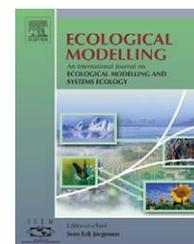


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# A semi-empirical growth estimation method for matrix models of endangered species

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## ARTICLE INFO

### Article history:

Received 3 December 2004

Received in revised form 25 October 2005

Accepted 15 November 2005

Published on line 28 December 2005

### Keywords:

Growth-transition matrix

Data poor

White abalone

Population viability analyses

Population dynamics

## ABSTRACT

Matrix models are critical for conservation planning of endangered species or any species with limited data. Sufficient growth data to construct growth-transition matrices required for size-structured population dynamics models may be lacking using traditional methods. We present a simple semi-empirical method for converting limited growth data into estimated transition probabilities required as elements in structured matrix models. Rather than approximating transition probabilities by counting actual transition frequencies between sparsely populated size classes, we assume that a selected function represents the entire data set, we obtain the model parameters by conventional curve fitting, and we construct the matrix model from the assumed model function. To illustrate the method, we use a sparse, scattered sample of growth data from the endangered white abalone. We use the slope and intercept of the von Bertalanffy model function to determine the growth-transition matrix elements, where the paucity and or scatter of the data preclude using the traditional counting method. The method we propose can accommodate both linear and non-linear mappings of size into growth rate, as we demonstrate with a Gaussian function which has been used to model growth of red abalone and red sea urchins. We illustrate how our method can convert confidence intervals from the model function into confidence intervals for the matrix elements. We suggest that this modelling procedure, which is simple to use and is suitable in data poor situations, will be broadly applicable for conservation practitioners in developing quantitative models to evaluate the population viability of endangered species.

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## 1. Introduction

Quantitative tools such as the suite of population viability analyses (PVA), including stage-structured matrix models, are now used in the conservation of endangered species (Caswell, 2001; Morris and Doak, 2002; Beissinger and McCullough, 2002). Elasticity analyses of matrix models can be conducted to determine which life stages and vital rates have the most

influence on population growth rate (de Kroon et al., 1986), an indicator of the life stages that recovery actions should target. Matrix models have been influential in shaping policy for a number of endangered species including the northern spotted owl (Lande, 1988), desert tortoise (Doak et al., 1994), and red cockaded woodpeckers (Heppell et al., 1994). The results and application of an elasticity analysis of a matrix model of loggerhead sea turtles are well documented (Crouse et al., 1987;

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doi:10.1016/j.ecolmodel.2005.11.019

Morris and Doak, 2002). Can these quantitative tools help us plan for the recovery of the endangered white abalone, *Haliotis sorenseni*, even when growth data are severely limited?

Abalone populations are declining around the world (Campbell, 2000; Shepherd et al., 2001). In California, depletion of the abalone complex has occurred (Dugan and Davis, 1993; Karpov et al., 2000; Rogers-Bennett et al., 2002) and the commercial fishery is now closed. White abalone were the first marine invertebrates to be listed as endangered, while black, *H. cracherodii*, and pinto abalone, *H. kamtschatkana*, are listed as species of concern. Today, white abalone are found only in remnant populations on deep offshore banks, having been nearly extirpated from their historic distribution by overfishing (Hobday et al., 2001; Lafferty et al., 2004). Recruitment failure has been observed (Davis, 1995; Rogers-Bennett et al., 2004) and recovery actions for this species are being considered by the NOAA Fisheries White Abalone Recovery Team, which is drafting a recovery plan. Quantitative analyses comparing the relative utility of recovery actions and the severity of threats would benefit the recovery planning process. These analyses, however, are hindered by a lack of size-specific vital rate data. Furthermore, for white abalone and many endangered species, collection of additional data may not be feasible.

While structured matrix models have aided in the management of some endangered species (Beissinger and Westphal, 1998), growth-transition data required to construct reliable size-based matrix models may be lacking. Meanwhile, identifying key life history stages to target recovery actions is crucial. Typically, growth information is obtained using tag-recapture data in which the numbers of organisms growing into the next stage (or size) or remaining in the current stage is observed (Caswell, 1989; Ebert, 1999). Growth transitions for endangered species, however, are likely to be based on data that are few and scattered. Small sample sizes can lead to sampling error when calculating growth transitions. Clumped data (e.g., data only for adults) can lead to distribution error. Low recapture rates or samples from limited portions of the size range make size class width selection difficult or arbitrary. Vandermeer (1978) and Moloney (1986) have developed algorithms that attempt to minimize sampling and distribution errors when selecting size class widths, but they do not solve them. In some cases, their algorithms suggest such small size class widths that the data for an endangered species cannot support them. Furthermore, Enright et al. (1995) demonstrated that the number of stage classes is important and can influence elasticity values.

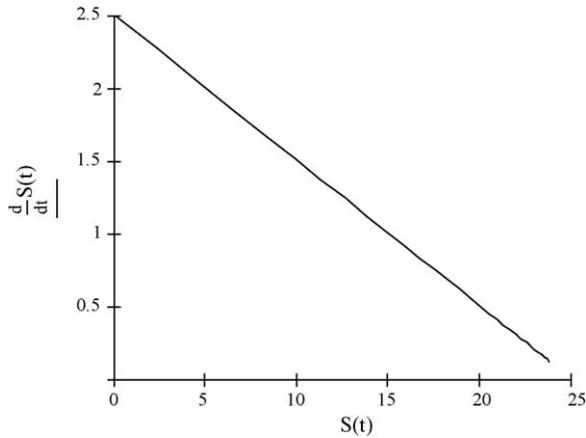
We present a semi-empirical method for extracting growth probabilities from an assumed mathematical model of growth as a function of size, which we call a “model function” as distinguished from the function obtained by empirical curve fitting. In the field of molecular modelling, purely theoretical models having no adjustable parameters lie at one end of the methodological spectrum and purely empirical curve fitting lies at the other. In between are semi-empirical models (Pople, 1999) consisting of theoretical models having one or more parameters that are determined by empirical comparison to experimental data. The method we present here is a semi-empirical treatment of a “poor” data set for white abalone, used because it is the only data set available or likely to be available in the foreseeable future.

In our method, the selected model function is assumed to represent a data set that may be sparse and scattered, for construction of structured matrix models of any dimension. We outline the mechanics of the modelling method using a hypothetical data set fitted by the simple first order von Bertalanffy growth model. As a practical application, we construct a size-based growth-transition matrix for the endangered white abalone which has model parameters that are identical to the hypothetical model population, but for which the actual growth data are limited. Growth transitions depend on the number of size classes selected (dimensions of the matrix) and is user defined to accommodate exploring stages (or sizes) at breaks relevant to life history or management and conservation planning. We show how the semi-empirical method can incorporate animal growth into more than one size class during a time step, as happens when the growth rate is larger than the class size interval. Finally, we describe how the modelling method can be used for non-linear growth models. As a practical application to a non-linear growth versus size model function, we treat growth data for the red abalone, *H. rufescens*, using a Gaussian function (Rogers-Bennett et al., in preparation). We illustrate how the 95% confidence limits from the model function generate upper and lower bounds of the growth-transition elements for use in elasticity analyses. We examine the benefits and assumptions inherent in the semi-empirical method.

