1}{\sqrt{2\pi}\sigma(x)}e^{-(y-\mu(x))^2/2\sigma(x)^2}.$$

Note that the use of a Gaussian distribution for the variability in growth was a data-based decision, and any other probability distribution could have been used to model the distribution of the residuals in Fig. 1c, had that been necessary.

The fecundity function $f(x, y)$ was estimated from the data in a similar way. Fecundity is split into $f(x, y) = f_1(x)f_2(x, y)$, where the function $f_1(x)$ is the mean number of offspring from a size-x individual, while $f_2(x, y)$ is the probability distribution of offspring size y for an adult of size x, which has $\int f_2(x, y) \, dy = 1$. In this case, the term "adult" refers to any individual large enough to reproduce, i.e., no smaller than the smallest individual observed to reproduce. The mean number of offspring was fitted by Poisson linear regression on adult size (Fig. 2a), and the linear model was not rejected against the nonlinear alternatives ($P > 0.3$ in all cases). One can view the fecundity data (Fig. 2a) as follows: plants of size x have some probability of having 0, 1, 2, or 3 offspring, and these probabilities vary with size x. Thus the mean number of offspring for a size-x plant is

$$f_1(x) = \Pr(n = 0, x) \times 0 + \Pr(n = 1, x) \times 1$$
$$+ \Pr(n = 2, x) \times 2 + \Pr(n = 3, x) \times 3.$$

The data in Fig. 2a do not appear to be linear, because each data point corresponds to one of the terms on the right-hand side of this equation (i.e., an actual discrete number of offspring). The linear regression line is an estimate of the expected total contribution from each term to the offspring production in a given year, which is the quantity that enters into the model. Note that when estimating the per capita fecundity f_1, all individuals must be included that are alive at the start of the time step, even if they die between times t and $t + 1$. Just as the survival function $s(x)$ should be fitted to remain between zero and one, f_1 should be fitted so that the number of offspring remains nonnegative for all adult sizes.

The distribution of offspring sizes (Fig. 2b) is strongly bimodal, with a cluster at size 0.2 (i.e., individuals with a single leaf that were assigned a stem diameter of 0.2 mm) and a smaller number of larger offspring. Sexual reproduction in this population was extremely rare (indeed not observed over the 3-yr span of our data set) and was omitted from the model. The size-0.2 offspring mostly originated as vegetative shoots, while the larger offspring are mostly fission of an adult into two smaller individuals (recorded in our data set as a death plus two births). The offspring size function $f_2(x, y)$, therefore, has two pieces corresponding to these different modes of reproduction. Size-0.2 offspring

were represented by a uniform distribution of offspring size in the interval [0.15, 0.25]. For the larger offspring, we used the same model as for $g(x, y)$: Gaussian, with mean and variance depending linearly on adult size x, fitted in exactly the same way (Fig. 2c, d). Because of the very small number of larger offspring, the linear model was selected a priori. The assumption of a Gaussian offspring size distribution is clearly arbitrary, given the small sample size. However, it should not be of great consequence, because production of the larger offspring is relatively infrequent. These two components of f_2 were weighted according to the proportion of size-0.2 vs. larger offspring in our data set (11/18 vs. 7/18).

As this example indicates, fitting the integral model requires some effort and judgement by the user to determine suitable functional forms. Parameter estimation in the matrix model is automatic (once stage boundaries are chosen), but this "advantage" depends on the often incorrect assumption that all vital rates are constant within size classes and jump instantly at class boundaries. If vital rates actually vary smoothly with size, then the inaccuracy that results from approximating the smooth variation by a staircase function with a few large jumps will be far larger than that resulting from using a regression equation with one degree of freedom too many or too few in the integral model. The integral model allows the user to seek an estimate within the biologically correct set of functions. Once a data set has been entered on the computer, fitting the model takes at most several minutes on current desktop computers (see the Supplementary Material). It is therefore quite feasible for a user to build several alternative integral models, for example with different polynomial orders for mean and variance functions.

In order to predict growth rates and sensitivities from the model, we need to determine the limits of integration in Eq. 1. The integration must run over all possible sizes, not just those observed in the data. We set the limits of integration based on the variance of growth. The lower limit of integration was set at the minimum observed size x_{min} minus three standard deviations of the growth increment at x_{min}, and the upper limit was set at the maximum observed size x_{max} plus three standard deviations of the growth increment at x_{max}. Setting the integration limits outside the data range means that the kernel must be extrapolated for x values outside $[x_{min}, x_{max}]$. Our solution to this problem was to use the nearest kernel value within the range of the observed data, so that

$$k(y, x) = \begin{cases} k(y, x) & \text{if } x_{min} \le x \le x_{max} \\ k(y, x_{min}) & \text{if } x \le x_{min} \\ k(y, x_{max}) & \text{if } x > x_{max}. \end{cases}$$

