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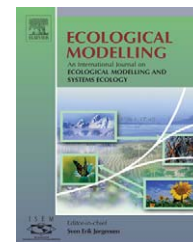
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A semi-empirical growth estimation method for matrix models of endangered species

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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 log-head sea turtles are well documented (Crouse et al., 1987;

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

19 Abalone populations are declining around the world
20 (Campbell, 2000; Shepherd et al., 2001). In California, deple-
21 tion of the abalone complex has occurred (Dugan and Davis,
22 1993; Karpov et al., 2000; Rogers-Bennett et al., 2002) and the
23 commercial fishery is now closed. White abalone were the
24 first marine invertebrates to be listed as endangered, while
25 black, *H. cracherodii*, and pinto abalone, *H. kamtschatkana*, are
26 listed as species of concern. Today, white abalone are found
27 only in remnant populations on deep offshore banks, having
28 been nearly extirpated from their historic distribution by over-
29 fishing (Hobday et al., 2001; Lafferty et al., 2004). Recruitment
30 failure has been observed (Davis, 1995; Rogers-Bennett et al.,
31 2004) and recovery actions for this species are being consid-
32 ered by the NOAA Fisheries White Abalone Recovery Team,
33 which is drafting a recovery plan. Quantitative analyses com-
34 paring the relative utility of recovery actions and the severity
35 of threats would benefit the recovery planning process. These
36 analyses, however, are hindered by a lack of size-specific vital
37 rate data. Furthermore, for white abalone and many endan-
38 gered species, collection of additional data may not be feasible.

39 While structured matrix models have aided in the manage-
40 ment of some endangered species (Beissinger and Westphal,
41 1998), growth-transition data required to construct reliable
42 size-based matrix models may be lacking. Meanwhile, iden-
43 tifying key life history stages to target recovery actions is
44 crucial. Typically, growth information is obtained using tag-
45 recapture data in which the numbers of organisms growing
46 into the next stage (or size) or remaining in the current stage
47 is observed (Caswell, 1989; Ebert, 1999). Growth transitions for
48 endangered species, however, are likely to be based on data
49 that are few and scattered. Small sample sizes can lead to
50 sampling error when calculating growth transitions. Clumped
51 data (e.g., data only for adults) can lead to distribution error.
52 Low recapture rates or samples from limited portions of the
53 size range make size class width selection difficult or arbitrary.
54 Vandermeer (1978) and Moloney (1986) have developed algo-
55 rithms that attempt to minimize sampling and distribution
56 errors when selecting size class widths, but they do not solve
57 them. In some cases, their algorithms suggest such small size
58 class widths that the data for an endangered species cannot
59 support them. Furthermore, Enright et al. (1995) demonstrated
60 that the number of stage classes is important and can influ-
61 ence elasticity values.

62 We present a semi-empirical method for extracting growth
63 probabilities from an assumed mathematical model of growth
64 as a function of size, which we call a “model function” as
65 distinguished from the function obtained by empirical curve
66 fitting. In the field of molecular modelling, purely theoretic-
67 al models having no adjustable parameters lie at one end
68 of the methodological spectrum and purely empirical curve
69 fitting lies at the other. In between are semi-empirical mod-
70 els (Pople, 1999) consisting of theoretical models having one
71 or more parameters that are determined by empirical com-
72 parison to experimental data. The method we present here
73 is a semi-empirical treatment of a “poor” data set for white
74 abalone, used because it is the only data set available or likely
75 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 Berta-
lanffy 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 conserva-
tion planning. We show how the semi-empirical method can
incorporate animal growth into more than one size class dur-
ing a time step, as happens when the growth rate is larger
than the class size interval. Finally, we describe how the mod-
elling 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 ani-
mal growth versus size $S(t)$ in which there are no age data, no
discrete stages, and for which the data set is limited. We pro-
pose 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 func-
tion 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 sub-
ject to some of the statistical problems (e.g., distribution error,
stochasticity, and sampling error) that afflict the usual meth-
ods of determining growth transitions for a Lefkovitch 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 ani-
mal 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) lin-
ear 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 ver-
tical axis in Fig. 1 while retaining $S(t)$ as the variable on the
horizontal axis. It is noteworthy that Walford considered only