## 2. Theory

We wish to determine the elements and uncertainties of a size-based growth-transition matrix from a distribution of animal growth versus size  $S(t)$  in which there are no age data, no discrete stages, and for which the data set is limited. We propose deriving the growth-transition probability matrix for a distribution over equal size classes of the rate of growth  $\frac{d}{dt}S(t)$  as a function of time  $t$  derived from an assumed model function fitted to tag-recapture data. The method involves finding the probability that an animal located anywhere in an earlier size class will make the transition to a later size class. Because it is based on a model function assumed to represent all data, the model function (as distinct from the data set) is not subject to some of the statistical problems (e.g., distribution error, stochasticity, and sampling error) that afflict the usual methods of determining growth transitions for a Lefkovich matrix (Caswell, 2001) from a limited number of growth frequencies.

Growth over a segment of the lifespan of an animal can be determined using the tag-recapture method by which the animal is captured at time  $t_1$  and marked so that at some later time  $t_2$  it can be identified and its growth over the interval  $(t_2 - t_1)$  can be determined. In general, the time of birth or larval settlement  $t_0$  is not known. Taking growth over, say, a 1-year interval, annual growth  $\Delta S(t)$  can be plotted against size at initial capture  $S(t_1)$  to yield a modified Walford plot (1946) as in Fig. 1. The Walford plot (Ebert, 1999) is a (presumed) linear approach of the function  $S(t+1)$  versus  $S(t)$  to the linear function  $S(t+1) = S(t)$ . In our modification of the Walford plot, we have subtracted  $S(t)$  from  $S(t+1)$  to obtain  $\Delta S(t)$  on the vertical axis in Fig. 1 while retaining  $S(t)$  as the variable on the horizontal axis. It is noteworthy that Walford considered only



**Fig. 1 – Growth as a function of abalone size (shell length). Five arbitrary size classes of 5 cm width leading to a 5 × 5 matrix are marked on the S(t) axis.**

growth data above the inflection point in the S(t) versus t curve (Walford, 1946).

The horizontal axis in Fig. 1 can be subdivided into size intervals, which, for simplicity, we shall take as equal. Adding a single observation of an animal’s annual growth to its initial size tells one whether the animal has progressed from its initial size class to the next higher class (or, occasionally, skipped one or more size classes).

Dividing the number of individuals that have progressed out of a size class by the number of individuals initially in that size class gives the frequency of transition from that class to the next. This frequency is often taken as a probability. Subtracting that probability from 1.0, gives the probability that an individual initially in the selected size class will stay there. These two probabilities are elements in the transition matrix.

By repeating this procedure over all size classes, one can construct a matrix with transition probabilities on the principal subdiagonal (or subdiagonals) and retention probabilities on the principal diagonal. Such a size-based growth-transition matrix is a (partial) Leslie or Lefkovich matrix (1965), shown as matrix 1, where  $r_1$  is the probability of retention in size class 1,  $g_2$  is the probability of growth into size class 2, and so on:

$$\mathbf{A} = \begin{pmatrix} r_1 & 0 & \dots & 0 & 0 \\ g_2 & r_2 & \dots & 0 & 0 \\ 0 & g_3 & \ddots & 0 & 0 \\ 0 & 0 & \ddots & r_{n-1} & 0 \\ 0 & 0 & \dots & g_n & r_n \end{pmatrix} \tag{1}$$

When the growth-transition matrix has been constructed, survival can be built into the model by multiplication of the growth transitions by the survival estimate. Fecundity information (the number of females produced by each female) can be included in the top row of the matrix. Non-zero fecundities lead to replenishment of the population through the smallest size class, augmenting the 1, 1 element of the matrix.

Once the final population matrix is constructed, it can then be multiplied into a population vector  $\mathbf{q}$ , consisting of a chosen population distribution of (in this case) five size classes, whereupon a new population vector is produced:

$$\mathbf{A}\mathbf{q}(t_2) = \mathbf{q}(t_3) \tag{2}$$

This process can be repeated indefinitely and if it is assumed that vital rates in the population matrix are constant over time, future population projections can be made (Caswell, 2001). The dominant eigenvalue of the matrix,  $\lambda$ , can be determined and if this is greater than 1.0 the model population is increasing. If it is less than 1.0, the model population is decreasing, given the assumptions made. Sensitivity and elasticity analyses can be obtained from the population matrix in order to examine which of the matrix elements has the most influence on population growth  $\lambda$ .

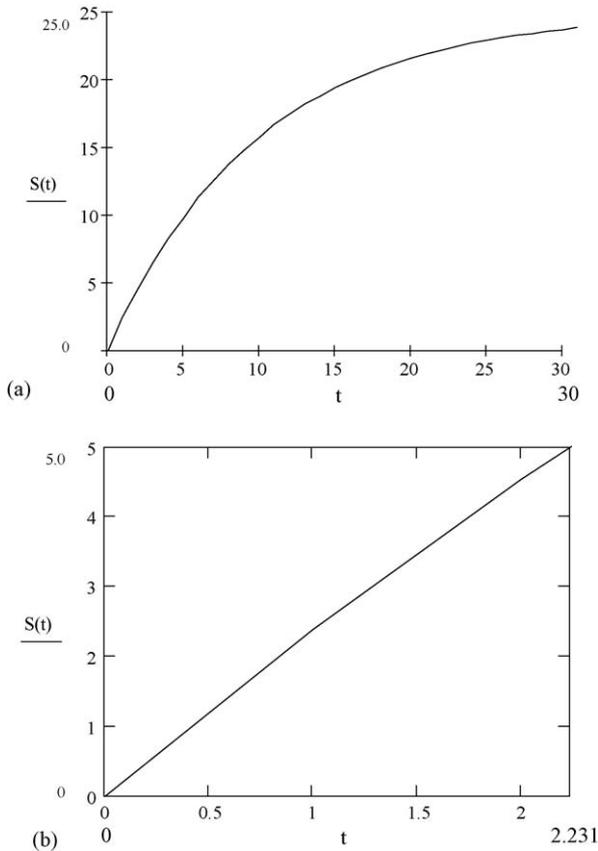
The method of tabulating growth transitions described above is not ideal. All valid criticisms involving treating a finite sample frequency distribution as though it were a probability distribution apply. In a finite sample of organism size, there will be an uneven size distribution within or among size classes, particularly in animals that exhibit pulsed settlement or reproduction. Sampling error can be serious in animals where an exposed part of the population may be over represented in the sample and a cryptic portion may be under represented. Moreover, criticisms of frequency distributions apply more to some size intervals than to others because there are fewer data points in some size intervals. Vandermeer (1978) and Moloney (1986) have proposed methods for minimizing errors arising from the arbitrary selection of size intervals (Caswell, 2001). In the semi-empirical method, a model function is assumed. None of the errors above exist within the model function, which is independent of the population. Once selected the model function is then made to coincide with the population as closely as possible by conventional fitting methods.

