Estimating growth and mortality in stage-structured populations

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Abstract. This paper presents a practical numerical method for separating and estimating growth and mortality coefficients in stage- or size-structured populations using only observations of the relative or absolute abundance of each stage. The method involves writing a system of linear ordinary differential equations (ODEs) modelling the rate of change of abundance. The solution of the differential system can be numerically approximated using standard (e.g. sixth-order Runge–Kutta–Felhberg) methods. An optimization problem whose solutions yield 'optimal' coefficients for a given model is formulated. The ODE numerical integration technique can then be employed to furnish required function and gradient information to the optimization algorithm. The data-fitting software package ODRPACK is then successfully employed to estimate optimal coefficients for the ODE population model. Simulation experiments with four- and eight-stage model populations illustrate that the method results in the successful estimation of coefficients of mortality and growth from abundance data.

Introduction

Growth and mortality are the principal processes that determine population dynamics. Estimation of these life-history parameters at different life stages and time intervals is crucial for understanding and interpreting the changes in population abundance and structure.

However, minimal assumption simple methods for estimating growth rates, mortality rates and stage duration in stage-structured populations require development [see the important contributions by Wood (1994) and by Wood and Nisbet (1991)]. Because methods for estimating such rates are not generally available, many depictions of 'ecosystems' that require such rates use contrived estimates. Furthermore, in the literature, estimates of growth are often confounded with mortality and vice versa; it is necessary to understand the statistical interaction of growth and mortality so that the two vital rates can be separated for use in ecosystem models [the importance of this interaction is discussed in detail by Beyer (1989)].

This paper describes a method for estimating the vital rates and stage duration from estimates of the change in abundance or indices of abundance of each stage as a function of time (as might be obtained from acoustic or optical monitoring methodologies). Subsequent sections illustrate how the abundance trajectories are developed as functions of time from a state diagram, discuss an analytical approach to the problem, demonstrate how mortality-rate and growth-rate parameters can be estimated using an optimization formulation of the problem and

modern parameter estimation software ODRPACK, and describe results of the numerical method applied to the simulated data from four- and eight-stage models. The paper concludes with a discussion.

Problem formulation

The stage-structured approach divides the population into recognizable stages, e.g. nauplii, juvenile or adult stages. It is also possible to think of dividing the population into length classes [as might be appropriate for the study of larval fish; see Beyer (1989)]. The problem is: given estimates of abundance at each stage or length class as a function of time, simultaneously estimate stage- or length-specific mortality and growth rates.

The state diagram in Figure 1 shows the configuration of the problem. The number of organisms in each stage at any instant of time is represented by $x_i(t)$ where i represents the ith stage for $i = 1, \ldots, n$ stages. The vector of x_is at any time t represents the state of the population at time t. The constants $k_{i,i-1}$ represent the growth rates from the $(i-1)$th to the ith stage, while the constants k_{0i} represent the mortality rate of the ith stage.

The dynamics of such a system are represented by the system of linear ordinary differential equations (ODEs):

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \vdots \\ \dot{x}_n \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{pmatrix} \tag{1}$$

which can be written more compactly as:

$$\dot{x} = Ax(t) \tag{2}$$

The structure of Figure 1 dictates that in the matrix A, the diagonal elements are $a_{ii} = -(k_{0i} + k_{i+1,i})$. The off-diagonal elements are zero, except for the lower sub-diagonal, where $a_{i+1,i} = k_{i+1,i}$. Consider as an example equation (3) representing the dynamics of four life history stages ($n = 4$):
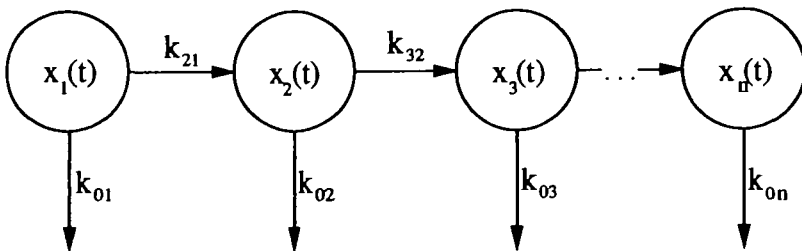

Fig. 1. Stage diagram showing the configuration of the mortality–growth estimate problem.

$$A = \begin{pmatrix} -(k_{01} + k_{21}) & 0 & 0 & 0 \\ k_{21} & -(k_{02} + k_{32}) & 0 & 0 \\ 0 & k_{32} & -(k_{03} + k_{43}) & 0 \\ 0 & 0 & k_{43} & -k_{04} \end{pmatrix} \quad (3)$$

Note that if we can determine a_{11} and a_{21}, for example, then we can determine both the growth and the mortality rates, k_{21} and k_{01}, since $k_{21} = a_{21}$ and $k_{01} = -(a_{11} + a_{21})$, etc.

Note also that $-a_{ii}$ is the total instantaneous loss for the ith stage. The apparent mortality rate is given by $-a_{ii}$. However, if growth is not taken into account, mortality will be overestimated. The magnitude of the overestimates is simply the growth rate $-a_{i,j-1}$ and vice versa.

Matrix stage-based population models were used to solve the 'forward problem'—to forecast population dynamics by multiplying the vector of population abundance by the population projection matrix at each time step (Caswell, 1978, 1980; Crouse *et al.*, 1987; Nakaoka, 1993).