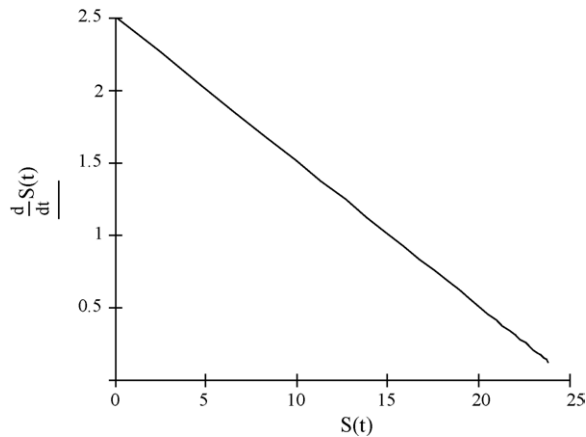


Fig. 1 – Growth as a function of abalone size (shell length). Five arbitrary size classes of 5 cm width leading to a 5×5 matrix are marked on the $S(t)$ axis.

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:

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

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, λ , 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 λ .

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

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 Lefkovitch 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:

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

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.

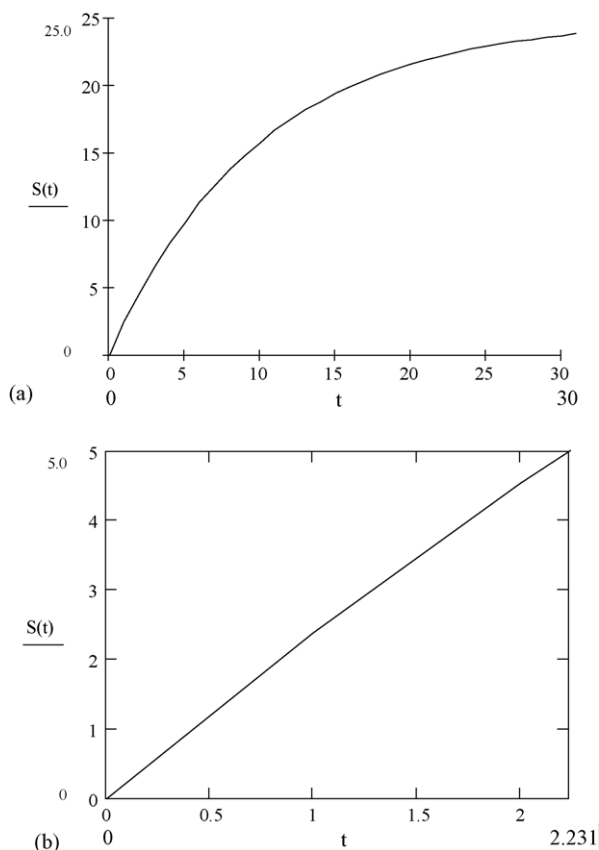


Fig. 2 – Size as a function of time over: (a) 30 years and (b) 2.23 years. The curve between $t=0$ and 2.23 is not quite linear.

215 1.00 year. In the discussion that follows, we shall imagine a
 216 single individual on an ideal growth trajectory or an infinite
 217 number of individuals on the same trajectory.

218 **3.2. The growth model**

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

221
$$\frac{d}{dt}S(t) = -kS(t) \tag{3}$$

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

227
$$S(t) = S_{\infty}(1 - e^{-kt}) = S_{\infty} - S_{\infty}e^{-kt}$$

228 that is,

229
$$\frac{S_{\infty} - S(t)}{S_{\infty}} = e^{-kt} \tag{4}$$

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

232
$$\frac{S_{\infty} - S(t)}{S_{\infty}} = e^{-kt} = \frac{25.0 - 5.0}{25.0} = e^{-0.100t}$$

233 or

234
$$\ln 0.800 = -0.2231 = -0.100t, \quad t = 2.231 \text{ years}$$

235 Because the von Bertalanffy model is linear in rate $\frac{d}{dt}S(t)$
 236 versus t , with a horizontal intercept at 25.0 cm and a slope of
 237 -0.100 year^{-1} , the vertical intercept in Fig. 1 is 2.50 cm year^{-1} .
 238 The horizontal intercept is never reached because t is never
 239 t_{∞} . For an animal that is exactly 5.00 cm at $t=2.231$ years, we
 240 would like to know how big the animal was 1.00 years earlier.
 241 We find:

242
$$t = 1.231 \text{ years}$$

$$25.0 - S(t) = 25.0e^{-0.1231} = 22.103$$

$$S(t) = 25.0 - 22.103 = 2.897 = 2.90 \text{ cm}$$

243 The animal may be anywhere on the growth curve from
 244 0 to 5.0 cm initially. We would like to know its probability of
 245 being close enough to the upper limit of 5.0 cm to make the
 246 transition into size class 2. Regarding the model function as
 247 representing many animals on the same growth curve (Fig. 2a
 248 and b), those with initial size greater than or equal to 2.90 cm
 249 will make it. Those with initial size less than 2.90 cm will not.
 250

251
$$\frac{5.00 - 2.90}{5.00} = 0.421 = 42\% \text{ make it;}$$

$$\frac{2.90}{5.00} = 0.579 = 58\% \text{ do not make it.}$$

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

254
$$\begin{pmatrix} .58 & \text{etc.} \\ .42 \\ 0 \\ 0 \\ 0 & \text{etc.} \end{pmatrix}$$

255 We can check this result and see how to extend the method
 256 by looking at the curve of $S(t)$ versus t between $t=0$ and 30 years
 257 and between 0 and 2.3 years in Fig. 2a and b. Verticals drawn at
 258 $t=1.2$ and 2.2 years intersect the growth curve at about $S(t)=2.9$
 259 and 5.0 cm. For more complicated functions, these points can
 260 be found using a commercial plotting or CAS program such as
 261 Mathcad@as in Fig. 2b.

262 For the time to grow to 10.0 cm, a similar calculation yields
 263 $t_{2/5} = 5.108$ years and the completed probability calculation for
 264 $t=4.108$ and 5.108 years, corresponding to sizes $S(t)=8.41$ and
 265 10.00 cm gives $\frac{10.00-8.41}{5.00} = 0.32$ as the proportion of animals
 266 in the lower size class that make it into the higher class.
 267 This yields 0.68 and 0.32 as the diagonal and subdiagonal
 268 matrix elements in column 2 of the 5×5 transition matrix.
 269 The remaining two calculations (exclusive of the 5, 5 element
 270

270 which is 1 by definition) give the transition matrix:

$$271 \begin{pmatrix} .58 & 0 & 0 & 0 & 0 \\ .42 & .68 & 0 & 0 & 0 \\ 0 & .32 & .79 & 0 & 0 \\ 0 & 0 & .21 & .89 & 0 \\ 0 & 0 & 0 & .11 & 1 \end{pmatrix} \quad (6)$$

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

4. Application: white abalone

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

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

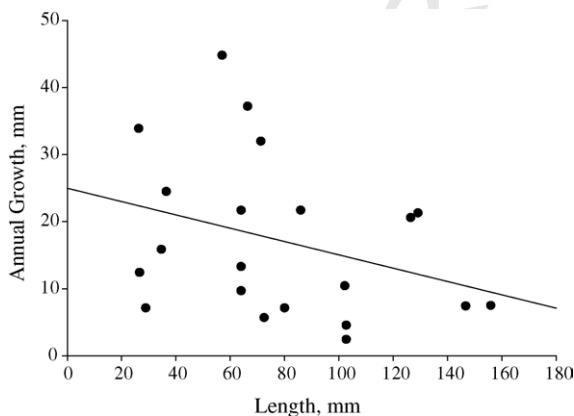


Fig. 3 – Annual Growth vs. length (scaled from cm to mm) for a sample of $N=21$ white abalone (Tutschulte, 1976). Although the data are scattered, the slope $-0.0993 \text{ year}^{-1}$ and intercept 252 mm are statistically identical to the model population, hence the $S(t)$ vs. t curves (Fig. 2) and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

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

301 By contrast, the transition matrix obtained by the tradi-
302 tional (counting) method is matrix 7, which bears little resem-
303 blance to matrix 6 derived from the semi-empirical model
304 function:

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 1 & .167 & 0 & 0 & 0 \\ 0 & .833 & .429 & 0 & 0 \\ 0 & 0 & .571 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 \end{pmatrix} \quad (7) \quad 305$$

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

$$\begin{pmatrix} .35 & 0 & 0 & 0 & 0 \\ .65 & .46 & 0 & 0 & 0 \\ 0 & .54 & .56 & 0 & 0 \\ 0 & 0 & .44 & .67 & 0 \\ 0 & 0 & 0 & .33 & .77 \end{pmatrix} \quad (8) \quad 310$$

