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Tagging Models for Estimating Survival Rates When Tag Visibility Changes over Time: Partial-Year Tabulation of Recaptures

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ARTICLE

Tagging Models for Estimating Survival Rates When Tag Visibility Changes over Time: Partial-Year Tabulation of Recaptures

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Abstract
Brownie tagging models are commonly used for estimating survival rates from multiyear tagging studies. The basic model, model 1, assumes that all tags have the same recovery rate. An alternative, model 0, allows newly tagged animals to have a different tag recovery rate than previously tagged animals. This feature might be necessary because new tags are less fouled and more visible than previously applied tags and thus have a higher reporting rate. Model 0 accommodates the different recovery rates through the use of additional parameters, which leads to larger standard errors than in model 1. Model 0′, a new model, also allows newly tagged animals to have a different tag recovery rate than previously tagged ones. It makes use of a known fouling time (the time it takes for tags on newly tagged animals to have the same visibility as tags on previously tagged animals) to divide the year into two parts. During the first part of the year the tags on newly tagged animals are more visible than those on previously tagged ones, while in the second part all tags have the same visibility. Dividing the year into parts and recording the recaptures in each part avoids the failure of the assumption that the reporting rate is constant for all tagged animals, achieves greater precision, and provides estimates of the survival rate at the end of the second year instead of at the end of the third year (as in model 0). The superiority of model 0′ over models 0 and 1 is demonstrated for several cases using Monte Carlo simulation. Simulations were based on the queen conch *Strombus gigas* fishery of the Turks and Caicos Islands, British West Indies. For that fishery, if the tag reporting rate is altered by 25% or more by fouling, it is beneficial to use model 0′ instead of model 1.

In multiyear tagging studies a sample of the population, termed a cohort, is captured, tagged, and released at the start of each of several years. Brownie et al. (1978, 1985) described a suite of models that enable the user to estimate age- and year-specific survival rates from tag recoveries that are tabulated by year. Annual survival rate, represented by S, is defined as the fraction of the population alive at the start of the year that is still alive at the end of the year. Additionally, Brownie models enable one to obtain estimates of the fraction of tagged animals that are caught and reported, termed the tag recovery rate and denoted by f.

The basic age-invariant and year-specific model described by Seber (1970), Youngs and Robson (1975), and Brownie et al. (1978, 1985) is known as model 1. Alternative models described by Brownie et al. (1978, 1985) enable the user to impose year-specific constraints on the parameters f and S and to allow newly tagged animals to have a different tag recovery rate than previously tagged animals. Today it is common to refer to all of these models as Brownie models.

The assumptions of Brownie models are well documented (e.g., Brownie et al. 1978, 1985; Pollock and Raveling 1982). Those for model 1 include the following: (1) the tagged sample

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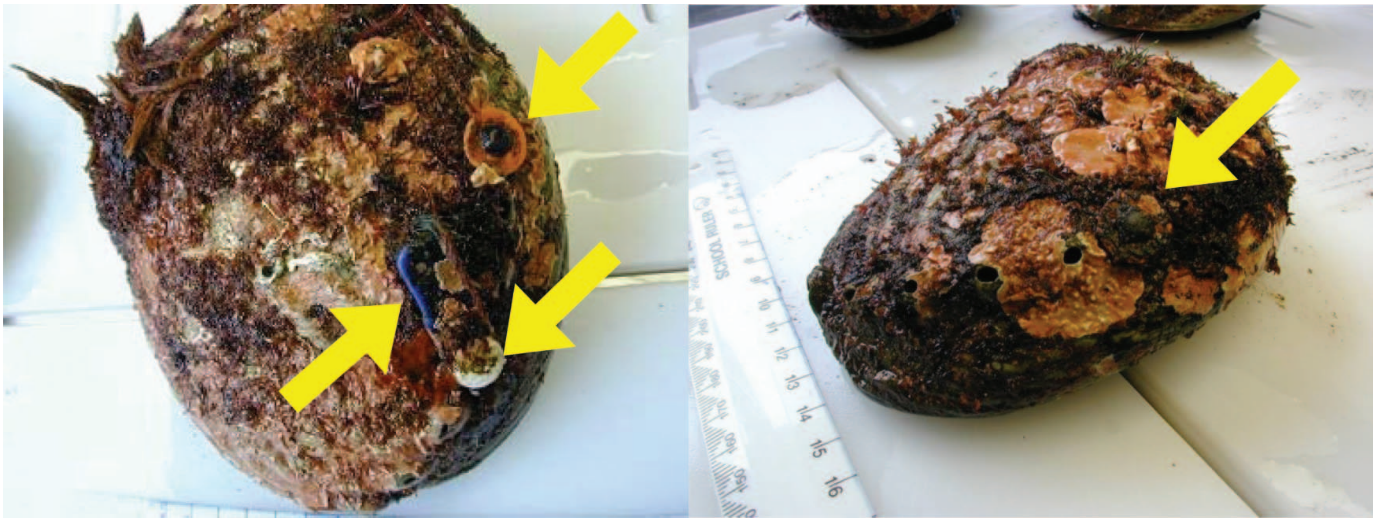

FIGURE 1. Blacklip abalone from Tasmania with three lightly fouled tags (left) and one highly fouled tag (right) (photos provided by David Tarbath, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania). The blue and white tags in the left photo are attached to the same respiratory pore of the shell. The arrows indicate the positions of the tags.

is representative of the target population; (2) short-term tag loss and tag-induced mortality (i.e., those occurring over a few days immediately after tagging) are constant from year to year; (3) there is no long-term tag loss (i.e., tag loss occurring over periods of months to years); (4) long-term survival is not affected by tagging or handling processes; (5) the fate of each tagged animal is independent of that of other tagged animals; (6) all animals within a tagged cohort experience the same S and f within a time period (known as homogeneous survival and tag recovery rates); and (7) the tag recovery rate, f, does not vary among cohorts within a given year.

Various models have been proposed that allow for violations of the assumptions of model 1. Here, we focus on a model described by Brownie et al. (1978) known as model 0 that allows for the violation of assumption 7, that is, newly tagged cohorts are allowed to have different tag recovery rates than previously tagged cohorts. Tagged cohorts might not be subject to the same tag recovery rate during a time period if tags become less visible over time due to factors such as tag fouling (for an example of the fouling of tags on blacklip abalone *Haliotis rubra* shells in Tasmania, see Figure 1).