To solve the 'inverse problem', the coefficients of the projection matrix are estimated based on the measurements of the change in abundance or the indices of abundance for each stage.

The problem formulation thus requires a sequence of estimates of abundances for each stage or length class. As a practical model, utilization of this technique may require acoustic or optical estimates. However, because the techniques admit statistical error, problems of misidentification, etc., can be evaluated statistically.

We observe that equation (2) is a linear approximation which seems adequate for relatively short observation intervals and please note that our procedure can be extended to account for non-linear extensions of equation (2).

Analytical solution

The system of linear differential equations (1) can be solved analytically, providing an algebraic expression for abundance $N(t)$ as a function of time t. A straightforward way of solving a system of differential equations (2) is to take its Laplace transform:

$$\mathbf{x}(s) = (sI - A)^{-1}\mathbf{x}(0) \quad (4)$$

where the initial conditions are given by $\mathbf{x}(0) = (K_1, K_2, \ldots, K_n)^t$ and the coefficients in A are unknown parameters. By applying the inverse Laplace transform operator to the solution in algebraic space, we obtain:

$$\mathbf{x}(t) = L^{-1}[(sI - A)^{-1}]\mathbf{x}(0) \quad (5)$$

the time trajectory of the abundance of each life history stage. Standard non-linear regression can be used to give straightforward estimates of the parameters.

To give the simplest example, consider the two-stage ($n = 2$) population. First, we write the appropriate differential equation:

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{pmatrix} -a & 0 \\ b & -c \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \qquad (6)$$

where a_{11}, a_{21} and a_{22} are represented, respectively, by $-a$, b and $-c$ for notational convenience. We note that $a = k_{01} + k_{21}$, $b = k_{21}$ and $c = k_{02}$. Setting $c = k_{02}$ implies that there is exactly zero growth in the last stage.

Assuming initial conditions $\mathbf{x}(0) = (K_1, K_2)^t$, we solve equation (6) by taking its Laplace transform and then inverting the transform as specified above, which yields:

$$\mathbf{x}(t) = \begin{pmatrix} K_1 e^{-at} \\ \dfrac{K_1 b e^{-at} - K_1 b e^{-ct} + K_2 c e^{-ct} - K_2 a e^{-ct}}{a - c} \end{pmatrix} \qquad (7)$$

The first row in the above column vector gives the trajectory or number of individuals as a function of time in the first stage, while the second row in the column vector gives the number of individuals as a function of time in the second stage.

To show the form of equation (7) by an example, let $a = 1.2$, $b = 0.5$, $c = 0.2$, $K_1 = 1000$ and $K_2 = 500$. These trajectories are plotted (see Figure 2). Because $a = 1.2$ and $b = 0.5$, it is clear that $k_{01} = 0.7$ while $k_{21} = 0.5$. This illustrates the
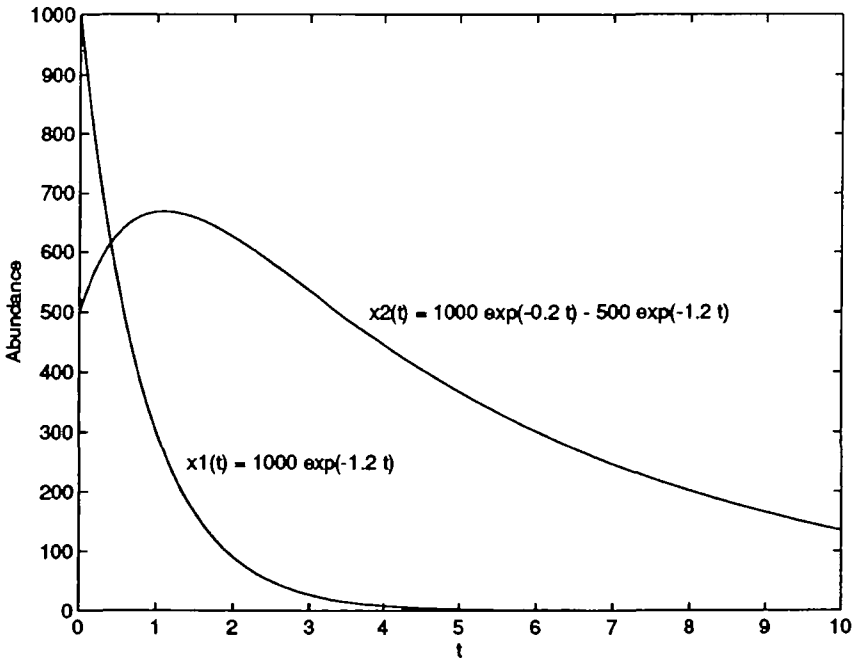

Fig. 2. Abundance of x_1 and x_2 in the two-stage model. They are trajectories according to equations (11) and (12). Note that as x_1 is depleted, x_2 increases. Then x_2 becomes depleted.