311 The last element on the diagonal is not 1 because S_∞ is 252
312 and the categories only go up to 175.

313 For six equal size categories, covering the entire range from
314 0 to $S_\infty = 25.2$ cm in Fig. 3, the categories should be 4.2 cm in
315 width ($6 \times 4.2 = 25.2$). This leads to the 6×6 transition matrix 9.
316 Because the size intervals are smaller (4.2 cm as compared to
317 5.0 cm), the probabilities for transition from one size class to
318 the next are greater in matrix 9 than they are in matrix 6. Other
319 things being equal, the probabilities of retention in a smaller
320 size class are less than they are in a larger size class:

$$\begin{pmatrix} .48 & 0 & 0 & 0 & 0 & 0 \\ .52 & .58 & 0 & 0 & 0 & 0 \\ 0 & .42 & .69 & 0 & 0 & 0 \\ 0 & 0 & .31 & .79 & 0 & 0 \\ 0 & 0 & 0 & .21 & .90 & 0 \\ 0 & 0 & 0 & 0 & .10 & 1 \end{pmatrix} \quad (9) \quad 321$$

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

$$\begin{pmatrix} .45 & 0 & 0 & 0 & 0 \\ .55 & .55 & 0 & 0 & 0 \\ 0 & .45 & .66 & 0 & 0 \\ 0 & 0 & .34 & .89 & 0 \\ 0 & 0 & 0 & .11 & 1 \end{pmatrix} \quad (10) \quad 327$$

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

5. Transitions over more than one size class

331 If the growth rate constant for the model is doubled to
332 $k=0.200\text{ year}^{-1}$ but all other characteristics of the model cal-
333 culation are the same, Fig. 2b is altered to give a curve that is
334 similar but twice as steep. One can determine the time nec-
335 essary to cover the first 5.00 cm growth interval as 1.116 years
336 and the size of the animal 1 year earlier as 0.57 cm. This leads
337 to the 1, 1 and 2, 1 element in matrix 11 which take the values
338 of 0.11 and 0.89, in which the augmented subdiagonal element
339 reflects the increase in the growth constant:

$$340 \begin{pmatrix} .11 & 0 & 0 & 0 & 0 \\ .89 & .33 & 0 & 0 & 0 \\ 0 & .67 & .55 & 0 & 0 \\ 0 & 0 & .45 & .77 & 0 \\ 0 & 0 & 0 & .23 & 1 \end{pmatrix} \quad (11)$$

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

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

364 According to the model function, the size is 6.53 cm at
365 $t=1.00$ years hence the ratio of animals transferring two
366 classes to those transferring one class is $6.53-5.00/5=0.31$ rela-
367 tive to 0.69. The ratio 0.69:0.31 is a refinement of the previous
368 estimate of 0.74:0.26. The corresponding column 1 matrix ele-
369 ments are:

$$370 \begin{pmatrix} 0 & \text{etc.} \\ .69 \\ .31 \\ 0 \\ 0 & \text{etc.} \end{pmatrix} \quad (12)$$

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:

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

The growth parameter $k=0.300\text{ year}^{-1}$ results in a sharp
change-over from subdiagonal dominance to diagonal domi-
nance as a result of the steep growth curve. The same
feature brings about a sharp change between diagonal ele-
ments 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 $a=22.0\text{ mm year}^{-1}$ (maxi-
mum 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 mm year^{-1} , 37.8, and 80.7 mm year^{-1} , respectively, for
the white abalone sample ($N=21$):

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

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 con-
tinued (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 induc-
tion period near $t=0$ giving a sigmoidal curve rather than the
exponential limiting form as in Fig. 2a.