The tag recovery rate f can be expressed as a product of its components (Pollock et al. 1991; Hoenig et al. 1998a):

$$f = \varphi \lambda u, \tag{1}$$

where φ is a composite factor representing the effective number of tags released, here defined as a combination of the short-term survival rate from tagging and the short-term probability of tag retention; λ is the tag reporting rate, or the probability that a tag will be reported if the fish is recaptured; and u is the exploitation rate, or the expected fraction of the population alive at the start of the year that dies due to harvesting during the year. The tag reporting rate can be further thought of as a combination of factors that affect the probability of a tag's being reported if the animal is recaptured, including the visibility of the tag.

If the visibility of the tag is constant over time and does not vary within cohorts, then visibility is of little interest except inasmuch as low visibility may cause a low rate of tag returns. If tag visibility changes with time at liberty, this will affect the tag reporting rate differently among cohorts, and thus the tag recovery rate, which introduces bias into the parameter estimates. In a variety of tagging studies, tag fouling has been reported to be prominent (Lowry and Suthers 1998; Tarbath 1999; Dicken et al. 2006; Verweij and Nagelkerken 2007). The use of antifouling materials to prevent fouling on tags may alleviate the problem of reduced tag visibility, but such materials could potentially harm the tagged animal. Other studies have reported issues with tag visibility over time. Tagging programs using visible implant elastomer tags have reported diminishing tag visibility over time as a result of thickening of the skin overlying the tags (Curtis 2006; Reeves and Buckmeier 2009). The problem of tag visibility varying with time at liberty may be more prevalent than discussed in the literature for a variety of reasons, including poor communication between fishers and scientists and researchers' not knowing how to incorporate the change of tag visibility into their models and therefore assuming that it has no effect or their not understanding the bias it may introduce into the parameter estimates.

Brownie et al. (1978, 1985) introduced a model, model 0, that can account for the tag recovery rate of new tags being different from that of older tags for the first year each cohort is at liberty. This model differs from model 1, which assumes that all cohorts have the same tag recovery rate in a given year. Under both models, all cohorts at liberty for more than 1 year have the same tag reporting rate (within a given year), presumably because they have the same tag visibility.

If it takes new tags less than 1 year to have the same visibility as those on previously tagged animals, better use can be made of the data by partitioning the year into parts. The tag returns can be tabulated by portions of the year that account for the change in visibility. That is, in the first part of the year, new tags are becoming fouled or are fouled; in the second part of the year, all tags are fouled. We present such a model, model 0′, and study its properties by Monte Carlo simulation. Model 0′ is compared with model 1 and model 0 to provide guidance as to which model(s) should be applied based on the availability of information on tag fouling. Additionally, the importance of the degree to which tag visibility (and thus tag reporting) affects model performance is evaluated.

BROWNIE MODELS

Model 1

We start with the basic year-specific model (model 1). The data consist of an upper-triangular or trapezoidal array made up of observed values of r_{ij}, which are the realizations of R_{ij}, the random variable representing the number of animals tagged in year i ($i = 1, 2, \ldots, I$) and recaptured in year j, ($j = i, \ldots, J$, with $J \geq I$). The expected recaptures of animals tagged in year i and recaptured in year j is

$$E(R_{ij}) = \begin{cases} N_i f_j, & i = j \\ N_i f_j \left(\prod_{k=i}^{j-1} S_k \right), & i < j \leq J \end{cases}, \tag{2}$$

where the expression $E(\cdot)$ denotes the expected value of the variable within the parentheses, R_{ij} is as defined above, N_i is the number tagged and released at the start of year i ($i = 1, \ldots, I$), S_j is the fraction of the population alive at the start of year j that is still alive at the end of year j ($j = 1, \ldots, J$–1), and f_j is the tag recovery rate in year j ($j = 1, \ldots, J$). Note that there is an implicit category for all animals of a cohort that are never seen again, denoted Y_i. This can be expressed as

$$Y_i = N_i - \sum_{j=i}^{J} r_{ij}. \tag{3}$$

Brownie-type models can be expressed as the product of independent multinomial distributions of tag returns over time, with each tagged cohort giving rise to a multinomial distribution. The general form of the likelihood function Λ for product multinomial models can be expressed as

$$\Lambda \propto \prod_{i=1}^{I} \left(\prod_{j=i}^{J} P_{ij}^{r_{ij}} \right) \left(1 - \sum_{j=i}^{J} P_{ij} \right)^{Y_i}, \tag{4}$$

where the symbol $\propto$ means "is proportional to," P_{ij} is the cell probability of recovering a tagged animal in year j given that it was tagged in year i, that is,

$$P_{ij} = \frac{E(R_{ij})}{N_i}, \tag{5}$$

and the other symbols are as defined previously. For model 1, the cell probabilities P_{ij} are found by substituting equation (2) into equation (5).

TABLE 1. Expected recaptures under Brownie model 0, where N_i is the number tagged and released at the start of year i ($i = 1, \ldots, 1[1 = 3]$); S_j is the fraction of the population alive at the start of year j that is still alive at the end of year j ($j = 1, \ldots, J$–1 [$J = 4$]); f_j is the expected fraction of the tagged population at large at the start of year j that is caught and reported during year j ($j = 2, \ldots, 4$); and $f_i{}^*$ is the expected fraction of the newly tagged animals in year i that is caught and reported in year i ($i = 1, 2, 3$), with the asterisks indicating that the fraction reported is different for the first year a cohort is at liberty than for previously tagged cohorts, as the tags are still new and unfouled.

		Expected number recaptured in year			
Year	Number tagged	1	2	3	4
1	N_1	$N_1 f_1^*$	$N_1 S_1 f_2$	$N_1 S_1 S_2 f_3$	$N_1 S_1 S_2 S_3 f_4$
2	N_2		$N_2 f_2^*$	$N_2 S_2 f_3$	$N_2 S_2 S_3 f_4$
3	N_3			$N_3 f_3^*$	$N_3 S_3 f_4$

Model 0

We now consider model 0, which pertains to the case in which the tag recovery rate in a given time period is different for the first year a cohort is at liberty than it is for previously tagged cohorts. For each cohort, the model (Table 1) incorporates an additional parameter, $f_i{}^*$, which is the tag recovery rate in year i for newly tagged animals (the asterisk indicating that the fraction reported is for a cohort in its first year at liberty). Allowing the tag recovery rates to be different for the first year a cohort is at liberty causes model 0 to have more parameters than model 1, which leads to less precision in the parameter estimates. However, the unequal recovery rates for newly tagged and previously tagged cohorts afford protection from bias due to model misspecification. Note that model 1 is a special case of model 0.