In the same way, y values outside $[x_{min}, x_{max}]$ were projected on the range of observed data. More accurate extrapolations beyond the range of the data may be
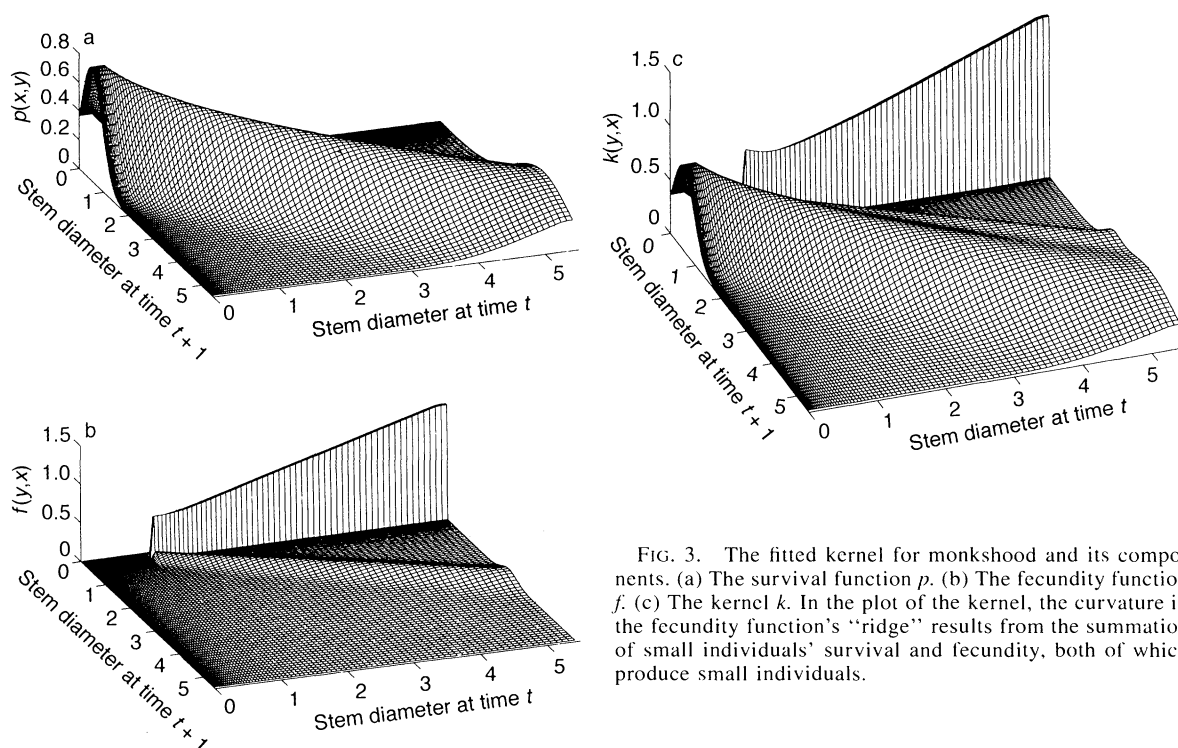
FIG. 3.   The fitted kernel for monkshood and its components. (a) The survival function p. (b) The fecundity function f. (c) The kernel k. In the plot of the kernel, the curvature in the fecundity function's "ridge" results from the summation of small individuals' survival and fecundity, both of which produce small individuals.

possible (e.g., linear extrapolation of log k), but such individuals are uncommon enough that the method used to extrapolate their vital rates has very little effect on the model's predictions.

The estimated fecundity function $f(x, y)$, survival function $p(x, y)$, and kernel $k(y, x) = f(x, y) + p(x, y)$ for monkshood are shown in Fig. 3. There are several features to notice. The straight "ridge" representing vegetative offspring dominates the fecundity function. The second, lower ridge represents larger offspring, which are less common and more variable in size. The main feature in the survival function is the ridge running near the diagonal, representing individuals who survive to the next year, without changing much in size. The location of the ridge shows that, in general, plants increase in size, but the amount of growth decreases as the stem diameter increases. Putting survival and fecundity together gives a kernel $k(y, x)$ that resembles a Lefkovitch (1965) matrix for a size-structured population: the large values in the "top row" represent newborns that all enter the smallest size class, and the ridge of smaller values near the diagonal represents survival with possible transition to a neighboring size class.

Matrix projection models for monkshood

For comparison with the integral model analysis, we constructed a matrix projection model using exactly the same data. We used five size classes with bound-

aries at the 20th, 40th, 60th, and 80th percentiles of the size distribution in the data set (0.2, 0.6, 1.154, and 1.702 mm, repectively). Classes included their upper boundary, e.g., all size-0.2 individuals are in class 1. The transition matrix resulting from this division is

Size class at time t

$$
\begin{array}{c}
\text{Size class} \\
\text{at time} \\
t + 1
\end{array}
\begin{bmatrix}
0.416 & 0.214 & 0.179 & 0.071 & 0.087 \\
0.177 & 0.214 & 0.075 & 0.114 & 0.029 \\
0.133 & 0.321 & 0.328 & 0.214 & 0.044 \\
0.062 & 0.036 & 0.313 & 0.429 & 0.2899 \\
0.0265 & 0.036 & 0.060 & 0.200 & 0.652
\end{bmatrix}.
\tag{4}
$$