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separation of growth and mortality constants. Inserting these constants in equation (7) results in:

$$x_1(t) = 1000e^{-1.2t} \tag{8}$$

and

$$x_2(t) = 1000e^{-0.2t} - 500e^{-1.2t} \tag{9}$$

The stage duration can be obtained by simple integration of equations (8) and (9):

$$\hat{T}_i = \int_0^\infty t x_i(t) \mathrm{d}t \tag{10}$$

Examination of the stage duration or average time in each stage is interesting because it can be used to calculate the length of the time that the population is exposed to a stage-specific risk. This is particularly important in the theory of larval fish mortality [see the discussion in Rothschild (1986, p. 114)].

To estimate parameters of equation (7), data sets using equations (8) and (9) were simulated and normally distributed noise was added to the data (see Figures 3 and 4).
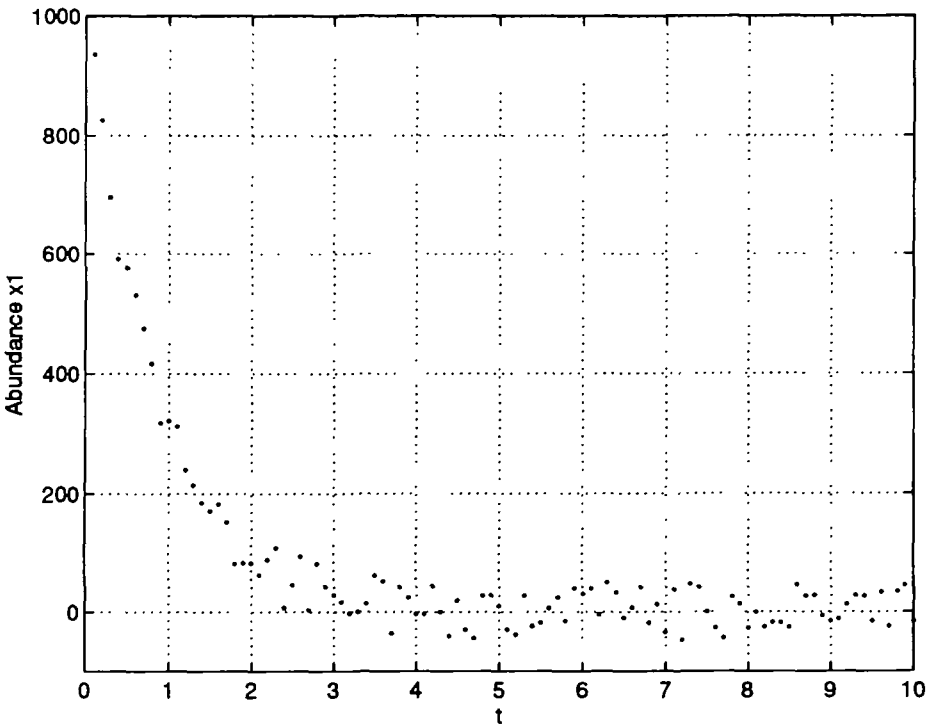

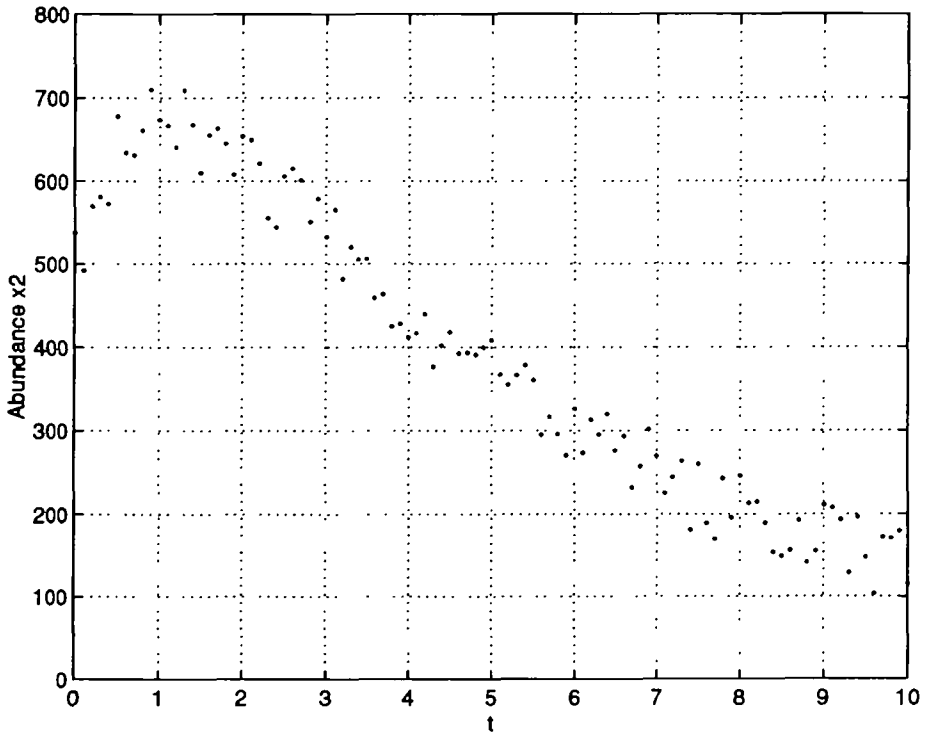**Fig. 3.** Simulated abundance dynamics of stage 1 with random noise (two-stage model).

Fig. 4. Simulated abundance dynamics of stage 2 with random noise (two-stage model).