To estimate the survival rate in the first year, 3 years of tag returns are needed instead of the 2 years needed for model 1. If recoveries are made for J years, then for the cohort tagged in year i there will be J–i–1 moment estimates of S_i. For example, for the cohort tagged in year 1, an estimate of S_1 is not possible in the second year (there will be three equations and four unknowns). This can be seen by looking at the moment estimates formed by the ratios of expectations (using R_{12} and R_{22} compared with R_{13} and R_{23}):

$$\frac{E(R_{12})}{E(R_{22})} = \frac{S_1 f_2}{f_2^*} \tag{6a}$$

$$\frac{E(R_{13})}{E(R_{23})} = \frac{S_1 S_2 f_3}{S_2 f_3} = S_1 \tag{6b}$$

(assuming equal numbers are tagged each year).

TABLE 2. Observed and expected recaptures under the new model 0′. The year is divided into two parts, (a) and (b). The observations consist of counts, r_{ijk}, that are the observed numbers of recaptures of animals tagged in year i that were recaptured in part k of year j. In the expected values, N_i is the number tagged and released at the start of year i, S_j is the fraction of the population alive at the start of year j that is still alive at the end of year j, S_{jk} is the fraction of the population alive at the start of year j that is still alive at the end of part k of year j, f_{jk} is the fraction of the tagged population at large at the start of year j that is caught and reported during part k of year j, and f^*_{ja} is the fraction of the newly tagged animals that is caught and reported in part (a) of year j, with the asterisk indicating that the fraction reported is different for part (a) of the first year a cohort is at liberty; $i = 1, \ldots, 3$; $j = 1, \ldots, 4$; and $k \in \{a,b\}$.

		Recaptures in time period							
Year	Number tagged	1a	1b	2a	2b	3a	3b	4a	4b
					Observed recaptures				
1	N_1	r_{11a}	r_{11b}	r_{12a}	r_{12b}	r_{13a}	r_{13b}	r_{14a}	r_{14b}
2	N_2			r_{22a}	r_{22b}	r_{23a}	r_{23b}	r_{24a}	r_{24b}
3	N_3					r_{33a}	r_{33b}	r_{34a}	r_{34b}
					Expected recaptures				
1	N_1	$N_1 f^*_{1a}$	$N_1 S_{1a} f_{1b}$	$N_1 S_1 f_{2a}$	$N_1 S_1 S_{2a} f_{2b}$	$N_1 S_1 S_2 f_{3a}$	$N_1 S_1 S_2 S_{3a} f_{3b}$	$N_1 S_1 S_2 S_3 f_{4a}$	$N_1 S_1 S_2 S_3 S_{4a} f_{4b}$
2	N_2			$N_2 f^*_{2a}$	$N_2 S_{2a} f_{2b}$	$N_2 S_2 f_{3a}$	$N_2 S_2 S_{3a} f_{3b}$	$N_2 S_2 S_3 f_{4a}$	$N_2 S_2 S_3 S_{4a} f_{4b}$
3	N_3					$N_3 f^*_{3a}$	$N_3 S_{3a} f_{3b}$	$N_3 S_3 f_{4a}$	$N_3 S_3 S_{4a} f_{4b}$

In practice, maximum likelihood estimates are found by maximizing equation (4) with appropriate cell probabilities obtained by substituting values in Table 1 for the values in equation (5). As before, Y_i is defined by equation 3.

NEW MODEL: MODEL 0′

The year can be divided into two parts. In the first part, part (a), newly tagged cohorts have new and highly visible tags that are becoming fouled and less visible; in the second part, part (b), the tags are fouled and have the same visibility as fouled tags on animals released in previous years. Dividing the year into two parts in this manner allows flexibility in the actual manner in which the tag fouling occurs since the division of the year into parts (a) and (b) does not depend on specifying the fouling process. The key is to make sure that the year is divided into parts (a) and (b) so that the tags on released animals in part (b) of the year during the first year at liberty have the same visibility as those on animals that have been at liberty for more than a year. The tag returns are tabulated separately for parts (a) and (b) of the year (Table 2).

For previously tagged cohorts there is a tag recovery rate parameter for each part of the year, namely, f_{ja} and f_{jb} for parts (a) and (b), respectively, of year j and a survival rate S_{ja} for part (a) of the year. Similar to model 0, model 0′ has an additional parameter in the form of an f^*_{ia} for the first part of the first year that cohort i is at liberty. In the second part of the first year a cohort is at liberty, the tag recovery rate is the same as for previously tagged cohorts (i.e., there is no asterisk on the recovery parameter; Table 2).

Because the year is divided into two parts, an estimate of survival can be made after two years; for example, for the survival rate in the first year the ratio of expectations is:

$$\frac{E\,(R_{12b})}{E\,(R_{22b})} = \frac{S_1 S_{2a} f_{2b}}{S_{2a} f_{2b}} = S_1. \tag{7}$$

This is in contrast to the situation for model 0, where an estimate can only be obtained after the end of the third year (equation 6b).

The likelihood is of the form

$$\Lambda \propto \prod_{i=1}^{I} \left(\prod_{j=i}^{J} \prod_{k\in\{a,b\}} P_{ijk}^{r_{ijk}} \right) \left(1 - \sum_{j=i}^{J} \sum_{k\in\{a,b\}} P_{ijk} \right)^{W_i}, \tag{8}$$

where P_{ijk} is the cell probability of recovering a tagged animal in part k of year j given that it was tagged in year i, that is,

$$P_{ijk} = \frac{E(R_{ijk})}{N_i},$$

and the other parameters are as defined previously. The likelihood is constructed as before using the cell probabilities from Table 2 (bottom). The recapture cell representing the tagged animals that are never seen again can be given by

$$W_i = N_i - \sum_{j=i}^{J} \sum_{k\in\{a,b\}} r_{ijk}, \tag{9}$$

where r_{ijk} are the observed recaptures of animals tagged in year i ($i = 1, 2, \ldots, I$) and recaptured in part k ($k \in \{a, b\}$) of year j ($j = i, \ldots, J$, with $J \geq I$). Estimates for the parameters can be found by maximizing equation (8).

