

ESTIMATING POPULATION PROJECTION MATRICES FROM MULTI-STAGE MARK–RECAPTURE DATA

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Abstract. Multi-stage mark–recapture (MSMR) statistics provide the best method for estimating the transition probabilities in matrix population models when individual capture history data are available. In this paper, we improve the method in four major ways. We use a Markov chain formulation of the life cycle to express the likelihood functions in matrix form, which makes numerical calculations simpler. We introduce a method to incorporate capture histories with uncertain stage and sex identifications, which allows the use of capture history data with incomplete information. We introduce a simple function that allows multinomial transition probabilities to be written as functions of covariates (time or environmental factors). Finally, we show how to convert transition probabilities estimated by the MSMR method into a matrix population model. These methods are applied to data on the North Atlantic right whale (*Eubalaena glacialis*).

Key words: capture–recapture studies; *Eubalaena glacialis*; multi-stage mark–recapture statistics; Markov chain; matrix population models; North Atlantic right whale; population projection matrix; survival probability; transition probability.

INTRODUCTION

Mark–recapture estimates of survival probability have been applied to many animal populations (e.g., Lebreton et al. 1992, Forsman et al. 1996, Weimerskirch et al. 1997, Hastings and Testa 1998, Caswell et al. 1999, Pease and Mattson 1999), and this method has become an important tool in population management. Mark–recapture estimates are based on capture histories of individually identified animals, which contain information on whether or not each individual was captured at each sampling occasion. For example, capture history data may be obtained by annual observations of banded birds or photographically identified whales. When such data are available, mark–recapture statistics are considered one of the best approaches for estimation of survival probability.

Modern demographic analysis goes beyond calculating survival, by breaking the life cycle into stages (which may be based on age, size, developmental or behavioral states, physiological condition, spatial location, or any other property that divides individuals into subgroups). The fate of individuals is described in terms of transition probabilities among these stages, and those transition probabilities form the basis for matrix population models (Caswell 2001). Nichols et al. (1992) introduced a method to estimate transition probabilities among stages from mark–recapture data, which we call the multi-stage mark–recapture (MSMR) method. This method extends the method originally

developed to estimate probabilities of movement among spatial locations (Arnason 1972, 1973, Brownie et al. 1993, Lebreton 1995). For the MSMR method, in addition to information on whether or not each individual was captured, the capture history data must also include the stage of captured individuals at each capture occasion. MSMR models account for inter-group heterogeneity in survival and capture probability by grouping similar individuals into stages. The development from single-stage to multi-stage mark–recapture statistics parallels the development from unstructured to structured population models. In fact, one motivation for the statistical development was the need to estimate parameters in stage-structured matrix population models from mark–recapture data (Nichols et al. 1992).

The analysis is based on maximization of a likelihood function that depends on all of the possible sequences of stage transitions compatible with an observed capture history. There can be very many of these sequences, and one of the most complicated parts of the method of Nichols et al. (1992) is writing them all down with their associated probabilities. In this paper, we describe the life cycle as a Markov chain, and take advantage of this description to write the likelihood in a simple matrix notation. A sketch of this method was given in Caswell (2001: Section 6.1.2.2). Here we give a complete presentation, and extend the method to incorporate uncertainty in stage and sex identifications, which allows the use of capture histories containing incomplete information. We also introduce a simple function that allows multinomial transition probabilities to be written as a function of covariates (e.g., environmental variables or time). Finally, we show how

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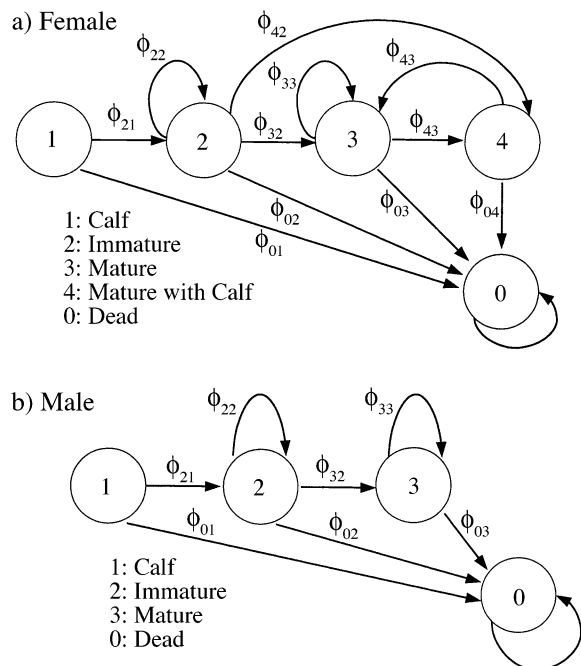


FIG. 1. A stage structure for (a) female and (b) male right whales. This structure is used as an example for the MSMR statistics.

to convert the estimated transition probabilities into a matrix population model.

MSMR STATISTICS

The MSMR method involves three main steps: (1) constructing an appropriate stage structure; (2) expressing the likelihood function in terms of parameters, based on available capture histories; and (3) finding the best parameter estimates using maximum likelihood theory. The parameters in the MSMR model are those that define the capture probabilities of each stage at each sampling occasion and the transition probabilities among stages between consecutive sampling occasions. The method assumes that individuals in the same stage are identical and independent, but that individuals in different stages may differ in their transition and capture probabilities. The MSMR method is very flexible and can be applied to almost any stage structure. Constructing a useful stage structure that is compatible with the life cycle of populations requires experience, in addition to sufficient mathematical and biological knowledge, and different stage structures are extensively reviewed in Caswell (2001). In this paper, methods for expressing the likelihood function and estimating parameters are described, assuming that an appropriate stage structure has been constructed.