### 3. Methods and results

#### 3.1. The model function

We propose selecting a model function, locating it on the  $\Delta S(t)$  versus  $S(t)$  coordinate system by a conventional fitting procedure, then calculating the transition matrix from the fitted curve. The philosophy behind this approach is that a model function better represents the entire data set than transition frequencies taken from a small sample with sparsely populated size intervals. Selection of a model function is, itself, a profound assumption which includes, in an average way, several error sources.

For illustrative purposes, we shall imagine a hypothetical animal that grows over an ideal growth trajectory (see Fig. 2) of  $S(t)$  versus  $t$ , where  $S(t)$  is the size at time  $t$ , to a limiting size of  $S_\infty = 25.0$  cm at very long  $t$ . The animal is observed very many times (strictly, infinitely many) over its growth period. The model function also describes very many animals, evenly distributed over the size range and observed at time  $t_1$  and some later time  $t_2$ . We shall take the time interval  $t_2 - t_1$  as



**Fig. 2 – Size as a function of time over: (a) 30 years and (b) 2.23 years. The curve between  $t=0$  and 2.23 is not quite linear.**

1.00 year. In the discussion that follows, we shall imagine a single individual on an ideal growth trajectory or an infinite number of individuals on the same trajectory.

**3.2. The growth model**

Initially, let us choose the simple first order von Bertalanffy model function:

$$\frac{d}{dt}S(t) = -kS(t) \tag{3}$$

with a growth constant  $k=0.100 \text{ year}^{-1}$  that is not dependent on the time. We would first like to know how long it will take for a hypothetical animal to reach the upper limit of the first size class, 5.0 cm, starting from  $S(t)=0$ . The growth equation (Fabens, 1965; Ebert, 1999) is found by integrating Eq. (3):

$$S(t) = S_{\infty}(1 - e^{-kt}) = S_{\infty} - S_{\infty}e^{-kt}$$

that is,

$$\frac{S_{\infty} - S(t)}{S_{\infty}} = e^{-kt} \tag{4}$$

Having stipulated that  $S_{\infty} = 25.0 \text{ cm}$ ,  $k=0.100 \text{ year}^{-1}$ , and  $S(t)$  for the upper limit of the first size class as 5.0 cm, we have:

$$\frac{S_{\infty} - S(t)}{S_{\infty}} = e^{-kt} = \frac{25.0 - 5.0}{25.0} = e^{-0.100t}$$

or

$$\ln 0.800 = -0.2231 = -0.100t, \quad t = 2.231 \text{ years}$$

Because the von Bertalanffy model is linear in rate  $\frac{d}{dt}S(t)$  versus  $t$ , with a horizontal intercept at 25.0 cm and a slope of  $-0.100 \text{ year}^{-1}$ , the vertical intercept in Fig. 1 is 2.50 cm  $\text{year}^{-1}$ . The horizontal intercept is never reached because  $t$  is never  $t_{\infty}$ . For an animal that is exactly 5.00 cm at  $t=2.231$  years, we would like to know how big the animal was 1.00 years earlier. We find:

$$\begin{aligned} t &= 1.231 \text{ years} \\ 25.0 - S(t) &= 25.0e^{-0.1231} = 22.103 \\ S(t) &= 25.0 - 22.103 = 2.897 = 2.90 \text{ cm} \end{aligned}$$

The animal may be anywhere on the growth curve from 0 to 5.0 cm initially. We would like to know its probability of being close enough to the upper limit of 5.0 cm to make the transition into size class 2. Regarding the model function as representing many animals on the same growth curve (Fig. 2a and b), those with initial size greater than or equal to 2.90 cm will make it. Those with initial size less than 2.90 cm will not.

$$\begin{aligned} \frac{5.00 - 2.90}{5.00} &= 0.421 = 42\% \text{ make it;} \\ \frac{2.90}{5.00} &= 0.579 = 58\% \text{ do not make it.} \end{aligned}$$

These probabilities are the elements in the first column of the transition matrix:

$$\begin{pmatrix} .58 & \text{etc.} \\ .42 & \\ 0 & \\ 0 & \\ 0 & \text{etc.} \end{pmatrix}$$

We can check this result and see how to extend the method by looking at the curve of  $S(t)$  versus  $t$  between  $t=0$  and 30 years and between 0 and 2.3 years in Fig. 2a and b. Verticals drawn at  $t=1.2$  and 2.2 years intersect the growth curve at about  $S(t)=2.9$  and 5.0 cm. For more complicated functions, these points can be found using a commercial plotting or CAS program such as Mathcad@as in Fig. 2b.

For the time to grow to 10.0 cm, a similar calculation yields  $t_{2/5} = 5.108$  years and the completed probability calculation for  $t=4.108$  and 5.108 years, corresponding to sizes  $S(t)=8.41$  and 10.00 cm gives  $\frac{10.00-8.41}{5.00} = 0.32$  as the proportion of animals in the lower size class that make it into the higher class. This yields 0.68 and 0.32 as the diagonal and subdiagonal matrix elements in column 2 of the  $5 \times 5$  transition matrix. The remaining two calculations (exclusive of the 5, 5 element

which is 1 by definition) give the transition matrix:

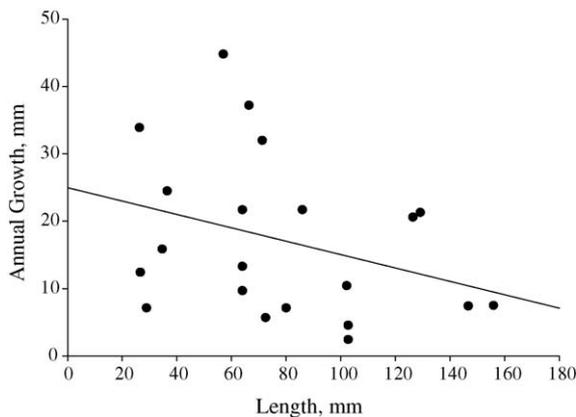
$$\begin{pmatrix} .58 & 0 & 0 & 0 & 0 \\ .42 & .68 & 0 & 0 & 0 \\ 0 & .32 & .79 & 0 & 0 \\ 0 & 0 & .21 & .89 & 0 \\ 0 & 0 & 0 & .11 & 1 \end{pmatrix} \tag{6}$$

The probability that an animal will progress from a lower size class to a higher size class (subdiagonal element) decreases as the animal ages. There is a corresponding increase in the probability that the animal will remain in its size class, ending up in the final size class from which the animal does not progress. These trends are smooth and monotonic for this model function because of the simple linear growth trend shown in Fig. 1 but they need not be either smooth or monotonic for other size class choices or other model functions (see below).