The top row entries of this matrix (in particular, toward the left) are primarily survival, rather than fecundity, which accounts for the fact that this row decreases from left to right, even though smaller individuals have lower fecundity (as in the integral model). For the same population (but using all years of available data) Dixon and Cook (1990) constructed a matrix model with five classes, but different class boundaries: seedling, juvenile, small (<2 mm), medium (2–4 mm), and large (>4 mm). In the *Results*, we discuss some of the results from this model. However unlike the matrix in Eq. 4, the Dixon and Cook (1990) matrix was not constructed from exactly the same data as our integral projection model for monkshood.
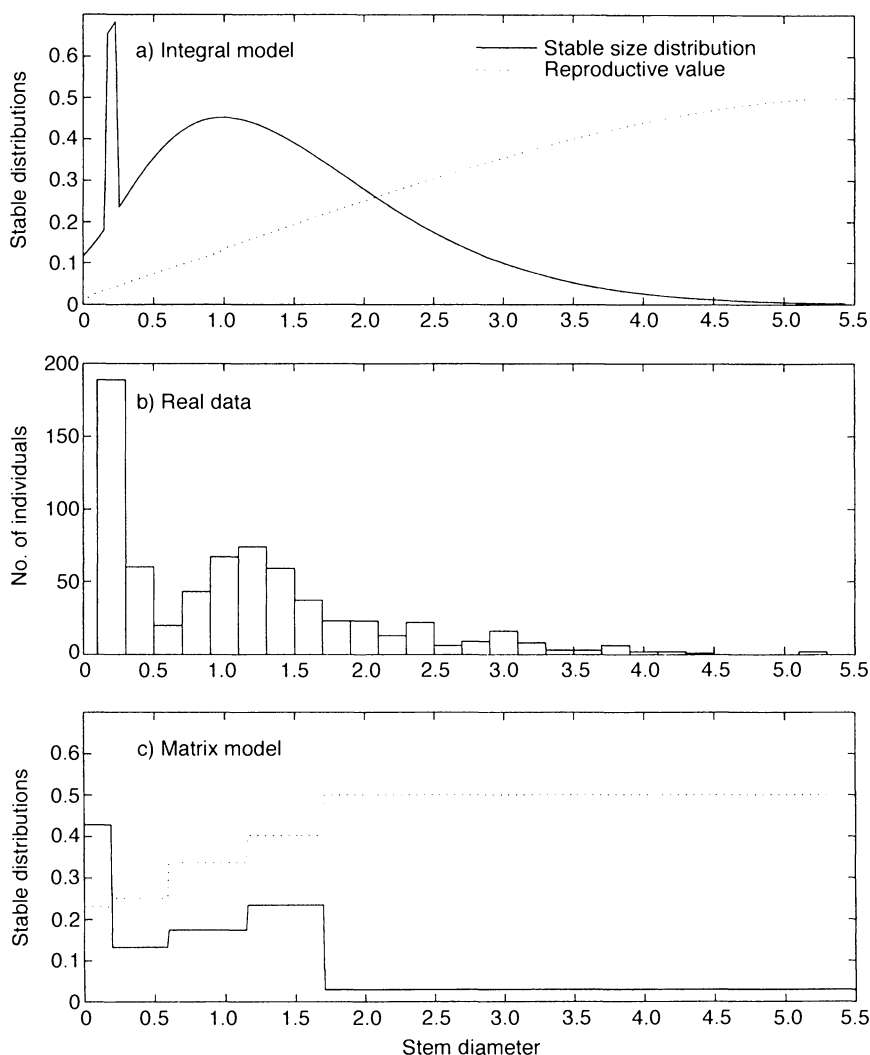
FIG. 4. (a) The stable size distribution (———) and relative reproductive value (· · · ·) for the integral projection model fitted to the monkshood data. (b) The distribution of plant sizes (stem diameter in millimeters) in the monkshood data set used for fitting the integral projection model. (c) The stable size distribution (———) and relative reproductive value (· · · ·) for the matrix model given in Eq. 4.

RESULTS

Asymptotic growth rate

The estimated asymptotic growth rate from the fitted integral model is model λ_{int} = 0.967, nearly identical to the estimate λ_{mat} = 0.969 from the matrix model. Easterling (1998) obtained similar results for artificial data sets: the matrix and integral models produce very similar estimates of λ, with very little difference in the bias or sampling variability of the estimates. For both integral and matrix models, bootstrap confidence intervals for the growth rate include 1.0 (Easterling 1998), so we cannot conclude that monkshood at this site is in decline. The same conclusion was reached by Dixon and Cook (1990).