To make our discussion more concrete, we will demonstrate the method using a stage structure (Fig. 1) developed to describe the life history of the North Atlantic right whale (*Eubalaena glacialis*). This is a two-sex, multi-stage model that distinguishes calves (stage

1), immature individuals (stage 2), and mature individuals (stage 3). In addition to these three stages, females also have a stage for individuals nursing a calf (stage 4); we call the individuals in this stage “mothers.” Stage 0 corresponds to death, and the probabilities ϕ_{0i} associated with the arrows going to stage 0 are stage-specific mortality rates. As usual, “mortality” includes both death and permanent emigration.

The objective of the MSMR approach is to estimate the transition probabilities associated with each arrow and the capture probabilities of each stage. In the next section, we will show how to construct matrices containing the transition and capture probabilities, and to account for uncertainty in the assignment of individuals to stages. Then we will show how to calculate the likelihood in terms of these matrices.

Transition and capture probability matrices

The transition matrix is constructed by first putting the transition probability ϕ_{ji} from (living) stage i to (living) stage j in the (j, i) position. To this matrix is appended a row containing the probabilities of transition from each stage to stage 0 (death) and a column containing the probabilities of transition from stage 0 to each stage. Because we treat death as a stage, the result is the transition matrix of an absorbing Markov chain, with death as an absorbing state. The matrix is column stochastic. The ability to treat transitions as a Markov chain is critical to our analysis. The transition matrix for females, corresponding to the stage structure in Fig. 1, is

$$\Phi_t^{(f)}(\theta) = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ \phi_{21}(t) & \phi_{22}(t) & 0 & 0 & 0 \\ 0 & \phi_{32}(t) & \phi_{33}(t) & \phi_{34}(t) & 0 \\ 0 & \phi_{42}(t) & \phi_{43}(t) & 0 & 0 \\ \phi_{01}(t) & \phi_{02}(t) & \phi_{03}(t) & \phi_{04}(t) & 1 \end{pmatrix} \quad (1)$$

where $\phi_{ji}(t)$ is the probability of females making transition from stage i to j between time t and $t + 1$. The upper left block of the matrix describes the transition among live stages; the lower left block of the matrix contains stage-specific probabilities of death. The 1 in the (5, 5) entry is the probability of dead individuals remaining dead in the following year. The notation $\phi_{ji}(t)$ in this paper corresponds to ϕ_{tij} in Nichols et al. (1992).

Similarly, the transition matrix for males, corresponding to the stage structure in Fig. 1, is

$$\Phi_t^{(m)}(\theta) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ \phi_{21}(t) & \phi_{22}(t) & 0 & 0 \\ 0 & \phi_{32}(t) & \phi_{33}(t) & 0 \\ \phi_{01}(t) & \phi_{02}(t) & \phi_{03}(t) & 1 \end{pmatrix} \quad (2)$$

We have written $\Phi_t^{(f)}$ and $\Phi_t^{(m)}$ as functions of a vector of parameters θ . These parameters can be the ϕ_{ji} themselves, or lower level parameters from which the ϕ_{ji} can be calculated. The objective is to estimate θ .

Capture probability matrices \mathbf{P}_t , defined for females and males separately, contain stage-specific capture probabilities on the diagonal and zeros elsewhere:

$$\mathbf{P}_t^{(f)}(\boldsymbol{\theta}) = \begin{pmatrix} p_1(t) & 0 & 0 & 0 & 0 \\ 0 & p_2(t) & 0 & 0 & 0 \\ 0 & 0 & p_3(t) & 0 & 0 \\ 0 & 0 & 0 & p_4(t) & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (3)$$

$$\mathbf{P}_t^{(m)}(\boldsymbol{\theta}) = \begin{pmatrix} p_1(t) & 0 & 0 & 0 \\ 0 & p_2(t) & 0 & 0 \\ 0 & 0 & p_3(t) & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \quad (4)$$

where $p_j(t)$ is the probability of capturing individuals in stage j at time t . This notation corresponds to p_{jt} in Nichols et al. (1992). As written here, $\mathbf{P}_t^{(f)}$ and $\mathbf{P}_t^{(m)}$ assume that dead individuals are never captured ($p_0^{(f)} = p_0^{(m)} = 0$), but such captures could be included.

Transition and capture probability matrices can be defined separately for females and males when information on sex identification is available, as in our example, but it is not always possible or necessary to have a two-sex model. In such cases, only a single transition and capture probability matrix is needed.