#### 4. Application: white abalone

Growth data for the endangered white abalone are shown in Fig. 3. The conventional least squares fit of the von Bertalanffy function to the data (Eq. (3), Fig. 1) is shown as a line through the points. Severe scatter is evident. One would be hesitant to rely on any single point or small group of points to determine characteristics of the sample, yet that is just what one does in determining transition probabilities using the traditional method by counting the number of abalone that make the transition from one arbitrarily defined size class to the next higher class.

The von Bertalanffy function produces a 5 × 5 transition matrix for this sample of white abalone that is identical to the hypothetical model matrix (matrix 6) with the exception that it is fitted to a very scattered data set rather than to an ideal hypothetical model. The point here is that if the slopes and intercepts of the (scaled) data set for white abalone or any



**Fig. 3 – Annual Growth vs. length (scaled from cm to mm) for a sample of N = 21 white abalone (Tutschulte, 1976). Although the data are scattered, the slope  $-0.0993 \text{ year}^{-1}$  and intercept 252 mm are statistically identical to the model population, hence the  $S(t)$  vs.  $t$  curves (Fig. 2) and transition matrices are the same (matrix 6).**

other data set are statistically identical, the growth curves and transition matrices will be the same no matter how much or little the data are scattered.

By contrast, the transition matrix obtained by the traditional (counting) method is matrix 7, which bears little resemblance to matrix 6 derived from the semi-empirical model function:

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 1 & .167 & 0 & 0 & 0 \\ 0 & .833 & .429 & 0 & 0 \\ 0 & 0 & .571 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 \end{pmatrix} \tag{7}$$

As we should expect, the probabilities are highly dependent upon the number of size classes chosen. For five equal size classes of 3.5 cm each, either the model population or the scattered sample of white abalone data yields the 5 × 5 matrix:

$$\begin{pmatrix} .35 & 0 & 0 & 0 & 0 \\ .65 & .46 & 0 & 0 & 0 \\ 0 & .54 & .56 & 0 & 0 \\ 0 & 0 & .44 & .67 & 0 \\ 0 & 0 & 0 & .33 & .77 \end{pmatrix} \tag{8}$$

The last element on the diagonal is not 1 because  $S_\infty$  is 252 and the categories only go up to 175.

For six equal size categories, covering the entire range from 0 to  $S_\infty = 25.2 \text{ cm}$  in Fig. 3, the categories should be 4.2 cm in width ( $6 \times 4.2 = 25.2$ ). This leads to the 6 × 6 transition matrix 9. Because the size intervals are smaller (4.2 cm as compared to 5.0 cm), the probabilities for transition from one size class to the next are greater in matrix 9 than they are in matrix 6. Other things being equal, the probabilities of retention in a smaller size class are less than they are in a larger size class:

$$\begin{pmatrix} .48 & 0 & 0 & 0 & 0 & 0 \\ .52 & .58 & 0 & 0 & 0 & 0 \\ 0 & .42 & .69 & 0 & 0 & 0 \\ 0 & 0 & .31 & .79 & 0 & 0 \\ 0 & 0 & 0 & .21 & .90 & 0 \\ 0 & 0 & 0 & 0 & .10 & 1 \end{pmatrix} \tag{9}$$

Calculation of a transition matrix for size classes that are unequal is a straightforward variation of the model method already described. Using the present method for size classes chosen as  $S(t) = 4.0, 4.0, 4.0, 6.5, 6.5 \text{ cm}$  in Fig. 1 (sum = 25.0 cm) gives transition matrix 10:

$$\begin{pmatrix} .45 & 0 & 0 & 0 & 0 \\ .55 & .55 & 0 & 0 & 0 \\ 0 & .45 & .66 & 0 & 0 \\ 0 & 0 & .34 & .89 & 0 \\ 0 & 0 & 0 & .11 & 1 \end{pmatrix} \tag{10}$$

In matrix 10, trends in the diagonal and subdiagonal elements are monotonic but not smooth because of the choice of the size classes.

**5. Transitions over more than one size class**

If the growth rate constant for the model is doubled to  $k=0.200\text{ year}^{-1}$  but all other characteristics of the model calculation are the same, Fig. 2b is altered to give a curve that is similar but twice as steep. One can determine the time necessary to cover the first 5.00 cm growth interval as 1.116 years and the size of the animal 1 year earlier as 0.57 cm. This leads to the 1, 1 and 2, 1 element in matrix 11 which take the values of 0.11 and 0.89, in which the augmented subdiagonal element reflects the increase in the growth constant:

$$\begin{pmatrix} .11 & 0 & 0 & 0 & 0 \\ .89 & .33 & 0 & 0 & 0 \\ 0 & .67 & .55 & 0 & 0 \\ 0 & 0 & .45 & .77 & 0 \\ 0 & 0 & 0 & .23 & 1 \end{pmatrix} \tag{11}$$

Matrix 11 should be compared with matrix 6 obtained at  $k=0.100\text{ year}^{-1}$ . The subdiagonal elements of matrix 11 decrease approximately linearly from left to right and they are slightly more than twice as large as the corresponding elements in matrix 6 (.89 compared to 2 (.42), etc.). They are not precisely double the subdiagonal elements in matrix 6 because the growth curve is not linear.

Increasing  $k$  to  $0.300\text{ year}^{-1}$  leads to 0.738 year necessary to reach the 5.00 barrier, that is, the probability of passing at least into the next class in 1 years is 1.0 with 0.26 years growth time "left over". This leads to a growth overflow into the third size class and a non-zero 3, 1 matrix element. If the growth curve were linear, we would expect a ratio of animals transferring from one size class to animals transferring to two classes to be about 0.74:0.26. Because of curvature, this expectation is nearly, but not quite true. When a curve is so steep, as in the case of the curve at  $k=0.300\text{ year}^{-1}$ , that the width of the size interval chosen is covered in less than 1 year, the amount of overflow can be calculated by drawing verticals at the lower and upper time limits of a 1.0 year time interval. Taking the ratio of growth beyond the upper limit to growth within the interval yields the subdiagonal and sub-subdiagonal elements in matrix 12.