Stable size distribution and reproductive values

The right and left eigenvectors corresponding to the dominant eigenvalue λ_{int} are the stable size distribution and reproductive value, respectively, for the integral projection model (Fig. 4a). The predicted stable size distribution is skewed heavily towards smaller plants, and is quite similar to the observed size distribution in the data set used to fit the model, including the spike of individuals in the size range corresponding to one-leaf vegetative offspring (Fig. 4b). The reproductive value curve reflects the fact that monkshood of almost any size can reproduce vegetatively. However, reproductive value increases monotonically with plant size, reflecting the fact that larger plants have higher sur-
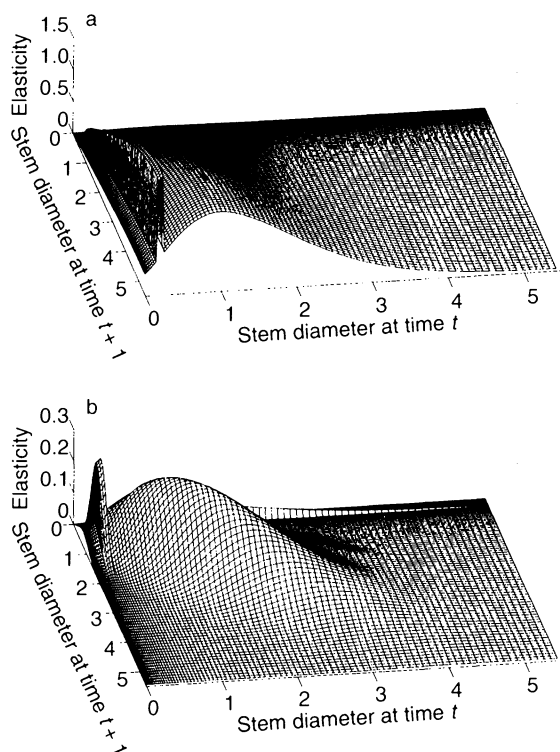
Fig. 5. (a) Sensitivity surface for the integral projection model fitted to the monkshood data. (b) Elasticity surface for the integral projection model fitted to the monkshood data.

vival, higher fecundity, and larger offspring, on a mean basis.

The stable size distribution and relative reproductive value curve for the matrix model are shown in Fig. 4c. The stable size distribution is similar to that observed, and has the same qualitative features as that from the integral projection model. The reproductive value curves are qualitatively different, with the matrix model estimating a far smaller difference in reproductive value between the smallest and largest individuals. A possible explanation for this discrepancy is discussed in the *Discussion*.

Sensitivity and elasticity analysis

Just as a matrix model has a matrix of sensitivity values for each matrix entry, the integral model has a *sensitivity surface* representing the sensitivity of the eigenvalue to changes in the kernel (Fig. 5a), and a corresponding elasticity surface (Fig. 5b), for all sizes. The sensitivity formula (Eq. 2) shows how the shape of the sensitivity surface is determined by the stable size distribution and reproductive value curves. On a slice through the sensitivity surface along a line of constant "stem diameter at time $t + 1$," the sensitivity surface is proportional to the stable age distribution: there is a sharp peak at the size of one-leaf vegetative offspring, and a second lower peak near stem diameters

of 1 mm. On a slice in the perpendicular direction, the sensitivity surface is proportional to relative reproductive value, and, therefore, increases sharply with increasing size. The elasticity surface is proportional to the product of the sensitivity surface and the kernel (see Eq. 3). Consequently, elasticities are high along the ridges representing birth and survival of one-leaf vegetative offspring and survival of larger individuals.

The sensitivity matrix for our 5×5 matrix model for Monkshood (Eq. 4) is

$$\text{Size class at time } t$$

$$\text{Size class at time } t+1 \begin{bmatrix} 0.132 & 0.069 & 0.139 & 0.186 & 0.159 \\ 0.117 & 0.061 & 0.123 & 0.164 & 0.140 \\ 0.181 & 0.095 & 0.190 & 0.254 & 0.217 \\ 0.213 & 0.112 & 0.224 & 0.300 & 0.257 \\ 0.264 & 0.138 & 0.277 & 0.370 & 0.317 \end{bmatrix} \quad (5)$$

and the elasticity matrix is

$$\text{Size class at time } t$$

$$\text{Size class at time } t+1 \begin{bmatrix} 0.055 & 0.027 & 0.023 & 0.014 & 0.013 \\ 0.024 & 0.009 & 0.009 & 0.014 & 0.004 \\ 0.032 & 0.017 & 0.068 & 0.063 & 0.010 \\ 0.013 & 0.005 & 0.074 & 0.132 & 0.076 \\ 0.008 & 0.004 & 0.017 & 0.076 & 0.213 \end{bmatrix}. \quad (6)$$

The highest sensitivities are in the lower right of the matrix representing large plant to large plant transitions. The larger elasticities are also for the transitions of large plants, in particular for survival of class four and class five plants. For the matrix model of Dixon and Cook (1990), for the same population (although using a different data set), the largest elasticities were for the survival of small and medium sized plants (stem diameter 0.2–4 mm).