Stage-assignment matrices

A stage-assignment matrix is defined for each individual each time it is captured. The diagonal elements of the matrix are proportional to the certainty of stage identification at time t (i.e., to the probability that the individual is in a given stage when it is captured). This probability should be known prior to estimating transition and capture probabilities. In our example, individual k is a female; its stage-assignment matrix is

$$\mathbf{U}_t^{(k)} = \begin{pmatrix} u_1^{(k)}(t) & 0 & 0 & 0 & 0 \\ 0 & u_2^{(k)}(t) & 0 & 0 & 0 \\ 0 & 0 & u_3^{(k)}(t) & 0 & 0 \\ 0 & 0 & 0 & u_4^{(k)}(t) & 0 \\ 0 & 0 & 0 & 0 & u_0^{(k)}(t) \end{pmatrix} \quad (5)$$

where $u_j^{(k)}(t)$ is the probability that individual k at time t is in stage j ($j = 1, 2, 3, 4$). Similarly, if individual k is male, its stage-assignment matrix is

$$\mathbf{U}_t^{(k)} = \begin{pmatrix} u_1^{(k)}(t) & 0 & 0 & 0 \\ 0 & u_2^{(k)}(t) & 0 & 0 \\ 0 & 0 & u_3^{(k)}(t) & 0 \\ 0 & 0 & 0 & u_0^{(k)}(t) \end{pmatrix} \quad (6)$$

Because we assume that the capture probability of dead individuals is zero, the value for $u_0^{(k)}(t)$ will not enter into the likelihood calculations. Multiplication of $\mathbf{U}_t^{(k)}$ by a scalar has no effect on the maximum likelihood estimates.

If the stage of the individual is known with certainty, its stage-assignment matrix contains a one in the corresponding diagonal entry and zeros elsewhere. On the other hand, if the stage of an individual is completely unknown, the identity matrix can be used for $\mathbf{U}_t^{(k)}$. This specifies a uniform probability distribution over the possible stages. Alternatively, if an independent assessment of the probability is available, it can be entered into the matrix. For example, in an age-structured model of fish, the age of fish is sometimes determined from their length using age-length keys (e.g., Fournier and Archibald 1982, Deriso et al. 1985, Quinn and Deriso 1999). Such a key could provide the probability distribution of ages of the fish, which can be entered into the stage-assignment matrices, for an age-structured model.

Likelihood

The likelihood of the parameter vector $\boldsymbol{\theta}$ contains contributions from the capture history of each individual. We denote by $l_k(\boldsymbol{\theta})$ the contribution to the likelihood from individual k ; it is proportional to the probability of the capture history. That probability is the sum of the probabilities of all possible sequences of transitions that could have been taken by the individual k . There may be many such possibilities. Their sum, however, can be calculated using the transition, capture probability, and stage-assignment matrices by the following algorithm. We assume that the individual is first captured at time t_1 .

- 1) Categorize individual k by its stage at its first capture, taking uncertainty in stage assignment into account,

$$\mathbf{U}_{t_1}^{(k)} \mathbf{e} \quad (7)$$

where \mathbf{e} is a vector of ones. This product is a vector whose entries are proportional to the probabilities of the initial stage of the individual at t_1 .

- 2) Calculate the probability distribution of the stage at t_2 by multiplying this vector by the transition matrix Φ_{t_1} :

$$\Phi_{t_1} \mathbf{U}_{t_1}^{(k)} \mathbf{e} \quad (8)$$

- 3) Calculate the probabilities of observation outcomes at t_2 . If individual k was captured at t_2 , multiply by the sighting matrix \mathbf{P}_{t_2} :

$$\mathbf{P}_{t_2} \Phi_{t_1} \mathbf{U}_{t_1}^{(k)} \mathbf{e} \quad (9)$$

If individual k was not captured at t_2 , multiply by $(\mathbf{I} - \mathbf{P}_{t_2})$:

$$(\mathbf{I} - \mathbf{P}_{t_2}) \Phi_{t_1} \mathbf{U}_{t_1}^{(k)} \mathbf{e} \quad (10)$$

where \mathbf{I} is the identity matrix.

- 4) Account for stage identification at t_2 by multiplying by the stage assignment matrix. If individual k was captured at t_2 ,

$$\mathbf{U}_{t_2}^{(k)} \mathbf{P}_{t_2} \Phi_{t_1} \mathbf{U}_{t_1}^{(k)} \mathbf{e}. \quad (11)$$

If individual k was not captured at t_2 ,

$$\mathbf{I}(\mathbf{I} - \mathbf{P}_{t_2}) \Phi_{t_1} \mathbf{U}_{t_1}^{(k)} \mathbf{e}. \quad (12)$$

- 5) Repeat steps 2–4 until the end of the capture history for individual k . The result is a vector whose i th entry is proportional to the probability of all the pathways by which individual k could have moved from its initial stage at t_1 to stage i at t_h and that are compatible with its capture history.
- 6) The final step is to sum the resulting vector of probabilities to obtain

$$l_k(\theta) = \mathbf{e}^T \mathbf{U}_{t_h}^{(k)} \cdots \Phi_{t_1} \mathbf{U}_{t_1}^{(k)} \mathbf{e}. \quad (13)$$

In this algorithm, the probability distribution of the individual's stage is updated sequentially over time, taking into account the new data available at each time step and possible stage transitions determined by the stage structure. Therefore, the right-hand side of Eq. 13 is the probability of the capture history for individual k , taking into account all possible transition sequences compatible with that history.

The likelihood $l_k(\theta)$ is calculated using only female or male matrices if the sex of individual k is known. If the sex of individual k is uncertain, algorithm (13) is repeated to get likelihoods $l_k^{(f)}(\theta)$ and $l_k^{(m)}(\theta)$ using the female- and male-specific matrices, respectively. Then, the likelihood $l_k(\theta)$ is

$$l_k(\theta) = p_f l_k^{(f)}(\theta) + (1 - p_f) l_k^{(m)}(\theta) \quad (14)$$

where p_f is the probability that the individual k is female. The probability p_f is 1 or 0 when the sex of the individual is known to be female or male, respectively. If the sex of the individual is unknown, a probability must be provided to calculate the likelihood.