MODEL EVALUATION BY SIMULATION

To evaluate the performance of model 0′, we used Monte Carlo simulation to generate data repeatedly under models 1 (no fouling), 0 (fouling that takes a year), and 0′ (fouling that takes only part of the year) and then fit all three models to each data set. The simulations consisted of 3 years of tagging data and 4 full years of recapture data, that is, recaptures for periods 1a, 1b, 2a, 2b, 3a, 3b, 4a, and 4b for model 0′ and periods 1, 2, 3, and 4 for models 1 and 0. The data were simulated with 1,000 animals tagged each year, for the 3 years of tagging. Ten thousand data sets were simulated for each scenario. Computations were done using the software environment R (R Development Core Team 2008), as described below. These computations could have also been done using the program SURVIV (White 1992) or MARK (White and Burnham 1999).

The function rmultinomial in the R package combinat (Chasalow 2005) was used to generate multinomial data sets with specified sample sizes and cell probabilities. The function nlm was used to minimize the negative log-likelihood functions (R Development Core Team 2008). Standard errors were estimated by inverting the Hessian matrix using the R function solve. The true standard error was determined from the variability of the 10,000 estimates of each parameter. The difference between these quantities is the bias of the estimator of standard errors. The output from the Monte Carlo simulations includes estimates of the parameters for each simulated data set as well as the bias, the percent bias of the average estimate (referred to as % bias), standard errors, and the bias of the estimated standard errors. Additionally, the root mean squared error (RMSE) for each parameter was calculated as

$$\text{RMSE} = \sqrt{\text{bias}^2 + \text{variance}} = \sqrt{\frac{\sum_{i=1}^{T}(\hat{\theta}_i - \theta)^2}{T}} \qquad (10)$$

(see Hogg et al. 2005), where T is the number of simulated data sets (10,000) and $\widehat{\theta}_i$ is the ith estimate of the parameter whose true value is θ.

In the simulations, the combined short-term survival rate from tagging and the short-term probability of tag retention, φ, was set equal to 1. Then equation (1) becomes

$$f = \lambda \text{u}. \qquad (11)$$

With the year split into two parts, there is a tag recovery parameter for each part of the year, given by $f_a{}^*$ and f_b for the newly tagged cohorts and f_a and f_b for the previously tagged cohorts in model 0′. These tag recovery parameters can be modeled as

$$f_a = \lambda_f u_a, \qquad (12)$$

$$f_a^* = \lambda_c u_a, \qquad (13)$$

and

$$f_b = \lambda_f u_b, \qquad (14)$$

where λ_c is the tag reporting rate during part (a) of the first year each cohort is at liberty (when the tags are clean and becoming fouled), λ_f is the tag reporting rate when the tags are fouled, u_a is the exploitation rate during part (a) of the year, and u_b is the exploitation rate during part (b) of the year. The exploitation rates are constrained by

$$u_a + u_b \leq 1 - S. \qquad (15)$$

Data Generated under Model 0′: Base Scenario

The parameters for the first set of simulations were loosely patterned after data from the queen conch *Strombus gigas* fishery of the Turks and Caicos Islands, British West Indies. The queen conch fishery was chosen because tag fouling is known to be a problem and the possibility of a tagging program was being explored. The exploitation rate, $u = 0.2$, was based on the ratio of the annual harvest plus local consumption to the estimated biomass at the start of the year as determined from a surplus production model (Kathy Lockhart, Department of Environment and Coastal Resources, Turks and Caicos Islands, personal communication). For these simulations it was assumed that tagging would occur during the summer when the conch fishery is closed. The tags were assumed to take 6 months to foul completely, so the year was split in half, with part (a) running from July to December and part (b) running from January to June. The percentage of the fishing effort occurring in part (a) of all years was set at 50% to reflect the seasonal distribution of the harvest.

The survival rates were calculated from the exploitation rate (u) of 0.2 and a natural mortality rate (M) of 0.3/year (SEDAR 2007) using Baranov's catch equation, which relates the exploitation rate to the two components, F and M, of the total instantaneous mortality rate:

$$u = \frac{F}{F + M}\left(1 - e^{-(F+M)}\right), \qquad (16)$$

and

$$S = e^{-(F+M)}. \qquad (17)$$

The survival rate in the first year, $S_1 = 0.57$, comes from solving equation (16) for F given M and then calculating S from equation (17). The survival rate in the second year, $S_2 = 0.62$, was altered from that in the first year to allow the years to have different survival rates.

A preliminary tag fouling study was conducted in the Turks and Caicos Islands on queen conchs. The conchs were tagged with custom-made tags (Hallprint custom code T6230; Hallprint Pty. Ltd., Hindmarsh Valley, South Australia) and vinyl tubing (spaghetti) tags (FLOY TAG, Inc., Seattle, Washington) secured around the spires of the conchs. After 4 months the tags were becoming fouled and, significantly, fouling and sedimentation of the shell began to obscure the tags. Unfortunately, the experiment ended prematurely and precise fouling times are not available. Conch fishermen typically free-dive in less than 10 m of water working off small boats with 50–65 hp engines and the conchs are collected by hand (see Medley and Ninnes 1999).

TABLE 3. Parameter values used in the simulations. All three models were parameterized with the year split into two parts, to make analysis with model 0′ possible, but for models 0 and 1 the parameters shown in the table are collapsed back into their form for a full year, which is the way they appear in the actual model parameterizations. Some parameters are confounded with others and therefore cannot be estimated on their own. For example, in model 0 and model 1, survival in the third year and the tag recovery rate in the fourth year, $S_3 f_4$, are confounded. Parameters that are confounded appear as products in the table. The simulations were conducted with 1,000 animals tagged each year.