According to the model function, the size is 6.53 cm at  $t=1.00$  years hence the ratio of animals transferring two classes to those transferring one class is  $6.53-5.00/5=0.31$  relative to 0.69. The ratio 0.69:0.31 is a refinement of the previous estimate of 0.74:0.26. The corresponding column 1 matrix elements are:

$$\begin{pmatrix} 0 & \text{etc.} \\ .69 \\ .31 \\ 0 \\ 0 & \text{etc.} \end{pmatrix} \tag{12}$$

Because the growth curve is so steep, small differences in choice of size versus growth time make a noticeable difference in the matrix. For example, if the growth model had produced  $S(t)=6.45\text{ cm}$  at  $t=1.00$  years, the 2, 1 and 3, 1 matrix elements would have been 0.71 and 0.29. Calculating elements in the second column in the same way as in the first, one arrives at 0.0, 0.71, and 0.29. The remaining elements are calculated as they were for matrix 6. The full matrix is:

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ .69 & 0 & 0 & 0 & 0 \\ .31 & .71 & .04 & 0 & 0 \\ 0 & .29 & .96 & .64 & 0 \\ 0 & 0 & 0 & .36 & 1 \end{pmatrix} \tag{13}$$

The growth parameter  $k=0.300\text{ year}^{-1}$  results in a sharp change-over from subdiagonal dominance to diagonal dominance as a result of the steep growth curve. The same feature brings about a sharp change between diagonal elements in the third and fourth columns showing that the system rapidly switches from growth to stasis in element 5, 5.

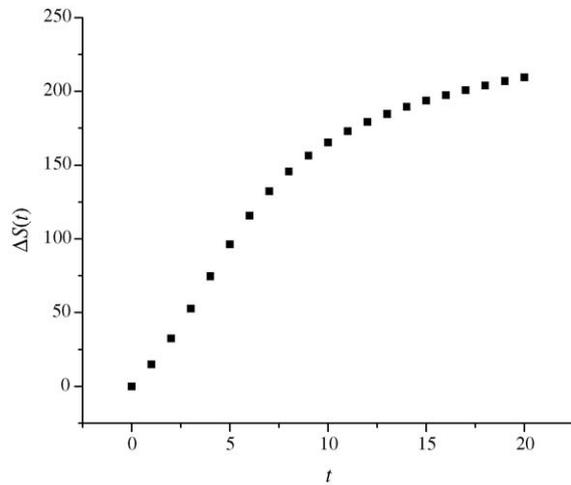
**6. Curvilinear functions: red abalone**

Functions that go through a maximum have been used to model growth (Rogers-Bennett et al., 2003) on the reasonable supposition that newly settled animals do not achieve their maximum growth immediately, but have a maximum growth rate sometime after birth (or settlement). The empirical fit of the Gaussian model function by a commercial curve fitting program (TableCurve®, www.systat.com) to tag-recapture data for both red and white abalone is shown in Fig. 5(top). It yields fitting parameters of peak height  $a=22.0\text{ mm year}^{-1}$  (maximum annual growth),  $\mu=62.0\text{ mm}$  (size at maximum growth), and  $\sigma=70.2\text{ mm}$  (standard deviation of annual growth away from its maximum value), for the red abalone sample ( $N=231$ ) and  $20.7\text{ mm year}^{-1}$ , 37.8, and  $80.7\text{ mm year}^{-1}$ , respectively, for the white abalone sample ( $N=21$ ):

$$\Delta S(t) = ae^{-(S-\mu)^2/2\sigma^2} \tag{14}$$

Fitting is by the Levenberg-Marquardt algorithm (Lourakis, 2005), which entails iterative solution of the normal equations arising from least squares successive approximations to the minimum sum of squares of residuals away from a non-linear function, the Gaussian in this case.

To obtain the  $S(t)$  versus  $t$  curve, we started at  $t=0$ ,  $S(t)\cong 0$ , and found  $\Delta S(t)=14.9$  by Eq. (14). The size at the end of 1 year is  $S(1)=14.9\text{ mm}$ . This value was substituted into Eq. (14) to give  $\Delta S(t)=17.6\text{ mm}$  for the second year, which was added to  $S(1)$  to give  $S(2)=32.5\text{ mm}$ . This recursive calculation was continued (by a simple program) to an arbitrary upper limit taken as  $S(\infty)=S_\infty$ , which was approximated by  $S(20)$  in this case. The result is 20 points on an  $S(t)$  versus  $t$  curve Fig. 4 which was roughly similar to Fig. 2a, but which showed an induction period near  $t=0$  giving a sigmoidal curve rather than the exponential limiting form as in Fig. 2a.



**Fig. 4 – A Gaussian model of red abalone growth shell length  $\Delta S(t)$  vs. time ( $t$ ) for abalone ( $N = 231$ ) growing 1 year in northern California (unpublished data, California Department of Fish and Game, Burge and Schultz).**

The  $S(t)$  versus  $t$  curve Fig. 4 was examined by using the Screen Reader option of TableCurve® (or Mathcad®) to yield precise beginning and end growth times of the curve at the limits imposed by size class selection (the vertical axis is taken to be a locus of points). With this information, we found the ratio of the probability that an animal grows from one size class to the next in the way already shown, except that for the abalone data sets, the size interval was taken as 5.0 cm. The 2, 1 sub-

diagonal element for the red abalone matrix treated here is:

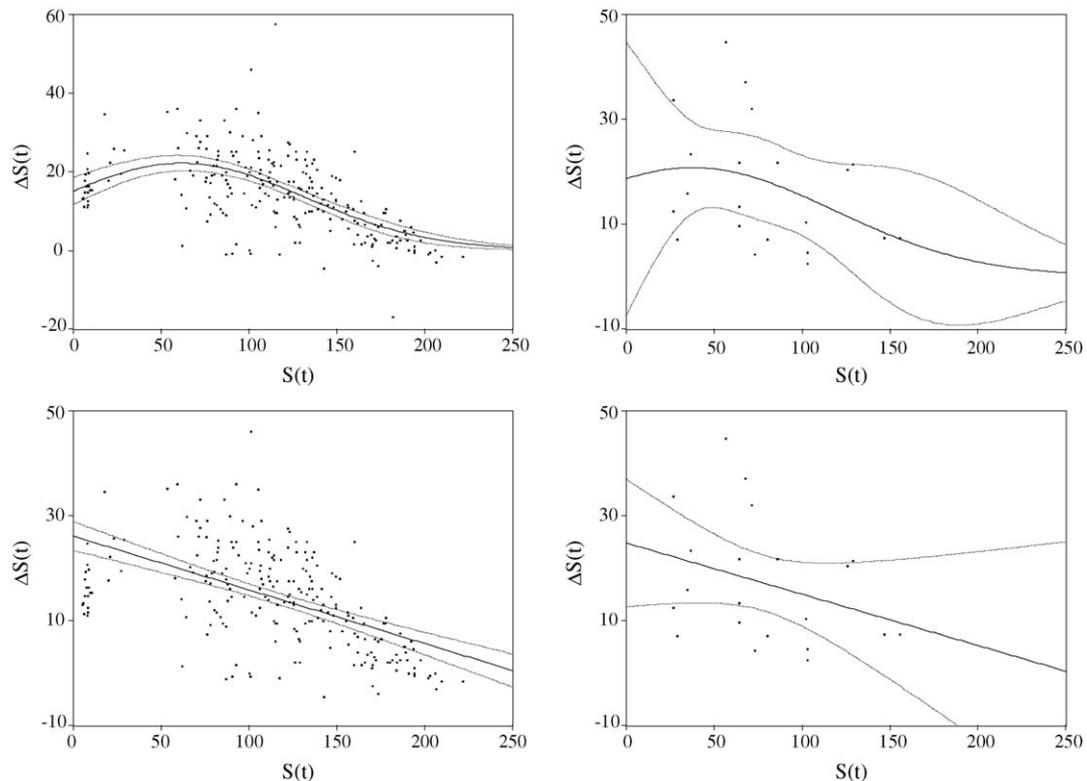
$$\frac{50.0 - S(t - 1)}{50.0} = \frac{50.0 - 30.1}{50} = 0.40$$

The full transfer matrix for this sample of red abalone by the Gaussian method is matrix 15:

$$\begin{pmatrix} .60 & 0 & 0 & 0 & 0 \\ .40 & .58 & 0 & 0 & 0 \\ 0 & .42 & .75 & 0 & 0 \\ 0 & 0 & .25 & .93 & 0 \\ 0 & 0 & 0 & .07 & 1 \end{pmatrix} \tag{15}$$

### 7. Curvilinear functions: white abalone

On the ground that red and white abalone are congeners and that the Gaussian function represents curvilinear red abalone growth (Fig. 5, top, left), it is reasonable to select it as a theoretical model function for white abalone. It is important to note that the data set is so “poor” that it forces neither the von Bertalanffy model nor the Gaussian model; we select the Gaussian function because it is plausible (Rogers-Bennett et al., 2003, in preparation). Data from well-known congeners have been used in lieu of data for lesser known endangered species (Caswell et al., 1998). It is when we fix the parameters  $a$ ,  $\mu$ , and  $\sigma$  by an empirical curve fitting routine (Lourakis, 2005) that the model becomes semi-empirical (Pople, 1999). The final curve has an empirical component because of the parameter fit, but it is semi-empirical because the theoretical function



**Fig. 5 – Gaussian models (top) and von Bertalanffy models (bottom) for the samples of red abalone,  $N = 231$  (left) and white abalone,  $N = 21$  (right) (Tutschulte, 1976) discussed in the text.**

was selected before infusion of empirical data into the model. The model function is independent of the data set but the parameters are not.

## 8. Confidence limits and summary of results

Using the *Interval* option of TableCurve® one can find the 95% confidence limit curves above and below the  $\Delta S(t)$  versus  $S(t)$  curve for model functions. Using the *Screen Reader* option, three numbers can be found, the value of the function at some specific  $S(t)$ , say the midpoint of the first size interval, and the upper and lower confidence limits on  $\Delta S(t)$  at that  $S(t)$ . For example, the upper 95% confidence limit is 2.3 mm year<sup>-1</sup> or 12% higher than  $\Delta S(t) = 19.2$  mm year<sup>-1</sup> at the midpoint of the first size category of the Gaussian model function for red abalone (Fig. 5, top, left).

We shall take confidence limits as being approximately symmetrical about the function so the lower confidence limit is  $\sim 2.3$  mm year<sup>-1</sup> below the central value. Thinking in terms of very many individuals progressing along the model function curve, an increase in speed of 12% will enable 12% more of them to cross the boundary from the first size class to the second than if the growth rate were exactly given by the model function. Therefore, the subdiagonal matrix element will be augmented by 12% and the element on the principal diagonal will be decremented by the same amount. A comparable calculation yields both the upper and lower confidence limits of all of the matrix elements except the 5, 5 element which is 1. For both confidence limits, the subdiagonal elements will be incremented or decremented within a range of  $0.12 \times 0.40 = 0.05$  ( $\pm 0.05$ ) and the diagonal element will be decremented or incremented ( $\mp 0.05$ ) by the same amount. These confidence limits pertain to the 1, 1 element in matrix 16.

The resulting transfer matrices are matrices 16–19, where **GR**, **BW**, **BR**, and **GW** designate Gaussian red, Bertalanffy white, Bertalanffy red, and Gaussian white, respectively.

$$\mathbf{GR} = \begin{pmatrix} .60 \mp .05 & 0 & 0 & 0 & 0 \\ .40 \pm .05 & .58 \mp .03 & 0 & 0 & 0 \\ 0 & .42 \pm .03 & .75 \mp .02 & 0 & 0 \\ 0 & 0 & .25 \pm .02 & .93 \mp .02 & 0 \\ 0 & 0 & 0 & .07 \pm .02 & 1 \end{pmatrix} \quad (16)$$

$$\mathbf{BW} = \begin{pmatrix} .58 \mp .17 & 0 & 0 & 0 & 0 \\ .42 \pm .17 & .68 \mp .10 & 0 & 0 & 0 \\ 0 & .32 \pm .10 & .79 \mp .14 & 0 & 0 \\ 0 & 0 & .21 \pm .14 & .89 \mp .20 & 0 \\ 0 & 0 & 0 & .11 \pm .20 & 1 \end{pmatrix} \quad (17)$$

$$\mathbf{BR} = \begin{pmatrix} .58 \mp .04 & 0 & 0 & 0 & 0 \\ .42 \pm .04 & .68 \mp .02 & 0 & 0 & 0 \\ 0 & .32 \pm .02 & .79 \mp .02 & 0 & 0 \\ 0 & 0 & .21 \pm .02 & .89 \mp .02 & 0 \\ 0 & 0 & 0 & .11 \pm .02 & 1 \end{pmatrix} \quad (18)$$

$$\mathbf{GW} = \begin{pmatrix} .52 \mp .26 & 0 & 0 & 0 & 0 \\ .48 \pm .26 & .67 \mp .16 & 0 & 0 & 0 \\ 0 & .33 \pm .16 & .79 \mp .15 & 0 & 0 \\ 0 & 0 & .21 \pm .15 & .93 \mp .17 & 0 \\ 0 & 0 & 0 & .07 \pm .17 & 1 \end{pmatrix} \quad (19)$$

Not surprisingly, the matrix elements are very similar for analysis of the two congeners. Indeed, ignoring confidence limits, **BW** = **BR**. There is little to choose between the models, i.e., the data set does not force either model function (the apparent quality of a von Bertalanffy representation of growth curves that go through a maximum is somewhat deceptive, as shown by Rogers-Bennett et al., 2003). The striking differences among the transfer matrices is not in their elements but rather in their uncertainties as seen by contrasting the red and white matrices 16 and 18 with matrices 17 and 19. This is, off course, a reflection of the difference in quality of the two data sets, red and white.