Some examples of probabilities of the capture histories of individuals with four capture periods are shown in Table 1. Because our example contains multiple stages, many possible capture histories exist, of which only a few are shown in Table 1. For simplicity, we assume that the sex of all individuals is known to be female.

None of the likelihoods in Table 1 contains \mathbf{P}_1 , because the probability of a capture history is always conditional on the first capture; therefore, capture probability at the first sampling time cannot be estimated. For the same reason, the likelihoods of individuals 5, 7, 8, 11, 12, and 13 do not begin at time $t = 1$, because capture histories prior to the first capture of an individual do not enter into probability calculations.

Given the likelihood functions $l_k(\theta)$ for all individuals, the likelihood associated with the data consisting of n capture histories is proportional to the product of the n likelihood functions:

$$L(\theta) \propto \prod_{k=1}^n l_k(\theta). \quad (15)$$

TABLE 1. Some possible capture histories of North Atlantic right whales corresponding to the example stage structure in Fig. 1 and their likelihood.

Individual (k)	Capture history†	Likelihood $l_k(\theta)$
1	3433	$\mathbf{e}^T \mathbf{U}_4^{(1)} \mathbf{P}_4 \Phi_3 \mathbf{U}_3^{(1)} \mathbf{P}_3 \Phi_2 \mathbf{U}_2^{(1)} \mathbf{P}_2 \Phi_1 \mathbf{U}_1^{(1)} \mathbf{e}$
2	122X	$\mathbf{e}^T (\mathbf{I} - \mathbf{P}_4) \Phi_3 \mathbf{U}_3^{(2)} \mathbf{P}_3 \Phi_2 \mathbf{U}_2^{(2)} \mathbf{P}_2 \Phi_1 \mathbf{U}_1^{(2)} \mathbf{e}$
3	22X3	$\mathbf{e}^T \mathbf{U}_4^{(3)} \mathbf{P}_4 \Phi_3 (\mathbf{I} - \mathbf{P}_3) \Phi_2 \mathbf{U}_2^{(3)} \mathbf{P}_2 \Phi_1 \mathbf{U}_1^{(3)} \mathbf{e}$
4	1X22	$\mathbf{e}^T \mathbf{U}_4^{(4)} \mathbf{P}_4 \Phi_3 \mathbf{U}_3^{(4)} \mathbf{P}_3 \Phi_2 (\mathbf{I} - \mathbf{P}_2) \Phi_1 \mathbf{U}_1^{(4)} \mathbf{e}$
5	X343	$\mathbf{e}^T \mathbf{U}_4^{(5)} \mathbf{P}_4 \Phi_3 \mathbf{U}_3^{(5)} \mathbf{P}_3 \Phi_2 \mathbf{U}_2^{(5)} \mathbf{e}$
6	12XX	$\mathbf{e}^T (\mathbf{I} - \mathbf{P}_4) \Phi_3 (\mathbf{I} - \mathbf{P}_3) \Phi_2 \mathbf{U}_2^{(6)} \mathbf{P}_2 \Phi_1 \mathbf{U}_1^{(6)} \mathbf{e}$
7	XX33	$\mathbf{e}^T \mathbf{U}_4^{(7)} \mathbf{P}_4 \Phi_3 \mathbf{U}_3^{(7)} \mathbf{e}$
8	X43X	$\mathbf{e}^T (\mathbf{I} - \mathbf{P}_4) \Phi_3 \mathbf{U}_3^{(8)} \mathbf{P}_3 \Phi_2 \mathbf{U}_2^{(8)} \mathbf{e}$
9	4XX3	$\mathbf{e}^T \mathbf{U}_4^{(9)} \mathbf{P}_4 \Phi_3 (\mathbf{I} - \mathbf{P}_3) \Phi_2 (\mathbf{I} - \mathbf{P}_2) \Phi_1 \mathbf{U}_1^{(9)} \mathbf{e}$
10	2X2X	$\mathbf{e}^T (\mathbf{I} - \mathbf{P}_4) \Phi_3 \mathbf{U}_3^{(10)} \mathbf{P}_3 \Phi_2 (\mathbf{I} - \mathbf{P}_2) \Phi_1 \mathbf{U}_1^{(10)} \mathbf{e}$
11	X3X4	$\mathbf{e}^T \mathbf{U}_4^{(11)} \mathbf{P}_4 \Phi_3 (\mathbf{I} - \mathbf{P}_3) \Phi_2 \mathbf{U}_2^{(11)} \mathbf{e}$
12	XX1X	$\mathbf{e}^T (\mathbf{I} - \mathbf{P}_4) \Phi_3 \mathbf{U}_3^{(12)} \mathbf{e}$
13	X3XX	$\mathbf{e}^T (\mathbf{I} - \mathbf{P}_4) \Phi_3 (\mathbf{I} - \mathbf{P}_3) \Phi_2 \mathbf{U}_2^{(13)} \mathbf{e}$
14	2XXX	$\mathbf{e}^T (\mathbf{I} - \mathbf{P}_4) \Phi_3 (\mathbf{I} - \mathbf{P}_3) \Phi_2 (\mathbf{I} - \mathbf{P}_2) \Phi_1 \mathbf{U}_1^{(14)} \mathbf{e}$

Notes: When the stage of the captured individual is i , $\mathbf{U}_i^{(k)}$ is a matrix with 1 in the i th row of the i th column and 0 elsewhere. Terms are as follows: Φ_t , transition probability matrix at time t ; $\mathbf{U}_i^{(k)}$, stage assignment matrix for individual k at time t ; \mathbf{P}_t , capture probability matrix at time t ; \mathbf{I} , identity matrix; \mathbf{e} , vector containing 1's in its entries.