These discrepancies between models result in part from the choice of stage boundaries in the matrix models. Matrix model sensitivity/elasticity values describe the effect of changing transition rates for an entire size class of individuals. Corresponding values for the integral model are obtained by integrating the sensitivity/elasticity surfaces over size limits corresponding to the matrix transition rate being changed. Thus the value from the integral model corresponding to the matrix model elasticity to transition rate a_{ij}, is given by

$$\bar{e}_{ij} = \int_{L_i}^{U_i} \int_{L_j}^{U_j} e(x, y) \, dy \, dx \quad (7)$$

where L_k and U_k are the lower and upper limits, respectively, of the kth size class in the matrix model.

Using the size class boundaries of our matrix model (Eq. 4), the integral model reproduces the conclusion from the matrix model that the highest elasticity is for the survival of individuals in the largest size category

a) Integral model

a) Integral model

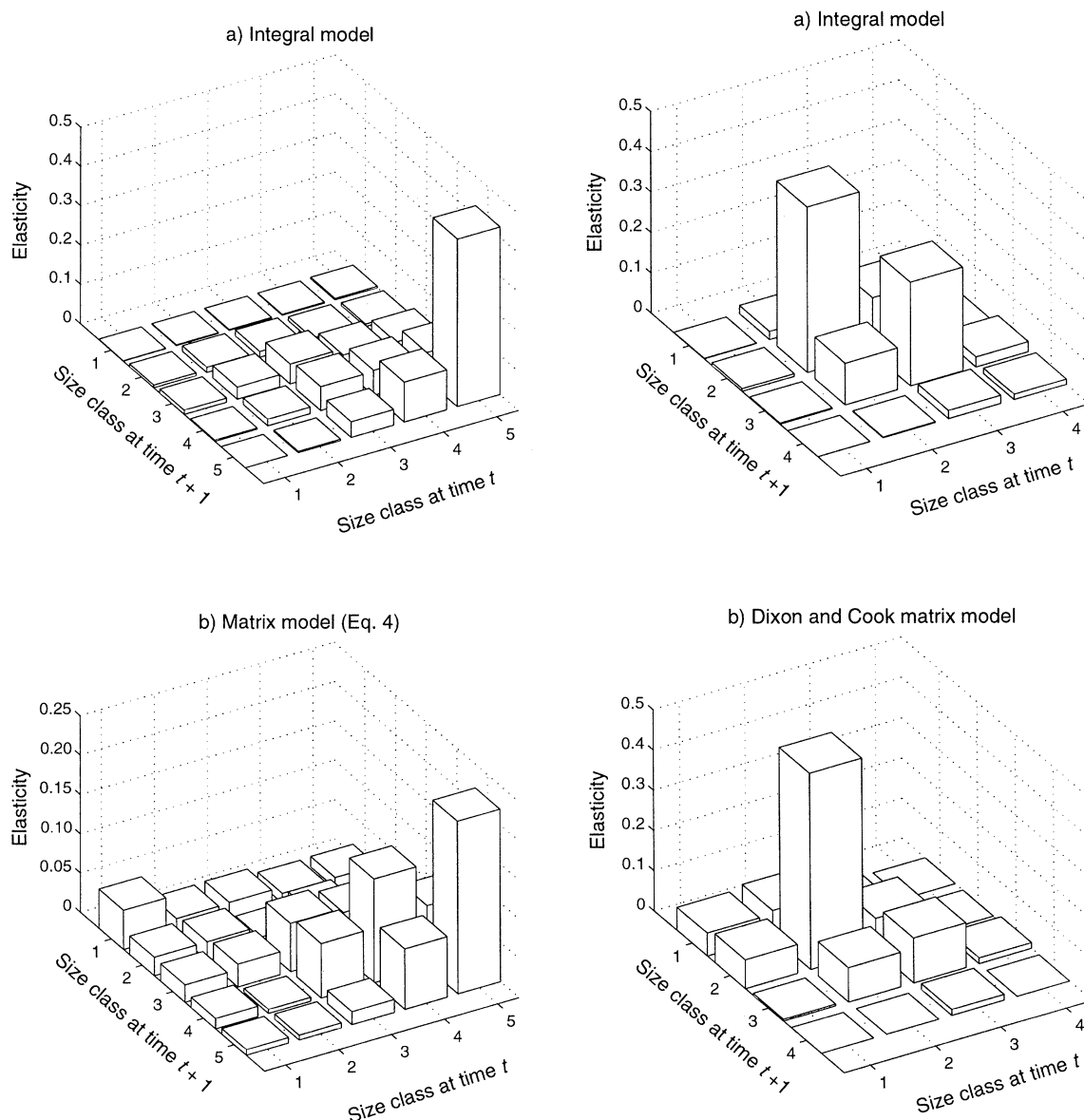b) Matrix model (Eq. 4)

b) Dixon and Cook matrix model

FIG. 6. Comparison of matrix model elasticities $e_{ij} = (a_{ij}/\lambda)\partial\lambda/\partial a_{ij}$ for monkshood, with corresponding values from the integral projection model (Eq. 7), for our matrix model (Eq. 4) with size class boundaries based on percentiles of the size distribution. The matrix model has five size classes with boundaries at 0.2, 0.6, 1.154, and 1.702 mm. (a) Integral model elasticity values. (b) Matrix model elasticity values.