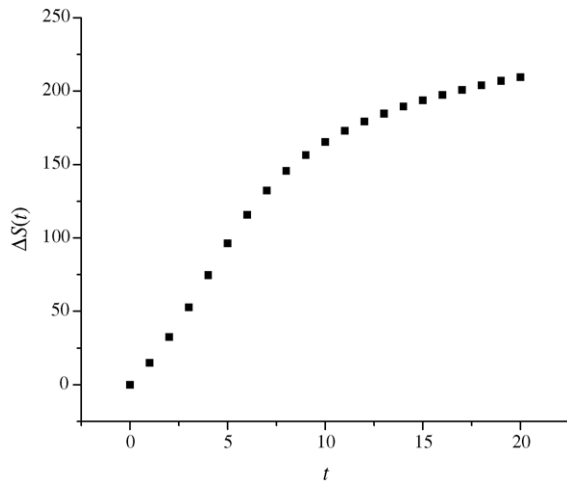


Fig. 4 – A Gaussian model of red abalone growth shell length $\Delta S(t)$ vs. time (t) for abalone ($N=231$) growing 1 year in northern California (unpublished data, California Department of Fish and Game, Burge and Schultz).

diagonal element for the red abalone matrix treated here is: 426

$$\frac{50.0 - S(t-1)}{50.0} = \frac{50.0 - 30.1}{50} = 0.40 \quad 427$$

The full transfer matrix for this sample of red abalone by the Gaussian method is matrix 15: 428

$$\begin{pmatrix} .60 & 0 & 0 & 0 & 0 \\ .40 & .58 & 0 & 0 & 0 \\ 0 & .42 & .75 & 0 & 0 \\ 0 & 0 & .25 & .93 & 0 \\ 0 & 0 & 0 & .07 & 1 \end{pmatrix} \quad (15) \quad 429$$

7. Curvilinear functions: white abalone 430

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 , μ , and σ 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 431

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

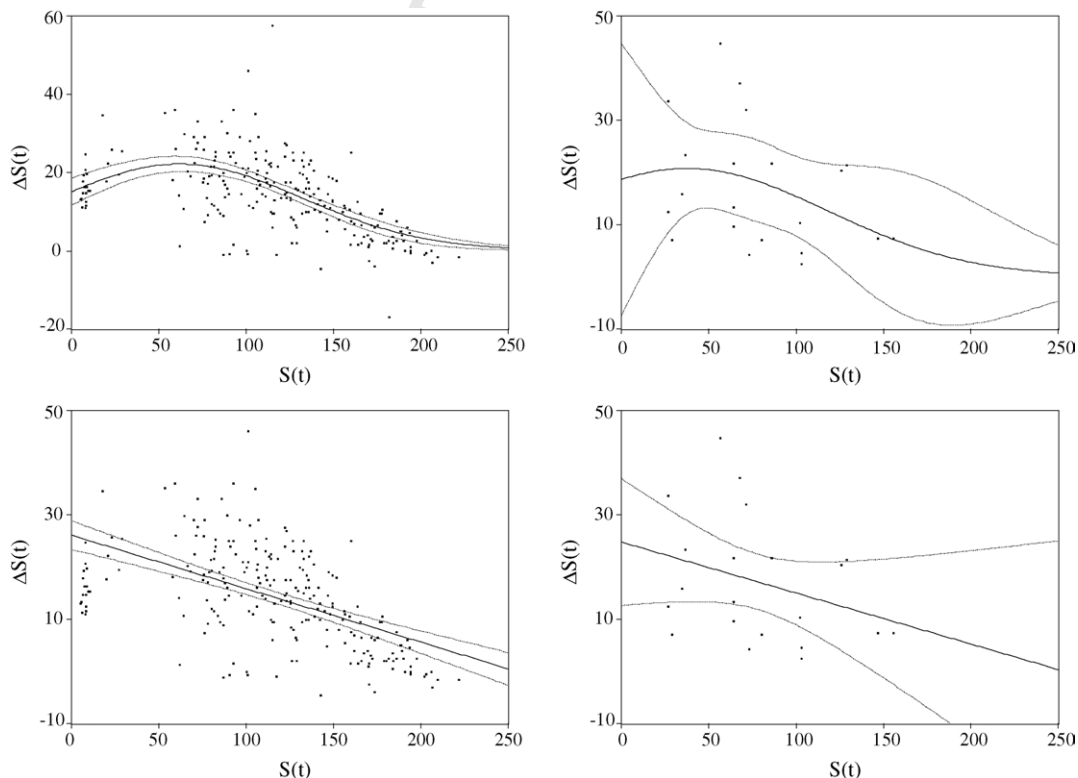


Fig. 5 – Gaussian models (top) and von Bertalanffy models (bottom) for the samples of red abalone, $N=231$ (left) and white abalone, $N=21$ (right) (Tutschulte, 1976) discussed in the text.