† X indicates that the individual was not captured; numbers indicate the stage of captured individuals.

Here, we assume that individuals are captured and make stage transitions independently, but based on identical probability distributions (i.e., we assume that the number of outcomes falling into the possible capture history sequences is multinomial).

Maximum likelihood estimates ($\hat{\theta}$) are found by maximizing $L(\theta)$. The likelihood function can be maximized numerically using software such as MATLAB (1999). For example, the MATLAB routine "fminu()" can be used to find the maximum likelihood by minimizing $-\log L(\theta)$.

TRANSITION PROBABILITIES AS FUNCTIONS OF COVARIATES

Transition probabilities $\phi_{ji}(t)$ may change over the course of a study, and the changes may be correlated with various factors. We would like to model the probabilities as functions of covariates measuring those factors. For example, population density and sampling effort were used to model the survival and capture probabilities in studies of the roe deer (*Capreolus capreolus*) and the common lizard (*Lacerta vivipara*), respectively (Lebreton et al. 1992), and time has been used to model the survival probability of the Northern Spotted Owl (*Strix occidentalis caurina*; Forsman et al. 1996) and the North Atlantic right whale (Caswell et al. 1999).

Covariates are incorporated in the transition probability using a link function. The link function must satisfy the constraint that each column of the transition matrix sums to 1, and each entry of the matrix must lie between 0 and 1. A flexible function that satisfies these properties is the polychotomous logistic function,

which is derived by expressing the log of the odds ratio as a linear function of the covariates (Hosmer and Lemeshow 1989). Let $x_i^{(d)}$ be the value of d th covariate at time t . The polychotomous logistic function is

$$\phi_{ji}(t) = \frac{\exp\left(\alpha_{ji} + \sum_d \beta_{ji}^{(d)} x_i^{(d)}\right)}{1 + \sum_j \exp\left(\alpha_{ji} + \sum_d \beta_{ji}^{(d)} x_i^{(d)}\right)} \quad (16)$$

where α_{ji} is an intercept parameter, and $\beta_{ji}^{(d)}$ is a slope parameter associated with the d th covariate. When all of the slope parameters are zero for all d , i , and j , the transition matrix is constant over time. The simple logistic function that is often used in mark-recapture literatures (e.g., Burnham et al. 1987, Lebreton et al. 1992) is a special case of the polychotomous logistic function for a binary outcome.

MATRIX POPULATION MODELS

Population projection matrices contain both transition probabilities and fertilities (see Caswell 2001). Because the transition probabilities are estimated by the MSMR method, we can construct the projection matrix if we know the fertility terms. In this section, we show an example of how those terms might be obtained, and how to compute confidence intervals for population growth rate calculated from the population matrix.

Conversion from a transition matrix to a population projection matrix

The right whale example provides enough information to write a two-sex model. To do so, we renumber the male stages in Fig. 1 as 5, 6, 7. Letting $\phi_{ji}(t)$ denote the transition probability as before, the projection matrix is:

$$\mathbf{A}_t = \begin{pmatrix} 0 & F_2(t) & F_3(t) & 0 & 0 & 0 & 0 \\ \phi_{21}(t) & \phi_{22}(t) & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_{32}(t) & \phi_{33}(t) & \phi_{34}(t) & 0 & 0 & 0 \\ 0 & \phi_{42}(t) & \phi_{43}(t) & 0 & 0 & 0 & 0 \\ 0 & F_6(t) & F_7(t) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_{65}(t) & \phi_{66}(t) & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_{76}(t) & \phi_{77}(t) \end{pmatrix}. \quad (17)$$

The upper-left and lower-right blocks describe production of females by females and males by males, respectively. The entries in the lower-left block describe production of males by females.

When constructing a population projection matrix, transition probability and fertility terms are often estimated from two separate data sets (Caswell 2001), but the fertility terms can be estimated directly using the MSMR method if the stage structure includes mothers that give birth between two consecutive sampling periods (i.e., stage 4 in our example). Each time an

individual enters this stage, it gives birth; therefore, transition probabilities into the fertile stage are also probabilities of giving birth. If the number of female and male births at each reproductive event are b_f and b_m , respectively, the fertility terms in the projection matrix are given by the product of the number of offspring and the transition probabilities:

$$F_2(t) = b_f \phi_{42}(t) \quad (18)$$

$$F_3(t) = b_f \phi_{43}(t) \quad (19)$$

$$F_6(t) = b_m \phi_{42}(t) \quad (20)$$

$$F_7(t) = b_m \phi_{43}(t). \quad (21)$$

An important assumption in these fertility terms is that mothers and their newborns have the same probability of being captured during sampling. To ensure that this condition is satisfied, when mothers are captured, their offspring should also be captured and entered into the database as new individuals. Similarly, when newborns are captured, their mothers should be captured and identified as mothers. Later, we will show one example of remedial methods when the equal ‘‘capturability’’ assumption is not met.