Model 1		Model 0′		Model 0	
Parameter	Value	Parameter	Value	Parameter	Value
f_1	0.092	f_{1a}^*	0.100	f_1^*	0.178
S_1	0.570	$S_{1a} f_{1b}$	0.040	S_1	0.570
f_2	0.091	S_1	0.570	f_2	0.091
S_2	0.620	f_{2a}	0.050	S_2	0.620
f_3	0.086	$S_{2a} f_{2b}$	0.041	f_3	0.086
$S_3 f_4$	0.050	S_2	0.620	$S_3 f_4$	0.050
		f_{3a}	0.048	f_2^*	0.170
		$S_{3a} f_{3b}$	0.038	f_3^*	0.186
		$S_3 f_{4a}$	0.028		
		$S_3 S_{4a} f_{4b}$	0.023		
		f_{2a}^*	0.090		
		f_{3a}^*	0.110		

The meats are removed from the shell by the boat driver while the divers continue collecting conchs; to remove the meat the shell is knocked (hammered) on the spire, which is where the tag is placed on the shell. Based on the nature of the fishery and the proposed tag reward (US$5 for the return of a tag to a fish processing plant), the tag reporting rate for newly tagged animals, λ_c, was set at 1.0. Information on the tag reporting rate for fouled animals, λ_f, was unavailable, so the initial value of 0.5 was used for the base case for model 0′ and then varied in later cases.

To compare model 0′ with models 1 and 0, it was necessary to generate data for two parts of each year, (a) and (b), and then combine the data from the parts of the year to analyze the data sets with models 1 and 0. All parameters were initially defined for parts of the year and then collapsed for use in other models (Table 3) using the following relationships:

$$f_1 = f_{1a} + S_{1a} f_{1b} \quad (18)$$

$$f_2 = f_{2a} + S_{2a} f_{2b} \quad (19)$$

$$f_3 = f_{3a} + S_{3a} f_{3b} \quad (20)$$

and

$$S_3 f_4 = S_3 f_{4a} + S_3 S_{4a} f_{4b}. \quad (21)$$

Note that some parameters are confounded and cannot be estimated; rather, the products are estimated (see Table 3).

The performance of the various models is described in terms of the bias, root mean squared error, true standard error, and mean estimated standard error for the survival rates during the first and second years and the recovery rates in the second and third years. These four parameters were chosen for comparison because they are the only interesting parameters in common when the data are analyzed under all three models (the fifth parameter in common, $S_3 f_4$, is confounded).

To determine the effect that the tag reporting rate for fouled animals (λ_f) has on model performance, the effect of tag fouling on tag visibility was varied in additional scenarios. In all cases, the tag reporting rate for clean, newly tagged animals (λ_c) was kept at 1.0. Simulations were run using λ_f values of 0.25, 0.50 (the base scenario for model 0′), 0.75, 0.80, and 0.90.

Data Generated under Model 1

The purpose of this scenario was to evaluate the penalty for applying model 0′ when model 1 is correct. Data were generated using parameters based on the queen conch fishery in the Turks and Caicos Islands (Table 3) assuming that fouling was not a problem, that is, the tag reporting rate for newly tagged animals was equal to that of previously tagged animals.

Data Generated under Model 0

Under model 0, it takes a full year for newly tagged animals to have the same tag visibility (and thus reporting rate) as previously tagged animals. For this simulation, the parameters were again based on information from the queen conch fishery of the Turks and Caicos Islands (see the description of the data from model 0′ and Table 3). The tag reporting rate for clean, newly tagged animals remained 1.0, and that for fouled animals was 0.5. In other words, the tag recovery rate of fouled animals was equal to one-half the value of the tag recovery rate of clean animals, such that $0.5(f_j) = f_j^*$.

Additional simulations were conducted to evaluate the performance of the models under various levels of tag visibility and thus various tag reporting rates. Simulations were run with the tag reporting rate for fouled tags set at 0.25, 0.50 (the base case for model 0), 0.75, 0.80, and 0.90.

SIMULATION RESULTS

Data Generated under Model 0′: Base Scenario

As expected, when we used data generated under the condition that tag fouling affects tag reporting and it takes less than a year for tags to fully foul (the case of model 0′ being appropriate), the parameter estimates for S_1, S_2, f_2, and f_3 were essentially unbiased whether estimated by model 0 (all parameters with % bias <3%) or model 0′ (all parameters with% bias <1%) (Table 4). Analysis with model 1 produced biased estimates for all four parameters: survival rates were underestimated (when $\lambda_f = 0.50$, the % bias of $\hat{S}_1 = -18\%$ and that of $\hat{S}_2 = -26\%$), and the fraction caught and reported in years 2 and 3, f_2 and f_3, were overestimated (the % bias of $\hat{f}_2 =$

TABLE 4. Simulation results for estimating survival rates in the first two years, S_1 and S_2, and the expected fraction that is caught and reported in years 2 and 3, f_2 and f_3, under the base scenario in which tag fouling occurs and takes half a year (data generated with model 0′). Values for all parameters appear in Table 3. The smallest values for bias,% bias, SE of the estimates, and root mean squared error (RMSE) are in bold italics. Mean $\widehat{SE}$ refers to the mean of the 10,000 estimated standard errors that come from the square root of the variance (obtained by calculating the inverse of the Hessian). The SE of the estimates refers to the true standard error (i.e., the standard deviation) of the 10,000 estimates of each parameter. The parameter λ_f is the tag reporting rate for fouled tags.