The problem in this 'inverse' approach is now formalized by rewriting equations (8) and (9) in the form:

$$x_1(t) = 1000e^{-\alpha t} \tag{11}$$

and

$$x_2(t) = 1000e^{-\beta t} - 500e^{-\alpha t} \tag{12}$$

Our intent is to estimate the values of α and β. This can be achieved using the standard non-linear regression techniques (Seber and Wild, 1989). Using only the data pictured (in Figures 3 and 4), approximate values of the parameters were recovered with virtually no error.

However, it is interesting to note that with an increase in the number of stages, the equations that need to be solved become more complicated. Perhaps more importantly, with an increase in the number of stages, one runs into the difficulty of generating equations with parameters to be estimated by non-linear regression analysis. Thus, while simple for two-stage population, this approach has significant drawbacks when extended to population models with more than two stages.

Yet, the simple example above highlights the fact that conventional estimates of mortality rate without estimates of growth rate, and estimates of growth rate without estimates of mortality rate, can have substantial systematic biases.

Numerical approach to the problem

Many difficulties with scalability and error estimation in the analytical technique described above for the solution of an ordinary least squares (OLS) problem can be overcome by formulating the problem as an orthogonal distance regression (ODR) problem. The (ODR) problem has been studied [see the papers by Boggs and Rogers (1990) and Boggs *et al.* (1987)] and a robust implementation in public domain software has also been released (Boggs *et al.*, 1989, 1992). The method and implementation have been successfully employed to solve many important application problems. Similarly, below is described the application of ODRPACK to the problem of estimating growth and mortality coefficients in stage-structured populations.

Let $x_D(t_i)$s denote observed (data) measurements of the numbers of organisms in given stages at times t_i ($i = 1, \ldots, p$). Further, let $x(t_i)$ approximate the solution to the differential equation (2) comprised of coefficients a_j, $j = 1, \ldots, 2n - 1$ (n is the number of stages in the model). In this case, coefficients in the matrix A are enumerated in the following way:

$$A = \begin{pmatrix} a_1 & 0 & 0 & \cdots & 0 \\ a_2 & a_3 & 0 & \cdots & 0 \\ 0 & a_4 & a_5 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & a_{2n-2} & a_{2n-1} \end{pmatrix}$$

We wish to minimize the residual sum of the differences between computed and observed data points subject to the computed values satisfying equation (2). The resulting new problem can be formulated:

$$\min_{\mathbf{a}} f(\mathbf{a}) = \sum_{i=1}^{p} \|x(t_i) - x_D(t_i)\|_2^2 \tag{13}$$

subject to the constraints

$$A\mathbf{x} = \dot{\mathbf{x}}, \ \mathbf{x}(0) = (\mathbf{x}_0) \tag{14}$$

$$a_{2i} + a_{2i-1} \leq 0, \ i = 1, \ldots, n - 1 \tag{15}$$

$$a_{2i-1} \leq 0, \ i = 1, \ldots, n \tag{16}$$

The implicit equality constraints (14) require that the coefficients satisfy the appropriate system of differential equations (2), while the inequality constraints

(15) and (16) guarantee that coefficients correspond to the structure of the problem illustrated in equation (3).

Also, since in practice the observation-error variance is proportional to the square of the abundance for mostly process errors and very large samples, we employ the appropriate weighting for the residual sum for the difference between computed and observed data:

$$\min_{\mathbf{a}} f(\mathbf{a}) = \sum_{i=1}^{p} \left\| \frac{\mathbf{x}(t_i) - \mathbf{x}_D(t_i)}{\mathbf{x}_D(t_i)} \right\|_2^2 \tag{17}$$

In short, the problem of approximating the coefficients of our model differential equation has been recast as a constrained optimization problem. The function to be minimized, equation (13), usually called the objective function, is a standard 'output least squares' function. We can write the equality constraints, (14), as one vector function $h(\mathbf{a}) = 0$:

$$h(\mathbf{a}) = (Ax - \dot{x}, x(0) - x_0)^t \tag{18}$$

of our parameters $\mathbf{a}$. Likewise, the inequality constraints can be written as a single vector function, say $g(\mathbf{a}) \leq 0$:

$$g(\mathbf{a}) = (a_{2i} + a_{2i-1}, a_{2i-1})^t \tag{19}$$

Although our constraints are linear, one can easily envision significantly more complicated and certainly highly non-linear ODEs replacing the linear system presently employed. For this reason, we chose to solve this optimization problem numerically (referred to in optimization as a non-linear programming problem) defined by equations (13), (14), (15) and (16) using the standard data-fitting software package ODRPACK (Boggs *et al.*, 1992). Optimization problem (13), (14) can be reformulated without difficulty as an explicit (ODR) problem (see Boggs *et al.*, 1992, p. 4) with implicit constraints (14) rewritten as a model function *f*:

$$\mathbf{x}(t) = f(t, \mathbf{a}) = A^{-1}\mathbf{x}(t) \tag{20}$$

ODRPACK has been designed for finding the parameters that minimize the sum of the squared weighted orthogonal distances from a set of observations to the curves or surfaces determined by the parameters.