Model (17) is female-dominant; males do not affect population dynamics. This assumption is often legitimate when the population size of males is large enough that searching for a partner does not limit reproduction by females. Thus, for calculation of population growth rate, the two-sex matrix may be reduced to the female matrix:

$$\mathbf{A}_t = \begin{pmatrix} 0 & F_2(t) & F_3(t) & 0 \\ \phi_{21}(t) & \phi_{22}(t) & 0 & 0 \\ 0 & \phi_{32}(t) & \phi_{33}(t) & \phi_{34}(t) \\ 0 & \phi_{42}(t) & \phi_{43}(t) & 0 \end{pmatrix}. \quad (22)$$

Confidence intervals for population growth rate

The long-term population growth rate implied by a projection matrix \mathbf{A}_t is given by the dominant eigenvalue λ of \mathbf{A}_t . A confidence interval for λ can be approximated from the MSMR statistics, using the eigenvalue sensitivity formula and the covariance matrix of the parameters.

The eigenvalue sensitivity formula is

$$\frac{\partial \lambda}{\partial a_{ji}} = \frac{v_j w_i}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (23)$$

where \mathbf{v} and \mathbf{w} are the left- and right-dominant eigenvectors of the population projection matrix (Caswell 1978, 2001). If the a_{ij} are functions of some other parameters θ_r , the sensitivity of λ to θ_r is:

$$\frac{\partial \hat{\lambda}}{\partial \theta_r} = \sum_j \sum_i \frac{\partial \hat{\lambda}}{\partial a_{ji}} \frac{\partial \hat{a}_{ji}}{\partial \theta_r}. \quad (24)$$

Now let $\boldsymbol{\theta}$ be a vector of parameters estimated by the

MSMR method. An approximate 95% CI for λ is calculated by

$$\hat{\lambda} \pm 1.96 \sqrt{\sum_{q,r} \hat{c}_{qr} \left(\frac{\partial \hat{\lambda}}{\partial \theta_q} \right) \left(\frac{\partial \hat{\lambda}}{\partial \theta_r} \right)} \quad (25)$$

where \hat{c}_{qr} is the (qr) th entry of the estimated covariance matrix $\hat{\mathbf{C}}$. The covariance matrix \mathbf{C} can be estimated by inverting the Hessian matrix (the information matrix; e.g., Burnham et al. 1987). This method of constructing the confidence interval is an application of the delta method (see Seber 1982: Chapter 1), taking advantage of the existence of the eigenvalue sensitivity formula (23).

APPLICATION TO THE NORTH ATLANTIC RIGHT WHALE

We have applied the MSMR method to data on the North Atlantic right whale (*Eubalaena glacialis*). The northern right whale is considered one of the most endangered large whale species in the world (Waring et al. 1999). The current population in the western North Atlantic contains fewer than 300 individuals. They migrate from the Bay of Fundy, which is a summer feeding ground, to the coast of Florida, which is a winter calving ground. Caswell et al. (1999) showed that the crude survival probability of individuals in this population has been declining since 1980.

Data on the North Atlantic right whale have been collected by the New England Aquarium and consist of annual sighting histories of photographically identified animals from 1980 to 1997 (Crone and Kraus 1990). For the purpose of our analysis, we consider individuals to have been marked on the occasion of their first identification, and recaptured when they were resighted during a subsequent year. Of the 372 individuals used for the analysis, 141 are known to be females and 143 to be males. We assumed the remainder to be either female or male with 50% probabilities. A few sightings of dead individuals exist, but are not included in this analysis.

Stage-assignment matrices

We attempted to assign each individual at each capture to one of the stages shown in Fig. 1. A whale was considered mature if it was known to be ≥ 9 yr old or, for females, if it had been observed with a calf. Stages could be assigned with certainty in 78% of the captures. The remainder were known to be either immature or mature; for these captures, we must calculate the entries u_2 , u_3 , u_5 , and u_6 of the stage-assignment matrices (5) and (6). In the absence of information to the contrary, we assume that these probabilities are constant over time and across individuals, but differ between females and males. Because we use different criteria to assign females and males to stages, we expect that the probability distribution of stages among the unknown-staged captures would differ for females and males.

When the stage of a captured individual is uncertain, the (2, 2) entry of the stage-assignment matrix is the probability that the individual is immature, given that the stage is uncertain. Similarly, the (3, 3) entry is the probability that the individual is mature, given that the stage is uncertain. The other entries are all zero. To express these probabilities in mathematical form, let X be a random variable giving the stage of an individual and let Y be a random variable taking the value 1 if the stage is known and 0 if the stage is uncertain. Then the two probabilities are:

$$u_2 = \Pr(X = 2 | Y = 0) \quad (26)$$

$$u_3 = \Pr(X = 3 | Y = 0) = 1 - u_2. \quad (27)$$

To calculate $\Pr(X = 2 | Y = 0)$, we use Bayes' Rule to derive

$$\Pr(X = 2 | Y = 0) = \frac{\Pr(X = 2) - \Pr(X = 2 | Y = 1)\Pr(Y = 1)}{1 - \Pr(Y = 1)}. \quad (28)$$