Model fitted	Parameter	True value	Mean estimate	Bias	% Bias	Mean $\widehat{SE}$	SE of estimates	RMSE
				$\lambda_f = 0.25$				
0′	S_1	0.570	0.579	***0.009***	***1.6***	0.118	0.119	***0.120***
1	S_1	0.570	0.329	–0.241	–42.3	0.051	***0.052***	0.247
0	S_1	0.570	0.582	0.012	2.1	0.143	0.147	0.147
0′	S_2	0.620	0.633	***0.013***	***2.2***	0.140	0.141	***0.142***
1	S_2	0.620	0.343	–0.277	–44.7	0.049	***0.048***	0.281
0	S_2	0.620	0.644	0.024	3.9	0.193	0.198	0.199
0′	f_2	0.043	0.044	***0.001***	***1.9***		0.010	***0.010***
1	f_2	0.043	0.101	0.058	134.2	0.009	***0.010***	0.058
0	f_2	0.043	0.045	0.002	5.1	0.015	0.015	0.015
0′	f_3	0.047	0.048	***0.001***	***1.1***		***0.010***	***0.010***
1	f_3	0.047	0.122	0.075	158.7	0.010	0.010	0.075
0	f_3	0.047	0.049	0.002	4.5	0.016	0.016	0.017
				$\lambda_f = 0.50$				
0′	S_1	0.570	0.575	***0.005***	***0.9***	0.082	0.082	***0.083***
1	S_1	0.570	0.467	–0.103	–18.2	0.053	***0.053***	0.116
0	S_1	0.570	0.577	0.007	1.2	0.102	0.102	0.103
0′	S_2	0.620	0.626	***0.006***	***0.9***	0.098	0.099	***0.099***
1	S_2	0.620	0.459	–0.161	–26.0	0.051	***0.050***	0.169
0	S_2	0.620	0.632	0.012	2.0	0.133	0.135	0.135
0′	f_2	0.091	0.092	***0.001***	***0.7***		0.014	***0.014***
1	f_2	0.091	0.125	0.034	37.2	0.010	***0.010***	0.035
0	f_2	0.091	0.093	0.002	2.1	0.021	0.021	0.022
0′	f_3	0.086	0.087	***0.001***	***0.8***		0.013	***0.013***
1	f_3	0.086	0.139	0.053	61.4	0.010	***0.010***	0.054
0	f_3	0.086	0.088	0.002	2.1	0.020	0.020	0.020
				$\lambda_f = 0.75$				
0′	S_1	0.570	0.573	***0.003***	***0.5***	0.064	0.065	0.065
1	S_1	0.570	0.541	–0.029	–5.0	0.049	***0.049***	***0.057***
0	S_1	0.570	0.575	0.005	0.9	0.080	0.080	0.081
0′	S_2	0.620	0.625	***0.005***	***0.8***	0.076	0.076	***0.076***
1	S_2	0.620	0.540	–0.080	–12.9	0.049	***0.049***	0.094
0	S_2	0.620	0.627	0.007	1.1	0.105	0.106	0.106
0′	f_2	0.134	0.135	***0.001***	***0.5***		0.017	0.017
1	f_2	0.134	0.146	0.012	9.2	0.010	***0.010***	***0.016***
0	f_2	0.134	0.136	0.002	1.2	0.025	0.025	0.025
0′	f_3	0.135	0.135	***0.000***	***0.2***		0.016	***0.016***
1	f_3	0.135	0.166	0.031	22.9	0.011	***0.011***	0.033
0	f_3	0.135	0.137	0.002	1.6	0.025	0.026	0.026

37% and that of $\hat{f}_3 = 61\%$). The estimates from analysis with model 0′ have the lowest bias and root mean squared error. Model 1 has the lowest estimated standard error for all four parameters but is not an attractive estimator for these situations because of the high bias and thus high RMSE.

As the effect of change in visibility on reporting rate decreases, model 1 begins to yield smaller RMSEs than model 0′ for S_1 and f_2 (Figure 2); this is because the estimates from model 1 are becoming closer to being essentially unbiased (when $\lambda_f = 0.75$, the % biases are as follows: $\hat{S}_1$, –5%; $\hat{S}_2$, –13%, $\hat{f}_2$, 9%; and $\hat{f}_3$, 23%; Table 4) and have better precision than model 0′ as a result of there being fewer parameters.

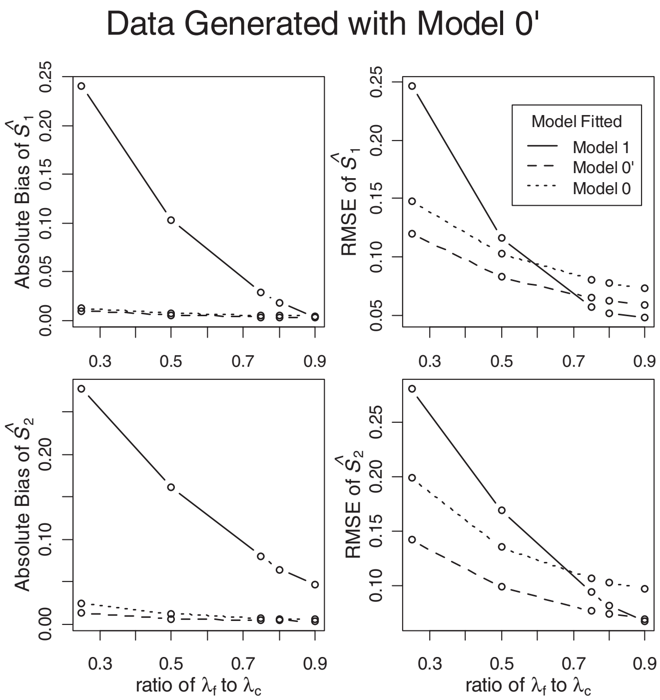

FIGURE 2. Absolute values of the biases and root mean squared errors (RMSEs) for the estimates of survival during the first year, $\hat{S}_1$, and the second year, $\hat{S}_2$ with respect to the ratio of the tag reporting rates for fouled (λ_f) and clean tags (λ_c). The data were generated for the situation in which tag fouling affects visibility and it takes a half year for tags to become fouled (data generated under model 0′). The tag reporting rate for clean tags was 1.0 and that for fouled tags was 0.25, 0.50, 0.75, 0.80, or 0.90. Note that when the tag reporting rate for fouled tags is 0.75 or more, model 1 has a lower RMSE for $\hat{S}_1$ than both models 0 and 0′. Additionally, model 0′ always has a lower RMSE than model 0 for both $\hat{S}_1$ and $\hat{S}_2$.

Data Generated under Model 1

Using data generated under the condition that tag fouling has no effect on the tag reporting rate (model 1 is appropriate) yields essentially unbiased estimates of S_1, S_2, f_2, and f_3 under all three models (Table 5). Model 1 produces estimates with the smallest standard error of the estimate and RMSE. Model 0′ produces estimates with RMSEs larger than those of model 1 but smaller than those of model 0 (the RMSE of model 0′ is 22% larger than that of model 1 for $\hat{S}_1$, 29% larger for $\hat{S}_2$, 75% larger for $\hat{f}_2$, and 63% larger for $\hat{f}_3$). Model 0 produces estimates with the largest RMSEs. Thus model 0 performs the worst (the RMSE of model 0 is 51% larger than that of model 1 for $\hat{S}_1$, 75% larger for $\hat{S}_2$, 175% larger for $\hat{f}_2$, and 150% larger for $\hat{f}_3$).

Data Generated under Model 0

When data are generated under model 0, tag fouling affects the tag reporting rate and it takes one full year for the tags to become fouled. When the tag reporting rate for previously tagged (fouled) animals is one-half that of newly tagged animals, only model 0 produces essentially unbiased estimates of S_1, S_2,

TABLE 5. Simulation results for estimating survival rates in the first two years, S_1 and S_2, and the expected fraction that is caught and reported in years 2 and 3, f_2 and f_3, when tag fouling does not affect visibility (data generated with model 1). See Table 4 for more details.