The matrices for white abalone are similar to each other but quite different from the matrix found by the counting method (matrix 7). The point is that for a poor data set, either model function, or presumably any plausible model function, is a better method of obtaining a self-consistent growth-transition matrix than the counting method. The counting method for red abalone produces matrix 20. Other than the 1, 1 and 2, 1 elements, matrix 20 begins to approximate matrices 16 and 18, which is not surprising for a larger and “better” data set.

$$\begin{pmatrix} .91 & 0 & 0 & 0 & 0 \\ .09 & .53 & .01 & 0 & 0 \\ 0 & .47 & .68 & 0 & 0 \\ 0 & 0 & .30 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} \quad (20)$$

## 9. Discussion

We have presented a simple method for calculating growth transitions using a model of growth fitted to tag-recapture data to construct a size-based matrix model. Assuming the model function, we circumvent problems like sampling and distribution error that have previously been minimized, but not eliminated, by the Vandermeer–Moloney algorithms. We do this by making the sweeping assumption that our model is a good representation of the data set. The transition matrix resulting from data sets with the same slope and intercept will be identical regardless of the scatter. We demonstrate how this method can be used for sparse data sets frequently associated with endangered species.

Our method is simple and yet flexible enough to accommodate matrices of varying sizes. In general, the smaller the size class the faster animals will transition out of size classes, whereas for larger size classes the probability of retention within the size class increases. Since size class width can have an impact on elasticity values of various matrix elements (Enright et al., 1995) these decisions of matrix size play an important role in conservation policy decisions. This method allows for the creation of multiple matrices of var-

ious size class widths, to examine the influence of matrix size, without being constrained by the limits of the data set. Furthermore, matrices which incorporate natural break points and sizes of importance for managers (e.g., minimum legal sizes for exploited species) can be explored freely without being constrained by limitations of the data set. Our method also allows for incorporation of confidence limits for each of the matrix elements relative to the model function. Conducting parameter uncertainty analyses is very helpful in setting future research priorities to target parameters which strongly influence model outcomes (Hunter et al., 2000).

Working from a model of growth is an improvement over the traditional method of obtaining growth transitions for matrices by observing the number of animals that grow out of or remain within a size class (Rogers-Bennett and Leaf, 2006). In a sparse data set, a change in one data point using the traditional method can have a large impact on the transition probabilities. In some cases, changes in survival transitions (which include both growth and survival in stage-based models) can have a large impact on elasticity values (Ebert, 1998) and consequently management decisions derived from the analysis. This is a highly undesirable feature of the traditional observation method and one that is eliminated by the model function method presented here.

Given the limitations of the traditional method other methods have been proposed to determine growth transitions, such as the direct estimation method (DEM) (Nichols et al., 1992). The DEM method, however, requires substantial amounts of data to estimate transition probabilities (survival combined with growth) between size classes. Alternatively, data from well-studied similar species can be used (Caswell et al., 1998), although selection of “similar” species is arbitrary (Heppell et al., 2000). Another method, the integral projection model, avoids the problems associated with dividing continuous variables such as age and size into discrete classes (Easterling et al., 2000), however, application of this method may be computationally challenging.

In principle, any statistical method can be used for estimating projection matrix parameters, whether the data set is rich or sparse. For example Lefkovich (1965) first proposed a regression method to aid in the estimation of growth and survival rates when there were limited data. Caswell and Tombley (1989) used this method in stage-based matrix models for estimating zooplankton demographic parameters. Caswell (2001) notes, however, that results are subject to unknown bias in data sparse situations. Davis (1995) has proposed a maximum likelihood method of data treatment. Values of the matrix parameters are estimated by searching for those that maximize the probability of seeing the results obtained experimentally over the time period. This method requires estimates of initial values of the parameters.

An iterative method for estimating growth and survival has also been suggested by Caswell (1989) for populations that are best described by stages of fixed duration. In this method, an initial population growth rate ( $\lambda$ ) is proposed and the matrix elements are computed from it. Next  $\lambda$  is changed for the new matrix and the process is repeated until the coefficients of the matrix are compatible with their eigenvalues. Growth-transition matrices have been estimated using von Bertalanffy

growth parameters for green sea urchins which are the basis of an important fishery in Maine (Chen et al., 2003).

Federico and Canziani (2005) describe a deterministic stage-based matrix model for the South American capybara (the largest living rodent) and they investigate the influence of different harvesting strategies on this population. Much of this work is preliminary, as the vital rates are, at present not known, however, early publication of this model is appropriate because resource managers need tools to aid in developing a management plan prior to exploitation (Federico and Canziani, 2005).

We suggest our method is simple and broadly applicable for generating growth information required for the construction of transition matrices for species with minimal data and for which size is a good predictor of vital rate. Tagging and recapture studies for endangered species, such as the white abalone, may be problematic since they may induce mortality and as such would not be recommended simply to improve growth data for quantitative modelling. Nevertheless quantitative modelling results are valuable (Heppell et al., 2000) and desperately needed for conservation and recovery planning (Gerber and Hatch, 2002; Morris et al., 2002). Consequently, we propose the semi-empirical modelling method presented here may be useful for constructing growth-transition matrices of endangered species or any species with limited data.

## Acknowledgements

We thank the NOAA White Abalone Recovery Team and their coordinator Melissa Neuman for encouraging us with this project. This publication was supported in part by the National Sea Grant College Program of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration under NOAA, Grant #NAO4OAR4170038, Project #RF-198, through the California Sea Grant Program; and in part by the California State Resources Agency. The views expressed here do not necessarily reflect the views of any of these organizations. Partial support was provided by the California Department of Fish and Game Marine Region. Special thanks to K. Rogers and Suzie's. Contribution #2288 Bodega Marine Laboratory, University of California, Davis.

## REFERENCES

- Beissinger, S., McCullough, D. (Eds.), 2002. Population Viability Analysis. University of Chicago Press, Chicago, Illinois, USA.
- Beissinger, S., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. *J. Wildl. Manage.* 62, 821–841.
- Campbell, A. (Ed.), 2000. Workshop on Rebuilding Abalone Stocks in British Columbia, vol. 130. Canadian Special Publication Fisheries Aquatic Sciences, pp. 1–150.
- Caswell, H., 1989. Matrix Population Models: Construction, Analysis and Interpretation. Sinauer, Sunderland.
- Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation, second ed. Sinauer, USA, 722 pp.
- Caswell, H., Tombley, S., 1989. Estimation of stage-specific demographic parameters for zooplankton populations: methods based on stage classified matrix projection models.