(Fig. 6). The differences between the matrix and integral model values in Fig. 6 are mostly due to the different reproductive value curves (Fig. 4a vs.4c). The integral model predicts a lower relative reproductive value for small individuals, and therefore assigns lower sensitivity and elasticity to transitions into the smaller size classes. Figs. 6a and 5b present the same information plotted in two different ways. The apparently large discrepancy between Figs. 6a and 5b is due to
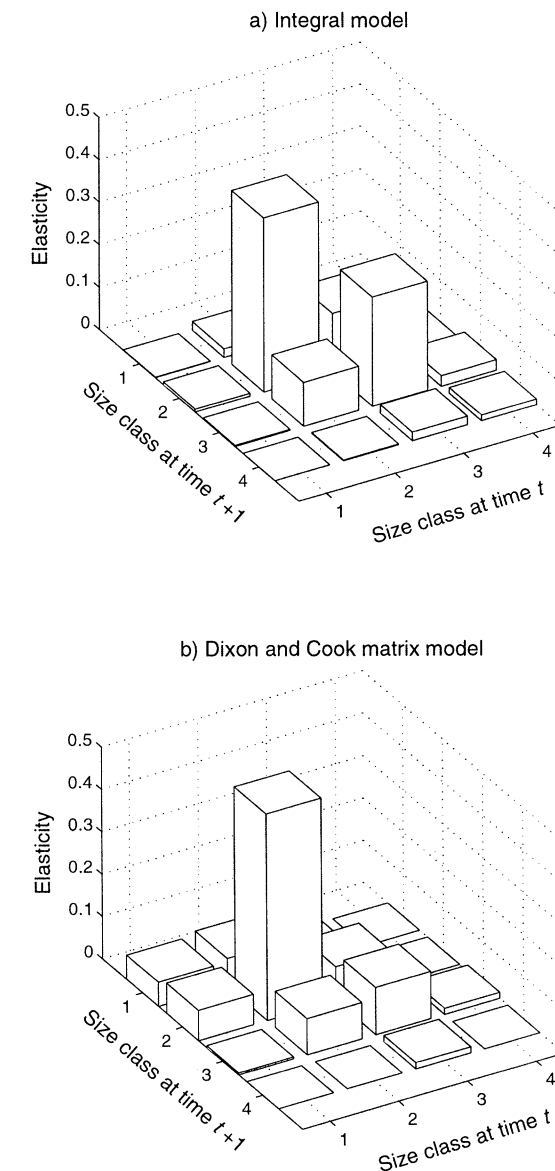
FIG. 7. Comparison of matrix model elasticities $e_{ij} = (a_{ij}/\lambda)\partial\lambda/\partial a_{ij}$ for monkshood, with corresponding values from the integral projection model (Eq. 7) (as in Fig. 6), but with the size class boundaries from the Dixon and Cook (1990) matrix model. The matrix model was derived from the same data as was used to fit the integral model and our matrix model (Eq. 4). The matrix model in this figure has four size classes with boundaries at 0.2, 2, and 4 mm. The fifth class in the Dixon and Cook (1990) model is sexually produced seedlings, which did not occur in our reduced data set. (a) Integral model elasticity values. (b) Matrix model elasticity values.

the variation in the width of the size classes used in Fig. 6, which causes wide variation in the area of the region of integration in Eq. 7. In particular, size class 5 (≥ 1.7 mm) is $>4\times$ as wide as any of the other size-classes, and this, more than anything else, produces the large value of $\bar{e}_{5,5}$.

Using, instead, the size class boundaries from the Dixon and Cook matrix model, the integral and matrix models both assign highest sensitivity to the survival of small-to-medium size individuals (Fig. 7). Again, the integral model predicts stronger size dependence of reproductive value, and assigns correspondingly lower elasticities to transitions into the smaller size classes. The differences between Figs. 6 and 7 are strikingly large, but can by reconciled by comparing the two sets of size class boundaries. In particular, all of size classes 2, 3, and 4 from Fig. 6 are included in size class 2 of Fig. 7, which gives size class 2 the bulk of the total elasticity. The majority of size class 5 from Fig. 6 is split between size classes 3 and 4 in Fig. 7, so that the large $\tilde{e}_{5,5}$ in Fig. 6 is (approximately) divided into four pieces ($\tilde{e}_{3,3}$, $\tilde{e}_{3,4}$, $\tilde{e}_{4,3}$, $\tilde{e}_{4,4}$) in Fig. 7. As these comparisons illustrate, the final rankings of elasticities in a matrix model can be driven by the choice of size classes for constructing the matrix; Figs. 6 and 7 are equally valid as reduced summaries of the sensitivity surface, but they would be interpreted very differently with regard to conservation priorities, based on the size of individuals. The integral model, in contrast, provides disaggregated information (Fig. 5a, b) that allows a user to compute elasticities for any projected changes in transition rates that could result from potential changes in population management.