Model fitted	Parameter	True value	Mean estimate	Bias	% Bias	Mean $\widehat{SE}$	SE of estimates	RMSE
0′	S_1	0.570	0.575	0.005	0.9	0.082	0.082	0.083
1	S_1	0.570	0.574	***0.004***	***0.7***	0.067	***0.068***	***0.068***
0	S_1	0.570	0.577	0.007	1.2	0.102	0.102	0.103
0′	S_2	0.620	0.626	0.006	0.9	0.098	0.099	0.099
1	S_2	0.620	0.624	***0.004***	***0.7***	0.077	***0.077***	***0.077***
0	S_2	0.620	0.632	0.012	2.0	0.133	0.135	0.135
0′	f_2	0.091	0.092	0.001	0.7		0.014	0.014
1	f_2	0.091	0.091	***0.000***	***–0.1***	0.008	***0.008***	***0.008***
0	f_2	0.091	0.093	0.002	2.1	0.021	0.021	0.022
0′	f_3	0.086	0.087	0.001	0.8		0.013	0.013
1	f_3	0.086	0.086	***0.000***	***–0.1***	0.008	***0.008***	***0.008***
0	f_3	0.086	0.088	0.002	2.1	0.020	0.020	0.020

TABLE 6. Simulation results for estimating survival rates in the first two years, S_1 and S_2, and the expected fraction that is caught and reported in years 2 and 3, f_2 and f_3, for the situation in which tag fouling occurs and takes a full year (data generated with model 0). See Table 4 for more details

Model fitted	Parameter	True value	Mean estimate	Bias	% Bias	Mean $\widehat{SE}$	SE of estimates	RMSE
				$\lambda_f = 0.25$				
0′	S_1	0.570	0.288	–0.282	–49.5	0.054	0.055	0.287
1	S_1	0.570	0.230	–0.340	–59.6	0.035	***0.036***	0.342
0	S_1	0.570	0.583	***0.013***	***2.3***	0.149	0.153	***0.153***
0′	S_2	0.620	0.348	–0.272	–43.9	0.063	0.061	0.279
1	S_2	0.620	0.256	–0.364	–58.7	0.035	***0.034***	0.366
0	S_2	0.620	0.645	***0.025***	***4.1***	0.198	0.205	***0.206***
0′	f_2	0.043	0.120	0.077	179.7		0.021	0.080
1	f_2	0.043	0.158	0.115	268.1	0.011	***0.012***	0.116
0	f_2	0.043	0.045	***0.002***	***5.3***	0.015	0.016	***0.016***
0′	f_3	0.043	0.116	0.073	170.2		0.018	0.075
1	f_3	0.043	0.173	0.130	303.4	0.012	***0.012***	0.131
0	f_3	0.043	0.045	***0.002***	***4.8***	0.015	0.016	***0.016***
				$\lambda_f = 0.50$				
0′	S_1	0.570	0.438	–0.132	–23.2	0.059	0.059	0.145
1	S_1	0.570	0.395	–0.175	–30.8	0.043	***0.043***	0.181
0	S_1	0.570	0.577	***0.007***	***1.2***	0.102	0.102	***0.103***
0′	S_2	0.620	0.477	–0.143	–23.1	0.067	0.066	0.158
1	S_2	0.620	0.404	–0.216	–34.8	0.042	***0.041***	0.220
0	S_2	0.620	0.632	***0.012***	***2.0***	0.133	0.135	***0.135***
0′	f_2	0.091	0.138	0.047	52.1		0.019	0.051
1	f_2	0.091	0.159	0.068	75.0	0.011	***0.011***	0.069
0	f_2	0.091	0.093	***0.002***	***2.1***	0.021	0.021	***0.022***
0′	f_3	0.086	0.137	0.051	59.2		0.018	0.054
1	f_3	0.086	0.173	0.087	100.9	0.011	***0.012***	0.088
0	f_3	0.086	0.088	***0.002***	***2.1***	0.020	0.020	***0.020***
				$\lambda_f = 0.75$				
0′	S_1	0.570	0.518	–0.052	–9.1	0.057	0.058	***0.078***
1	S_1	0.570	0.503	–0.067	–11.8	0.045	***0.045***	0.081
0	S_1	0.570	0.575	***0.005***	***0.9***	0.080	0.081	0.081
0′	S_2	0.620	0.574	–0.046	–7.4	0.068	0.068	***0.082***
1	S_2	0.620	0.519	–0.101	–16.4	0.046	***0.046***	0.111
0	S_2	0.620	0.627	***0.007***	***1.1***	0.105	0.106	0.106
0′	f_2	0.134	0.158	0.024	17.8		0.019	0.031
1	f_2	0.134	0.164	0.030	22.5	0.011	***0.011***	0.032
0	f_2	0.134	0.136	***0.002***	***1.3***	0.025	0.025	***0.025***
0′	f_3	0.133	0.155	0.022	16.8		0.018	0.029
1	f_3	0.133	0.178	0.045	33.5	0.011	***0.011***	0.046
0	f_3	0.133	0.135	***0.002***	***1.6***	0.025	0.025	***0.025***

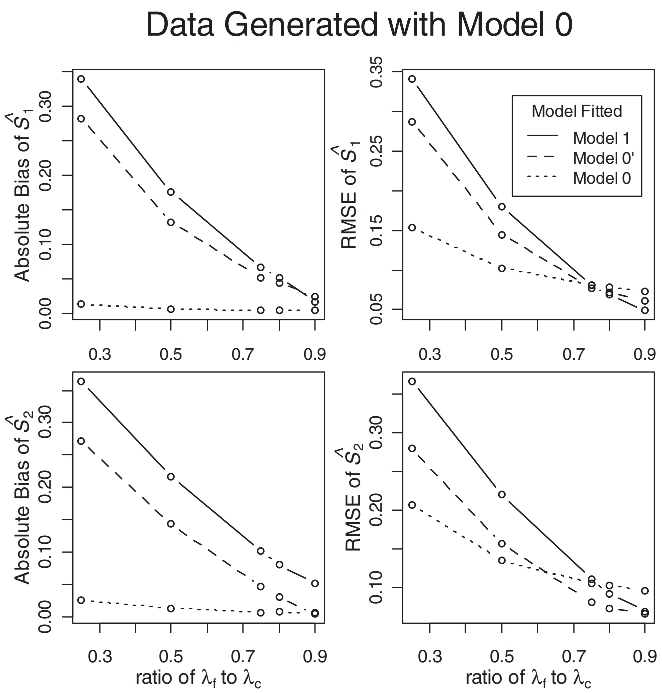

FIGURE 3. Absolute value of the biases and root mean squared errors (RMSEs) for the estimates of survival during the first year, $\hat{S}_1$, and the second year, $\hat{S}_2$. The data were generated for the situation in which tag fouling affects visibility and it takes a full year for tags to become fouled (data generated under model 0). The tag reporting rate for clean tags was 1.0 and that for fouled tags was 0.25, 0.50, 0.75, 0.80, or 0.90. Note that when the tag reporting rate for fouled tags is 0.75 or more, model 0′ has a lower RMSE than model 0.