Here, $\Pr(Y = 1)$ is the probability that the stage of an immature or mature individual is known, and can be estimated from the capture history data as

$$\Pr(Y = 1) = \frac{N_2 + N_3}{N_2 + N_3 + N_u} \quad (29)$$

where N_2 , N_3 , and N_u are numbers of captures of immature, mature, and uncertain stages, respectively. $\Pr(X = 2 | Y = 1)$ is the probability that the stage of an immature or mature individual is immature, given that the stage is known. This probability can be calculated from the capture history data as

$$\Pr(X = 2 | Y = 1) = \frac{N_2}{N_2 + N_3}. \quad (30)$$

Finally, $\Pr(X = 2)$ is the probability that the stage is immature, given that the stage is either immature or mature, regardless of whether the stage is known or uncertain. To estimate this probability, we estimated the parameters for a time-invariant projection matrix from the subset of the data containing only certain captures. From the stable stage distribution \mathbf{w} (i.e., the right eigenvector associated with the dominant eigenvalue) of this matrix, we calculated the proportion of individuals in stage 2 among stages 2 and 3 and used it as our estimate of $\Pr(X = 2)$:

$$\Pr(X = 2) = \frac{w_2}{w_2 + w_3}. \quad (31)$$

For males, the same method was applied to the male stages (5 and 6). It should be noted that these calculations work best when the capture probabilities of stages 2 and 3 (5 and 6 for males) are similar. Otherwise, each count in (29) and (30) should be divided by the corresponding capture probability (Nichols et al.

TABLE 2. Dependence of the best capture model for the North Atlantic right whale on effort level and time.

Stage†	Northern effort‡	Southern effort§
Immature female (2)	yes	yes
Mature female (3)	yes	yes
Mature female with calf (4)	no	no
Immature male (6)	yes	yes
Mature male (7)	yes	yes

† The sighting probability of calves cannot be estimated because the capture of a calf is always the first capture of that individual.

‡ The Northern region includes Bay of Fundy, Brown's Bank, Great South Channel, and Massachusetts Bay.

§ The Southern region includes the coast of Florida and Georgia.

1994). The end result of these calculations is in $u_2 = 0.87$, $u_3 = 0.13$, $u_5 = 0.30$, and $u_6 = 0.70$.

Capture probabilities

Capture probabilities were modeled as binary logistic functions of estimated sampling effort levels in the northern and southern regions, which are major feeding and calving grounds, respectively. These effort levels were approximated by the number of sampling dates per year in each region. We created models by including all possible combinations of effort levels for all possible combination of stages. This resulted in 1024 models. The best capture model among the 1024 candidate models was selected using Akaike Information Criteria, AIC (Akaike (1973)). Because the sample size is large, we did not use the small-sample adjustment to AIC (i.e., AIC_c in Burnham and Anderson [1998]). The difference in AIC between the best and the second-best capture models was about 2, indicating that the support for the best model relative to the second best model is high (Burnham and Anderson 1998). Furthermore, the four best models differ only in how capture probability of mothers depends on effort; in all cases, the capture probability was consistently close to 1 throughout the sampling period. Therefore, we used only the best model shown in Table 2. The capture probabilities of immature males and females did not differ significantly in the best model, based on a likelihood ratio test. Therefore, we set these two capture probabilities equal and used the resulting capture probability model for further analysis.

Transition probabilities

Although we know that the vital rates have varied over time (Fujiwara and Caswell 2001), for this example we fit a model in which the transition probabilities are constant over time (i.e., no covariates). We also assumed that the survival probabilities of female and male calves are the same. This model gives a time-averaged picture of right whale demography. Estimated capture and transition probabilities are shown in Fig. 2 and Table 3, respectively.

The population projection matrix for female right whales is:

$$\mathbf{A} = \begin{pmatrix} 0 & 0.5\phi_{42}\sqrt{\phi_{34}} & 0.5\phi_{43}\sqrt{\phi_{34}} & 0 \\ \phi_{21} & \phi_{22} & 0 & 0 \\ 0 & \phi_{32} & \phi_{33} & \phi_{34} \\ 0 & \phi_{42} & \phi_{43} & 0 \end{pmatrix} \quad (32)$$

This matrix is the same as (22), but with a particular set of assumptions defining the fertility terms. Consider $F_2(t)$ in (22). When a female moves from stage 2 to stage 4 (with probability ϕ_{42}), she gives birth; the newborn is female with probability 0.5. To appear as a calf in stage 1 at $t + 1$, the newborn calf must survive long

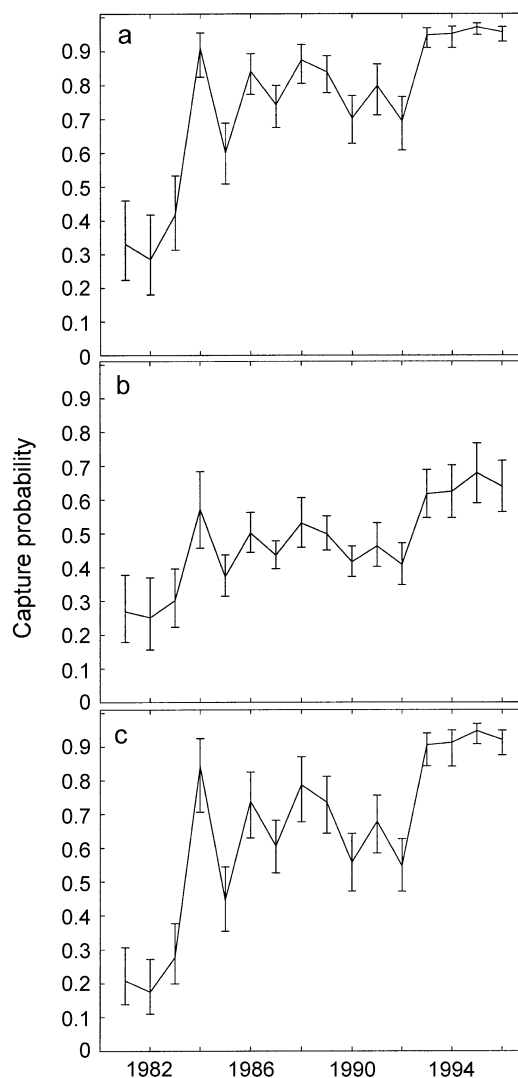


FIG. 2. Stage-specific capture probabilities, 1981–1996, for (a) immature male and female, (b) mature female, and (c) mature male right whales. Error bars indicate point-wise 95% confidence intervals (CI) estimated from 1000 parametric bootstrap samples generated assuming a multivariate normal distribution of the logit of parameters. The covariance matrix of the distribution was estimated as the inverse of the Hessian matrix (see Burnham et al. 1987, Lebreton 1995). Mothers had a constant capture probability of 0.99 (95% CI = [0.98, 1.00]).