DISCUSSION

Results of integral projection versus matrix models

The integral projection model is a new tool for analyzing structured population data, and this paper is only an initial trial at fitting the model to data, and using the fitted model for some of the usual purposes of the matrix projection model. In theory, there is a well-defined set of circumstances in which the integral projection model can offer decisive advantages over alternatively structured population models: a better representation of transient dynamics (Easterling 1998), and all of the useful output from a matrix model, without any artifacts due to the location of artificial class boundaries. Our monkshood case study emphasizes that the class boundary effects are not statistical niceties, but can have an enormous impact on the interpretation of the sensitivity analysis and the management priorities that would be implied. Aggregating size-specific elasticities into class-specific elasticities (via Eq. 7) can blur potentially significant features, such as the "ridges" in elasticity for vegetative production of one-leaf individuals (Fig. 5).

The findings of Enright et al. (1995) demonstrate that this problem is quite general. Relative sensitivities and elasticities within and between species are sensitive to the location of stage class boundaries, and, in particular, to stage duration (the fraction of the life span typically spent in each stage). The solutions proposed by Enright et al. (1995) (i.e., holding stage duration constant, or

using the same number of stages for all species) minimize the effects of stage duration, but do so at the considerable price of laying down stage boundaries at locations unrelated to any natural (or management-imposed) breakpoints. Like the algorithms of Vandermeer (1978) and Moloney (1986), these are ways to make the best of a bad situation. Using an integral projection model for the sensitivity analysis removes the artifacts due to stage duration, without introducing new artifacts due to biologically inappropriate stage boundaries. The exactly size-specific results from an integral model can be applied to any size-dependent thresholds for management effects (e.g., size limits on harvest of individuals). A user can estimate the effects of alternative management options more easily and more flexibly than with a matrix model, which is inherently tied to the size categories (or combinations of them) used in constructing the model. Given the critical role of sensitivity analysis results for conservation planning (e.g., Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 1994, 2000, Schemske et al. 1994, de Kroon et al. 2000), the additional effort of constructing the integral projection model will often be outweighed by the potential benefits.

The matrix and integral models also produce very different estimates of the size-dependent variation in reproductive value for monkshood. One might expect that a matrix model will produce an "average" or "typical" reproductive value for individuals in a size category, but this is not necessarily true. As a simple example to illustrate what can happen, consider a five-stage population that is really age structured, with juveniles (ages 1–4) having no fecundity and survival S_J, adults ($\geq$age 5) having survival S_A and per capita fecundity b. To allow analytic calculations we choose b so that the population is stationary ($\lambda = 1$); this occurs if $S_A + bS_J^4 = 1$. This population is governed by a Leslie matrix $\mathbf{L}$ with S_J's on the subdiagonal, $\mathbf{L}_{5,5} = S_A$ and $\mathbf{L}_{1,5} = b$. If we construct a matrix model by grouping the population into "small" (age 1), "medium" (age 2–4), and "large" ($\geq$age 5) individuals, the matrix giving the transition rates for the population at stable age distribution is

$$\begin{bmatrix} 0 & 0 & b \\ S_J & \alpha & 0 \\ 0 & \beta & S_A \end{bmatrix}$$

where $\alpha = (S_J + S_J^2)/(1 + S_J + S_J^2)$, $\beta = S_J - \alpha$. For these matrices, it is straightforward to show that the 3 × 3 matrix assigns to "medium" individuals the actual reproductive value of age-2 individuals. So, rather than producing a "typical" reproductive value for medium-size individuals, the matrix model yields the actual reproductive value of the smallest individual in the size class. This particular example is extreme, but it underscores the point that grouping individuals into size

classes inevitably entails aggregation errors that will affect the final patterns.

When to use the integral projection model

The integral projection model has many of the same properties that have made the matrix projection model popular: approximation of the population growth rate, eigenvectors representing reproductive value and stable size distribution, and sensitivity analysis for changes in specific vital rates. Given these similarities, a decision of which kind of model to use for data fitting should be made based on the available data, the study system, and the goals of the study.

Available data.—The integral and matrix projection models are both adapted to fitting data on the observed fate of marked individuals between two census times. Both models are derived directly from the "rules" describing individual changes in state between one time period and the next, and the "rules" describing state-dependent fecundity (distribution of offspring number and size). The correspondence between the fitting problem and the data makes the fitting process relatively simple. For our monkshood study, the only statistical tools that we used were least squares and binary regression. Fitting continuous-time structured population models to discrete-time census data is a far more complex process (see e.g., Wood 1994, Ellner et al. 1997, Kendall et al. 1999). These models (partial differential equation, ordinary differential equation, delay differential equation, or the continuous-time integral projection model) are based on instantaneous process rates, while the data reveal the result of those processes acting over an extended period of time. Fitting these models, therefore, entails the rarely easy *inverse* problem of estimating instantaneous rate equations from finite-time outcomes (see Wood [1997] for a review).