Presently, a drawback of the approach is that one cannot impose constraints. While the problem is not naturally constrained, one can imagine constraints representing maximum or minimum bounds on variations in population in a given cycle or similar constraints. For this reason, the authors are also investigating a constrained optimization approach to the problem employing ideas from sequential quadratic programming (SQP) (see the paper by Boggs *et al.*, 1994). Similar ideas have been successfully employed in other areas of science and engineering (see Kearsley, 1996).

Numerical results

To test the numerical approach, several simulated data sets were generated for both four-stage and eight-stage populations. This was done in the following way:

(i) Coefficients of growth and mortality were randomly picked from the set of reasonable values for growth and mortality rates. We generated 100 coefficient sets for this experiment.
(ii) Numerical solutions of the ODEs with the above coefficients generated a set of observations of abundance of each stage (numerical tests here were performed with $p = 25$ such simulated observations).
(iii) For each coefficient set, 100 levels of normally distributed noise (with standard deviation from 0.16 to 0.24 for four-stage and from 0.09 to 0.12 for eight-stage population models) were added to the simulated data corresponding to random fluctuations within a given percentage of deviation from the 'actual' value (CV of 16–24%), thus generating sets of observations like one would expect to collect in the field. These observations are shown as asterisks, pluses, crosses and circles in Figures 5, 7 and 8.

The resulting data sets were assumed to be the 'observed' data. First we estimated growth and mortality coefficients from the data without the 'noise' using the optimization-based numerical approach described in the previous sections.
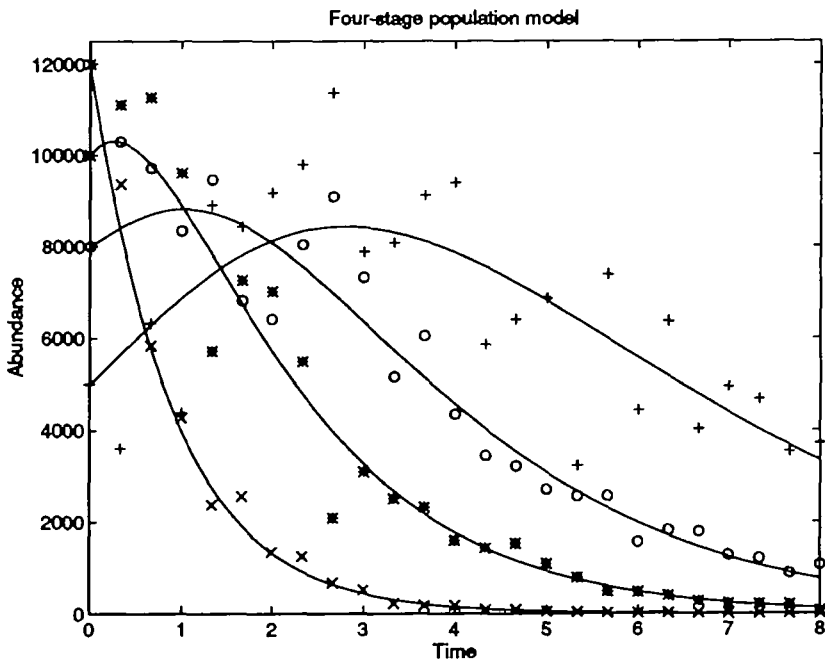

Fig. 5. Simulated abundance dynamics of the four-stage population model. Asterisks, pluses, crosses and circles represent the 'observed' data, and solid lines represent the solution.
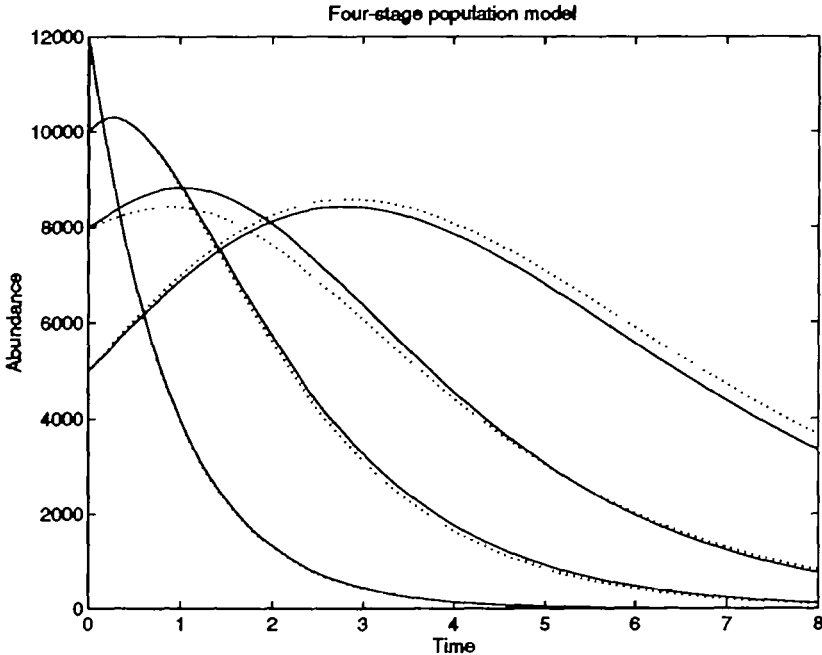
Fig. 6. Typical estimated abundance trajectories (dotted lines) as compared to the original trajectories (solid lines) of the four-stage population model.