TABLE 3. Estimated transition probabilities for the North Atlantic right whale.

Transition probability	Mean	95% CI
ϕ_{21}	0.92	[0.74 0.98]
ϕ_{22}	0.86	[0.81 0.89]
ϕ_{32}	0.08	[0.06 0.12]
ϕ_{42}	0.02	[0.01 0.03]
ϕ_{33}	0.80	[0.77 0.83]
ϕ_{43}	0.19	[0.16 0.22]
ϕ_{34}	0.83	[0.77 0.88]
ϕ_{66}	0.76	[0.72 0.79]
ϕ_{76}	0.19	[0.16 0.23]
ϕ_{77}	0.95	[0.94 0.96]

Notes: The confidence intervals were estimated from 1000 parametric bootstrap samples generated assuming multivariate normal distributions of parameters. The covariance matrix of the distribution was estimated as the inverse of the Hessian matrix (Burnham et al. 1987, Lebreton 1995).

enough to be catalogued. Although newborn calves have distinct markings, they are harder to distinguish individually than other stages. Therefore, calf survival is estimated from the time when the calf is seen sufficiently well to permit identification, which is not necessarily on its first sighting. We assumed that calves, on average, are identified midway through their first year, and that the mother must survive this long (with probability $\phi_{34}^{0.5}$) in order for the calf to survive. $F_3(t)$ is calculated in a similar manner.

From this matrix, we estimated the long-term population growth rate and its confidence interval. They are $\lambda = 1.01$ (95% CI = [1.00, 1.02]). This result shows that the North Atlantic right whale population has been growing by 1% annually, on average, from 1980 to 1997. (In fact, a time-varying model estimated by this same procedure concludes that the growth rate has declined from $\lambda = 1.03$ to $\lambda = 0.98$ over this time period (Fujiwara and Caswell 2001).) This matrix can now be analyzed to obtain the stable stage distribution, reproductive value, damping ratio, sensitivity and elasticity of λ , and other demographic statistics.

DISCUSSION

The method presented here estimates a population projection matrix from mark-recapture data, which is one of the most commonly available data types for animal populations. Once the population projection matrix is estimated, it is subject to complete demographic analysis; such analyses provide powerful tools for conservation biology (e.g., Caswell 1989, 2001, Tuljapourkar and Caswell 1997). They can be used to assess the causes of past population declines and to predict the effect of possible future management actions. Because population projection matrices contain many parameters, it has been difficult to estimate them accurately. This has been especially true for animals that are not captured at every sampling period.

The likelihood calculations here are simpler than those described in Nichols et al. (1992). This allows

the use of mathematical software packages such as MATLAB, so the transition and capture probability models need not be limited to those available in mark-recapture packages such as MARK (White and Burnham 1999), MSSURVIV (Hines 1994), or SURVIV (White 1983).

Our method permits the use of capture histories with uncertain stage and sex. Individuals with such uncertainties tend to have lower survival rates than the rest of a population, because individuals that survive longer have more chances for accurate assessment of stage and sex identification. For example, right whales are considered mature at 9 yr of age. If animals that die within nine years from their first capture are excluded because their stage is uncertain, then we would overestimate the survival probability. Observations with uncertain stage or sex should never be discarded in parameter estimation. Our approach is one way to deal with this problem.

The stage structure that we used in this paper contains as a stage females that have given birth between consecutive sampling periods. This stage makes the conversion of the transition matrix into a population projection matrix relatively simple. Because the purpose of the MSMR statistics often is to estimate a population projection matrix, we recommend the use of this type of stage structure when possible.

The polychotomous logistic function is a flexible way to allow transition probabilities to decrease or increase with a covariate while satisfying the requirement that each column of the transition matrix sum to one. When time is used as a covariate, the polychotomous function allows inferences about temporal trends in stage-specific transition rates. This approach has been applied to the North Atlantic right whale data (Fujiwara and Caswell 2001).

Multi-stage mark-recapture data arise in many applications. For example, Nichols and Kendall (1995) use them in population genetics context to test trade-offs between survival and reproduction. Hestbeck et al. (1991) use them to estimate spatial movement of individuals. We have applied them to deal with the problem of temporary emigration (Fujiwara Caswell 2002). We hope that the extensions of the analytical method presented here will make them even more useful.

Mark-recapture data are expensive to collect, and they should be analyzed as completely as possible. If information on the stage of individuals (e.g., age, size, other developmental stages, or geographic locations) is collected in addition to the basic mark-recapture data, then MSMR statistics can be applied. The stage information need not be complete because our method incorporates uncertainties in stage identifications. The value of being able to use matrix population models for conservation makes it worthwhile to collect stage-specific data whenever possible.

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