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

8. Confidence limits and summary of results

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

459 We shall take confidence limits as being approximately
460 symmetrical about the function so the lower confidence limit
461 is ~ 2.3 mm year⁻¹ below the central value. Thinking in terms
462 of very many individuals progressing along the model func-
463 tion curve, an increase in speed of 12% will enable 12% more
464 of them to cross the boundary from the first size class to the
465 second than if the growth rate were exactly given by the model
466 function. Therefore, the subdiagonal matrix element will be
467 augmented by 12% and the element on the principal diagonal
468 will be decremented by the same amount. A comparable calcu-
469 lation yields both the upper and lower confidence limits of all
470 of the matrix elements except the 5, 5 element which is 1. For
471 both confidence limits, the subdiagonal elements will be incre-
472 mented or decremented within a range of $0.12 \times 0.40 = 0.05$
473 (± 0.05) and the diagonal element will be decremented or incre-
474 mented (∓ 0.05) by the same amount. These confidence limits
475 pertain to the 1, 1 element in matrix 16.

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

$$479 \mathbf{GR} = \begin{pmatrix} .60 \mp .05 & 0 & 0 & 0 & 0 \\ .40 \pm .05 & .58 \mp .03 & 0 & 0 & 0 \\ 0 & .42 \pm .03 & .75 \mp .02 & 0 & 0 \\ 0 & 0 & .25 \pm .02 & .93 \mp .02 & 0 \\ 0 & 0 & 0 & .07 \pm .02 & 1 \end{pmatrix} \quad (16)$$

$$480 \mathbf{BW} = \begin{pmatrix} .58 \mp .17 & 0 & 0 & 0 & 0 \\ .42 \pm .17 & .68 \mp .10 & 0 & 0 & 0 \\ 0 & .32 \pm .10 & .79 \mp .14 & 0 & 0 \\ 0 & 0 & .21 \pm .14 & .89 \mp .20 & 0 \\ 0 & 0 & 0 & .11 \pm .20 & 1 \end{pmatrix} \quad (17)$$

$$481 \mathbf{BR} = \begin{pmatrix} .58 \mp .04 & 0 & 0 & 0 & 0 \\ .42 \pm .04 & .68 \mp .02 & 0 & 0 & 0 \\ 0 & .32 \pm .02 & .79 \mp .02 & 0 & 0 \\ 0 & 0 & .21 \pm .02 & .89 \mp .02 & 0 \\ 0 & 0 & 0 & .11 \pm .02 & 1 \end{pmatrix} \quad (18)$$

$$482 \mathbf{GW} = \begin{pmatrix} .52 \mp .26 & 0 & 0 & 0 & 0 \\ .48 \pm .26 & .67 \mp .16 & 0 & 0 & 0 \\ 0 & .33 \pm .16 & .79 \mp .15 & 0 & 0 \\ 0 & 0 & .21 \pm .15 & .93 \mp .17 & 0 \\ 0 & 0 & 0 & .07 \pm .17 & 1 \end{pmatrix} \quad (19)$$

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

495 The matrices for white abalone are similar to each other but
496 quite different from the matrix found by the counting method
497 (matrix 7). The point is that for a poor data set, either model
498 function, or presumably any plausible model function, is a bet-
499 ter method of obtaining a self-consistent growth-transition
500 matrix than the counting method. The counting method for
501 red abalone produces matrix 20. Other than the 1, 1 and 2, 1
502 elements, matrix 20 begins to approximate matrices 16 and
503 18, which is not surprising for a larger and “better” data set.

$$504 \begin{pmatrix} .91 & 0 & 0 & 0 & 0 \\ .09 & .53 & .01 & 0 & 0 \\ 0 & .47 & .68 & 0 & 0 \\ 0 & 0 & .30 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} \quad (20)$$

9. Discussion

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

517 Our method is simple and yet flexible enough to accom-
518 modate matrices of varying sizes. In general, the smaller the
519 size class the faster animals will transition out of size classes,
520 whereas for larger size classes the probability of retention
521 within the size class increases. Since size class width can
522 have an impact on elasticity values of various matrix ele-
523 ments (Enright et al., 1995) these decisions of matrix size
524 play an important role in conservation policy decisions. This
525 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, *in press*). 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) have 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 (λ) is proposed and the matrix elements are computed from it. Next λ 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.

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