- In: MacDonald, L., Manley, B., Lockwood, J., Logan, J. (Eds.), Estimation and Analysis of Insect Populations. Springer-Verlag, New York, NY, pp. 93–107.
- Caswell, H., Brault, S., Read, A.J., Smith, T.D., 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. *Ecol. Appl.* 8, 1226–1238.
- Chen, Y., Hunter, M., Vadas, R., Beal, B., 2003. Developing a growth-transition matrix for the stock assessment of the green sea urchin (*Strongylocentrotus dorebachiensis*) off Maine. *Fishery Bull.* 101, 737–744.
- Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68, 1412–1423.
- Davis, G.E., 1995. Recruitment of juvenile abalone (*Haliotis* spp.) measured in artificial habitats. *Mar. Freshwater Res.* 46, 549–554.
- de Kroon, H., Plaiser, A., van Groenendael, J., Caswell, H., 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67, 1427–1431.
- Doak, D., Kareiva, P., Klepetka, B., 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. *Ecol. Appl.* 4, 446–460.
- Dugan, J.E., Davis, G.E., 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fisheries Aquat. Sci.* 50, 2029–2042.
- Easterling, M.R., Ellner, S.P., Dixon, P.M., 2000. Size-specific sensitivity: applying a new structured population model. *Ecology* 81, 694–708.
- Ebert, T.A., 1998. An analysis of the importance of Allee effects in management of the red sea urchin *Strongylocentrotus franciscanus*. In: Mooi, T. (Ed.), *Echinoderms*. Balkema, San Francisco, Rotterdam, pp. 619–627.
- Ebert, T.A., 1999. *Plant and Animal Populations*. Academic Press, San Diego, USA, 312 pp.
- Enright, N.J., Franco, F., Silvertown, J., 1995. Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. *Oecologia* 104, 79–84.
- Fabens, A.S., 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 104, 265–289.
- Federico, P., Canziani, G.A., 2005. Modeling the population dynamics of capybara *Hydrochaeris hydrochaeris*: a first step towards a management plan. *Ecol. Modell.* 186, 111–121.
- Gerber, L.E., Hatch, L.T., 2002. Are we recovering? An evaluation of recovery criteria under the U.S. Endangered Species Act. *Ecol. Appl.* 12, 668–673.
- Heppell, S.S., Walters, J.R., Crowder, L.B., 1994. Evaluating management alternatives for red-cockaded woodpeckers—a modeling approach. *J. Wildl. Manage.* 58, 479–487.
- Heppell, S.S., Caswell, H., Crowder, L.B., 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81, 654–665.
- Hobday, A.J., Tegner, M.J., Haaker, P.L., 2001. Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Rev. Fish Biol. Fisheries* 10, 493–514.
- Hunter, C.M., Moller, H., Fletcher, D., 2000. Parameter uncertainty and elasticity analyses of a population model: setting research priorities for shearwaters. *Ecol. Modell.* 134, 299–323.
- Karpov, K.A., Haaker, P.L., Taniguchi, I.K., Rogers-Bennett, L., 2000. Serial depletion and the collapse of the California abalone (*Haliotis* spp.) fishery. *Can. J. Fisheries Aquat. Sci.* 130, 11–24.
- Lafferty, K.D., Behrens, M.D., Davis, G.E., Haaker, P.L., Kushner, D.J., Richards, D.V., Taniguchi, I.K., Tegner, M.J., 2004. Habitat of endangered white abalone, *Haliotis sorenseni*. *Biol. Conserv.* 116, 191–194.
- Lande, R., 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75, 601–607.
- Lefkovich, L.P., 1965. The study of population growth in organisms grouped by stages. *Biometrics* 21, 1–18.
- Lourakis, M.I.A., 2005. A Brief Description of the Levenberg–Marquardt Algorithm Implemented by Levmar (<http://scholar.google.com> search; levmar); also [www.ics.forth.gr/~lourakis/levmar](http://www.ics.forth.gr/~lourakis/levmar) link:note.
- Moloney, K.A., 1986. A generalized algorithm for determining category size. *Oecologia* 69, 176–180.
- Morris, W.F., Doak, D.F., 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, USA, 480 pp.
- Morris, W.F., Bloch, P.L., Hudgens, B.R., Moyle, L.C., Stinchcombe, J.R., 2002. Population viability analysis in endangered species recovery plans: past use and future plans. *Ecol. Appl.* 12, 708–712.
- Nichols, J.D., Sauer, J.R., Pollock, K.H., Hestbeck, J.B., 1992. Estimating transition probabilities for stage-based population projection matrices using capture–recapture data. *Ecology* 73, 306–312.
- Pople, J.A., 1999. Quantum chemical models. Nobel prize address December 1998. *Rev. Mod. Phys.* 71, 1267–1274.
- Rogers-Bennett, L., Leaf, R.T., 2006. Elasticity analyses of size-based red and white abalone matrix models: management and conservation. *Ecol. Appl.* 16, 213–224.
- Rogers-Bennett, L., Haaker, P.A., Huff, T.O., Dayton, P.K., 2002. Estimating baseline abundances of abalone in California for restoration. *CalCOFI Rep.* 43, 97–111.
- Rogers-Bennett, L., Rogers, D.W., Bennett, W.A., Ebert, T.A., 2003. Modeling red sea urchin (*Strongylocentrotus franciscanus*) growth using six growth functions. *Fishery Bull.* 101, 614–626.
- Rogers-Bennett, L., Allen, B.L., Davis, G.E., 2004. Measuring abalone (*Haliotis* spp.) recruitment in California to examine recruitment overfishing and recovery criteria. *J. Shellfish Res.* 23, 1201–1207.
- Rogers-Bennett, L., Rogers, D.W., Schultz, S.A. Modeling Growth and Mortality of Red Abalone (*Haliotis rufescens*) in Northern California, in preparation.
- Shepherd, S.A., Rodda, K.R., Vargas, K.M., 2001. A chronicle of collapse in two abalone stocks with proposals for precautionary management. *J. Shellfish Res.* 20, 843–856.
- Tutschulte, T.C., 1976. *The Comparative Ecology of Three Sympatric Abalones*. Dissertation U.C. San Diego, CA, USA, 335 pp.
- Vandermeer, J., 1978. Choosing category size in a stage projection matrix. *Oecologia* 32, 79–84.
- Walford, L.A., 1946. A new graphic method of describing the growth of animals. *Biol. Bull.* 90, 141–147.