These coefficients were then estimated from the 'observed' data sets using the same numerical approach.

Figures 6, 9 and 10 show the results of the typical estimations from the 'observed' data sets for four- and eight-stage populations. The original trajectories are shown as solid lines and the trajectories produced from the estimated coefficients are shown as dotted lines. Also, Tables I and II show the original and estimated coefficients (with 95% confidence intervals) for these estimations.

As seen from Figures 11 and 12, the accuracy of the estimated coefficients does not appear overly dependent on the level of noise. On the contrary, the CV of coefficients does not appear overly dependent on the level of noise the CV of coefficients remains close to constant as a function of the CV of noise. However, after using our technique to solve identification problems consisting of >100 different coefficient sets, we observed that the selection of a coefficient set greatly influenced the solution and the procedure for finding the solution. In other words, slight perturbations of the coefficient set for which the problem is well conditioned could cause the problem to become ill conditioned.

Discussion

It was shown in numerical experiments that the proposed method allows estimation of rates of mortality and transition to the next stage (growth, maturation, etc.) with sufficient precision. In particular, the scheme appears to work
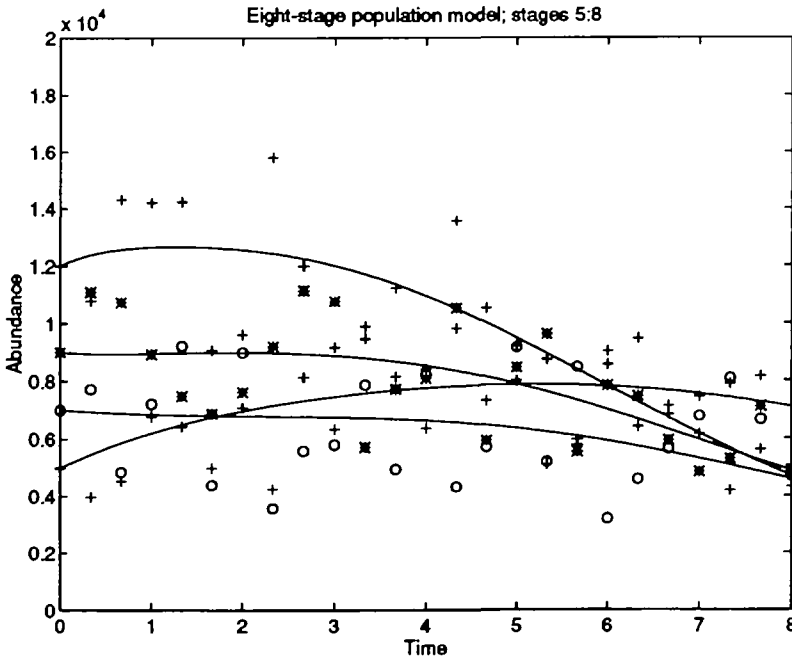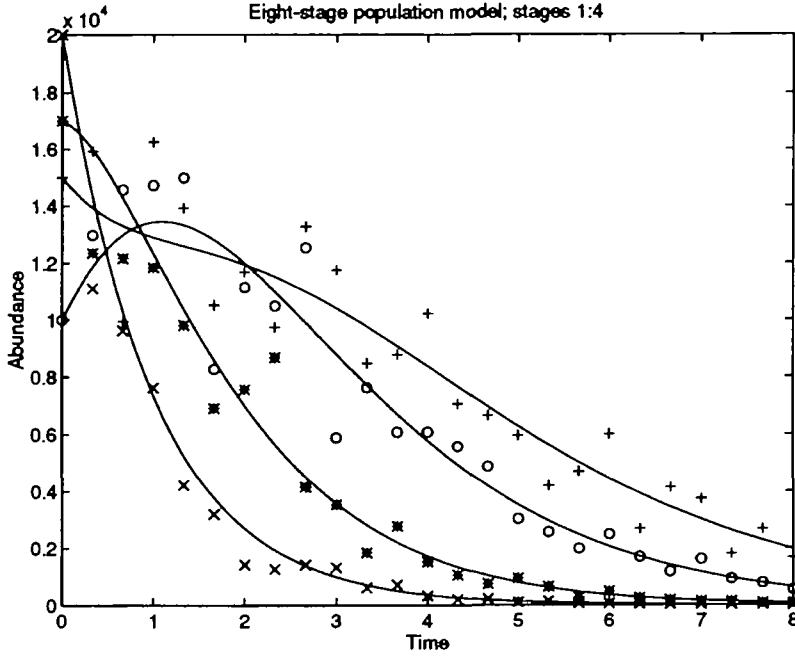
Figs 7 and 8. Simulated abundance dynamics of the eight-stage population model. Asterisks, pluses, crosses and circles represent the 'observed' data, and solid lines represent the solution.
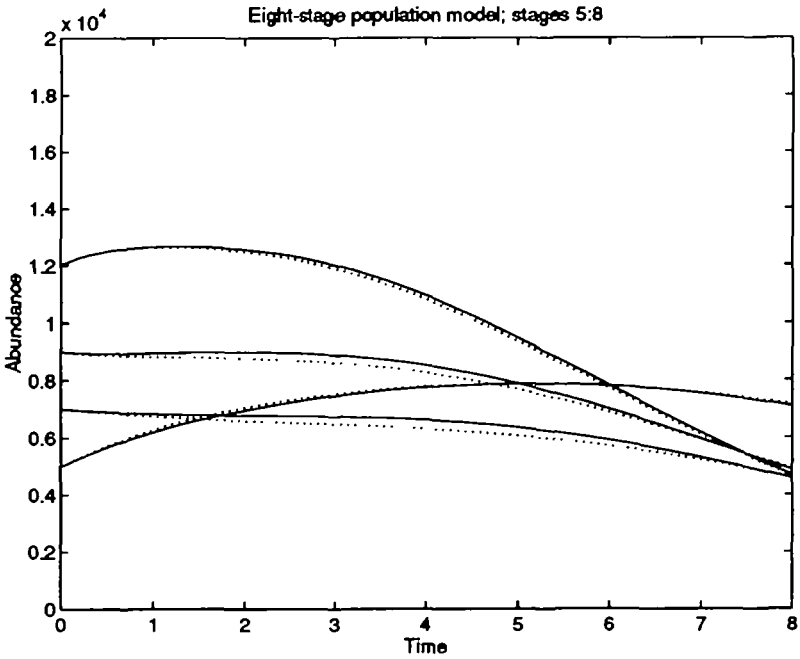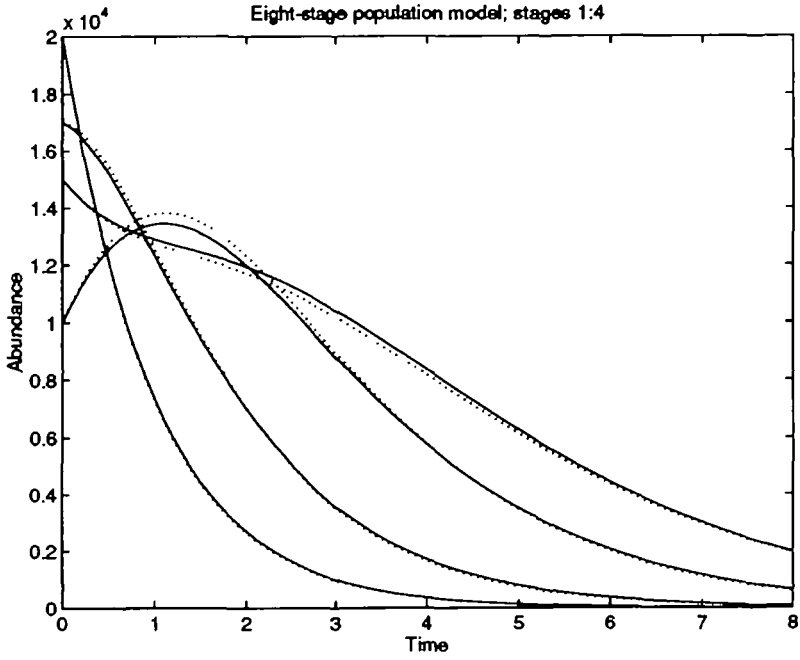
Figs 9 and 10. Typical estimated abundance trajectories (dotted lines) as compared to the original trajectories (solid lines) of the eight-stage population model.