f_2, and f_3 (Table 6). Model 0 has the lowest RMSE for every parameter when $\lambda_f = 0.25$ or 0.50.

For estimating S_1 and S_2, the most appropriate model shifts from model 0 to model 0′ as the ratio of reporting rates (previously tagged : newly tagged) approaches 1.0 (Figure 3).

DISCUSSION

There are three important factors to consider when choosing between models 1, 0, and 0′. First, the time period that must elapse for new tags to have the same tag reporting rate as older tags (the length of part [a] of the year) must be bounded, that is, known to be less than some specified period of time. When part (a) is neither very short nor close to a full year, model 0′ may be appropriate. As part (a) of the year becomes shorter model 1 becomes more appropriate, and as part (a) becomes longer (close to 1 year) model 0 becomes appropriate. If part (a) takes longer than 1 year, a new model should be parameterized to account for this.

Second, the timing of the fishery relative to the timing of the fouling (which determines parts [a] and [b] of the year) should be considered. When fishing occurs in both parts (a) and (b) of the year, model 0′ should remain appropriate (given fouling that lasts less than a year). However, if all the fishing effort takes place in period (b), then the recaptures for all (a) periods will be zero and model 1 will be a more appropriate model. If all the fishing effort takes place in period (a), then model 0 should be the most appropriate model.

Finally, the magnitude of the change in visibility affects which model is the most appropriate. If the change in visibility is small (i.e., tag visibility does not greatly vary between cohorts in a given part of a year), then model 1 is more appropriate than model 0′ or model 0.

If tag fouling is known to occur in much less than a year and affects the reporting rate greatly, then model 0′ will outperform model 1 (Figure 2) and models 0′ and 0 will both provide unbiased estimates. Even when it takes a full year for the tags to foul, model 0′ can outperform model 0 (in terms of lower RMSE) as the influence of tag fouling on the tag reporting rate becomes smaller, making λ_f closer in value to λ_c (Figure 3). Furthermore, when fouling takes less than a year, model 0′ can outperform models 1 and 0.

As the change in visibility due to tag fouling becomes smaller, model 1 produces smaller RMSEs when tag fouling takes a year (model 0) and when tag fouling takes less than a year (model 0′). This emphasizes the importance of considering the magnitude of change in visibility when selecting a model. As the ratio of the tag reporting rate for fouled tags to new tags becomes closer to 1.0, model 1 becomes the most appropriate model (Figures 2, 3).

If fouling is known to affect the tag reporting rate but the time necessary for a tag to become fouled has not been determined, models 0′ and 0 are valid candidates since they provide unbiased estimates when tag fouling takes less than a year. If possible, a study should be done to determine the time to tag fouling. Such a study may be inexpensive and require only modest effort, and it may provide key information for choosing between models 0 and 0′.

For the queen conch fishery of the Turks and Caicos Islands, model 0′ should be used if the change in tag visibility causes the tag reporting rate to decline by 25% or more (Table 4; Figure 2). Otherwise, model 1 will suffice. This highlights the importance of studying the effect that a change in tag visibility has on the tag reporting rate.

The problem of changing tag visibility is similar to that of tag loss. Model 0′ is parameterized such that the change in tag visibility takes an appreciable amount of time, which is less than a year, and then the tag visibility remains constant over time. Thus, one can think of two time periods: one when the visibility is constant over time and one when it is not. In contrast, tag loss is of two types. Type I, or short-term, tag loss occurs so rapidly that it happens before fishing begins (Beverton and Holt 1957). Short-term tag loss essentially modifies the effective number tagged. Type II, or long-term, tag loss is similar to changing visibility over time except that it is usually described as occurring progressively and continuously rather than leveling off. If it can be assumed that the rate of tag loss declines to 0.0 in less than a year, then model 0′ would be appropriate. However, most of the literature supports the idea of ongoing, progressive tag loss.

Tabulating the recaptures by part of a year rather than a full year should not be a problem. It has been shown by Pollock and Raveling (1982) that when conducting a tagging study it is important to determine the year of tag recapture for Brownie models because misreporting the year causes biased estimates. Thus, assuming that the advice of Pollock and Raveling is followed, determining whether the tag return is from part (a) or part (b) of the year should add little or no additional cost to the study.

In cases in which tag fouling occurs, takes less than a year, and causes a change in the tag reporting rate, model 0′ can greatly improve the efficiency of the tagging study (in terms of smaller standard errors). Furthermore, model 0′ provides the first estimate of survival during the first year, S_1, at the end of the second year, which is a full year before model 0 provides an estimate.

The current study is one of the first works to demonstrate the value of tabulating tag returns with a greater periodicity than the periodicity of tagging (e.g., tabulating by parts of the year when tagging occurs annually) for studies with the Brownie experimental design. One other example of the value of tabulating recaptures in this way is given in Waterhouse and Hoenig (2011), where partial-year tabulation is used for dealing with the delayed mixing of newly tagged animals with the population at large. This method of dealing with changing tag visibility could easily be extended to instantaneous-rates models and could be extended to incorporate estimates of fishing effort (Hoenig et al. 1998b). Another class of tagging models utilizes the exact times of recapture of animals (see Leigh et al. 2006). The approach of Leigh et al. (2006) is innovative and promising, though more complicated than the models considered here. The relative performance of the various approaches remains to seen, for example, with respect to their robustness to failures of assumptions. It is yet to be seen what further benefits can accrue from tabulating recapture data on a finer scale than the tagging periodicity.

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