Study system.—If the study population is structured by continuous individual-level state variables, without any natural breakpoints that can be used to define meaningful stage classes, then continuous-state models (integral projection or partial differential equation) correspond better to the biological reality than discrete-state models (matrix projection or ordinary differential equation). A "natural breakpoint" can be operationally defined in terms of the relationship between individual-level state variables and vital rates. If vital rates vary in a step-like manner (changing quickly over small regions of the individual-level state variables, and remaining relatively constant between these regions), then the "step" locations form a natural set of stage class boundaries. If the state-dependent variation in vital rates is smooth, the user of a continuous-state model can accurately represent that fact in the model, and, moreover, can exploit smoothness by using statistical techniques for optimizing the fit of smooth functions to data (e.g., Wahba 1990, Green and Silverman 1994). Relative to partial differential equation models, the integral projection model offers greater flexibility

in describing the distribution of size-dependent growth increments (see *Integral projection model*). If this unpredictable component of individual-state dynamics is small, or can be modeled well enough by adding a suitable diffusion-in-state term to a partial differential equation, the choice of models would be a matter of personal preference or convenience in fitting the data.

Goals.—The easiest model to fit and analyze is the discrete-state, discrete-time case: the matrix projection model. If that model gives you all that you need, there is no point in working any harder. The integral model and the matrix model give very similar estimates for the growth rates of the monkshood population, which are similar to Dixon and Cook's (1990) results, using a different set of stage boundaries in a matrix model. Simulation studies on a set of theoretical cases (Easterling 1998) also indicate that a matrix projection model estimates the population growth rate λ, as well as the integral projection model, and with no greater bias, even if vital rates vary smoothly with size. Population growth results from the aggregate (hence the average) net reproductive output of the entire population. One might expect that a matrix model will produce a "typical" reproductive value for individuals in a size category (e.g., the mean or something close to it), but this is not necessarily true. Nevertheless, the process of first averaging over individuals within classes to construct a matrix model appears to have little effect on the estimated growth rate.

However, the eigenvectors (reproductive value and stable state distribution) are about the state-dependent differences between individuals, as are the state-dependent sensitivities that are computed from the eigenvectors. In these, the difference between a matrix model and an integral model is clearly displayed.

The integral projection model also gives a more detailed depiction of state-dependent differences in reproductive value and stable frequency. The stable size distribution and reproductive value are smooth functions in the integral projection model (Fig. 4), while they are step functions in the matrix model. The matrix model only has a single reproductive value for each class. Sections of the reproductive value curve for monkshood are very steep in the integral model (e.g., sizes ranging 0.5–2 mm). The smallest and largest sizes in this range have very different reproductive values according to the model, and grouping them into one size category would lose this information. A larger matrix may come closer to representing this large change for individuals of similar sizes, but not without additional variance in parameter estimates, due to the reduced sample size in each class.

How to use the integral projection model

Several objectives must be reached before the integral model becomes a standard part of the experimental ecologist's toolkit. First, the merits of alternative ways of fitting the kernel need to be explored. With a matrix

model, one must arbitrarily break apart the size distribution, and then use data from each category for parameter estimation. This has two problems: categorization, and poor estimation of parameters in sparsely sampled categories. Both of these problems are overcome with an integral model. However, to construct an integral model one needs to define the size-dependent growth and survival functions. There are countless ways to estimate a probability density from sample data, and the conditional densities for individual size and offspring size are the essential components of the model. While these can be flexible (e.g., splines), any specific functional form is a construct laid over the real data, and, when data are sparse, it may be difficult to decide between alternative functional forms (of course, a similar comment applies to the choice of stage boundaries in a matrix model). In such cases, a user's best option would be to build a set of models with alternative functional forms, in order to verify that (for example) results are robust against departures from a Gaussian approximation to the conditional size distribution.

Second, the integral model should be expanded to other situations, such as a density-dependent model or a time-varying model. In principle these are straightforward, requiring only the addition of a covariate (e.g., density, rainfall) to each of the functions making up the kernel. In practice, the increased dimension will increase the data requirements for fitting the kernel.

Finally, the methods need to be readily available to any potential user with the appropriate data. The fitting and analysis are straightforward to code in a matrix language such as Matlab, GAUSS, or SAS IML, but a typical user may be deterred by the effort involved. As a step in that direction, Matlab code for the examples presented here is available, along with a users' manual (see the Supplementary Material). It is also possible to "trick" existing code for matrix projection models into producing numerical solutions for the integral model (we describe how to do this at the end of the Appendix and provide sample S-plus code in the Supplementary Material). This approach is computationally inefficient, but it may be the most attractive option at present for users who already have experience working with matrix models.

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APPENDIX

Methods for computing the dominant eigenvalue and eigenvectors may be found in ESA's Electronic Data Archive: *Ecological Archives* E081-007-A1.

SUPPLEMENTARY MATERIAL

Matlab code for the examples presented, along with a user's manual, is available in ESA's Electronic Data Archive: *Ecological Archives* E081-007-S1.