Table I. Actual and computed coefficients with 95% confidence intervals for the four-stage population model

Actual coefficients	Estimated coefficients	95% confidence intervals
−1.1	−1.10884936	−1.33069617 to −0.88700255
0.8	0.83513807	0.12226160 to 1.54801451
−0.7	−0.72974590	−0.98901686 to −0.47047494
0.6	0.48441035	0.09880331 to 0.87001738
−0.6	−0.52764224	−0.77575753 to −0.27952695
0.5	0.51978080	0.20587469 to 0.83368691
−0.4	−0.38332264	−0.60042499 to −0.16622030

Table II. Actual and computed coefficients with 95% confidence intervals for the eight-stage population model

Actual coefficients	Estimated coefficients	95% confidence intervals
−1.0	−1.01948904	−1.19968538 to −0.83929269
0.7	0.65711214	−0.12456032 to 1.43878460
−0.9	−0.88231027	−1.29305566 to −0.47156484
0.8	0.80611938	0.33502469 to 1.27721408
−0.7	−0.68607393	−0.95137870 to −0.42076916
0.5	0.52101167	−0.09053107 to 1.13255442
−0.6	−0.62544568	−1.12095822 to −0.12993314
0.5	0.50472084	−0.02825008 to 1.03769176
−0.5	−0.51035757	−0.95532174 to −0.06539341
0.5	0.64875412	−0.85221896 to 2.14972721
−0.7	−0.88235942	−2.77042540 to 1.00570655
0.6	0.31064101	−0.85460328 to 1.47588530
−0.8	−0.42090184	−1.87956801 to 1.03776433
0.5	0.67517411	−0.46673167 to 1.81707989
−0.4	−0.56101227	−1.58690365 to 0.46487911

successfully when data are provided in a large number of stages. It appears that casting the model coefficients as solutions to a 'constrained optimization problem' is a viable strategy for finding their approximate values based on observations.

The assumption of constant rates of mortality and growth within each stage is a non-trivial but 'standard' assumption. If the actual process rates are not constant within the stages under consideration, the resulting coefficients would be incorrectly estimated. There are two solutions to this difficulty. The processes could be analysed at shorter time intervals (which means more frequent sampling), such that the rates of mortality and growth could be considered to be constant. Another way to overcome this difficulty is to replace our elementary linear model $\dot{\mathbf{x}} = A\mathbf{x}$ with a more complicated non-linear model $\dot{\mathbf{x}} = \phi(\mathbf{x})$. This is one of the very strong advantages of the numerical approach presented here—in no way does it depend specifically on the particular model employed. Therefore, if we have notions regarding how the process changes in time, we can incorporate these in the selection of appropriate objective and/or constraint functions to be handled by the minimization algorithm.
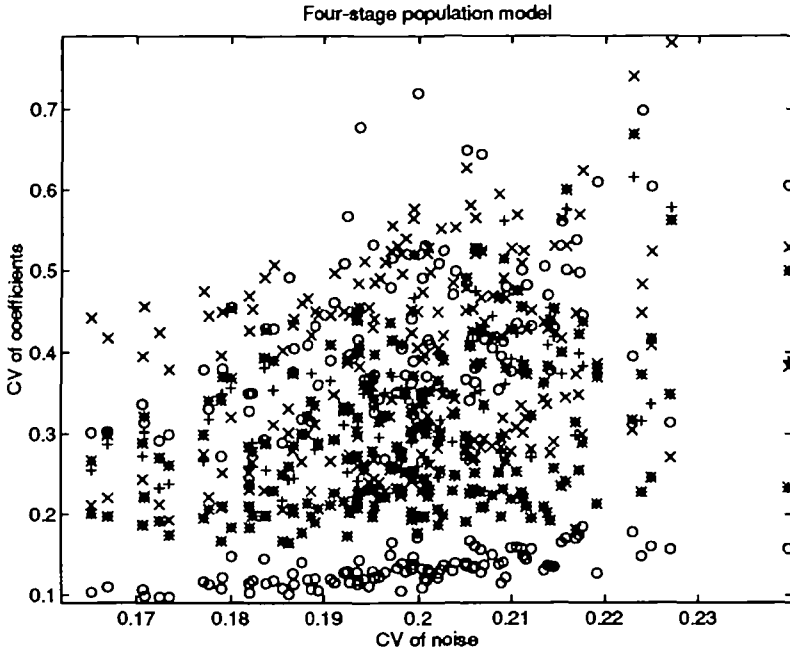
Four-stage population model

Fig. 11. Uncertainty in estimated coefficients as a function of uncertainty in the population data for the four-stage population model.
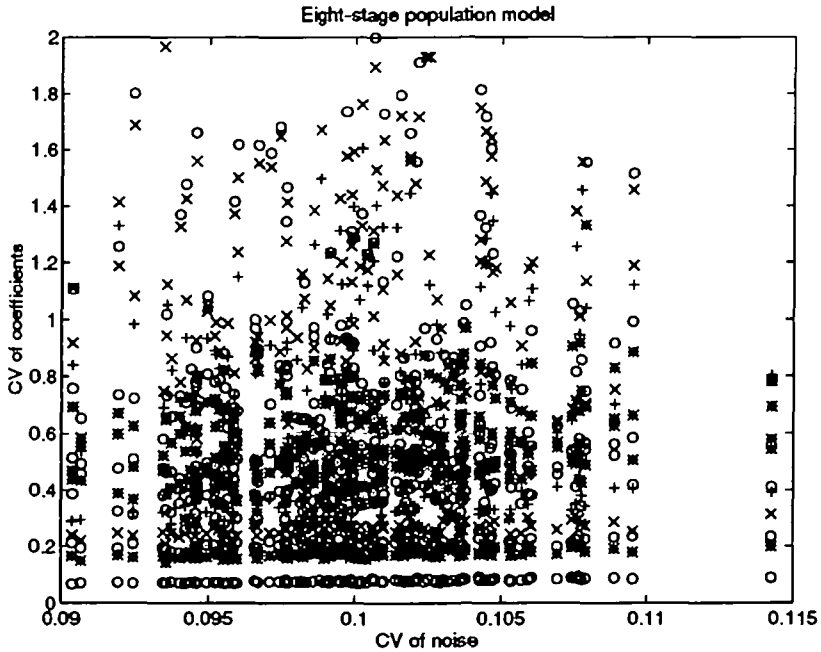
Eight-stage population model

Fig. 12. Uncertainty in estimated coefficients as a function of uncertainty in the population data for the eight-stage population model.

An analysis of larger collections of real field data in terms of the method applicability, development and testing of non-linear models must be conducted. Alternative formulations of our development and testing of non-linear models are the potential perspectives for the future method development. In addition to employing more sophisticated biological models, an examination of potential statistical models that more delicately describe how noise and inaccuracies affect observational data would be of interest.

Finally, we mention that the formulation and numerical solution of parameter identification problems arising in marine sciences is becoming a very active field (for example, see DeAngelis and Coutant, 1979; DeAngelis and Mattice, 1979; Banks *et al.*, 1991; Somerton, 1992). We intend to continue our contribution by studying alternative optimization formulations in search of those that allow more complicated models and demonstrate superior numerical results. The theoretical and numerical characteristics of some alternative formulations are presently being investigated.

Acknowledgements

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