

Models for tagging data that allow for incomplete mixing of newly tagged animals

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Abstract: The Brownie models for tagging data allow one to estimate age- and year-specific total survival rates as well as tag recovery rate parameters. The latter can provide estimates of exploitation rates if the tag reporting, tag shedding, and tag-induced mortality rates can be estimated. A limitation of the models is that they do not allow for newly tagged animals to have different survival rates than previously tagged animals because of lack of complete mixing. We develop a model that allows for the animals to be incompletely mixed, or not fully recruited, into the population during the entire year in which they are tagged. There is a penalty in terms of precision associated with the use of this model. To increase the precision, we also developed a model for which it is assumed that animals become fully mixed (recruited) after a portion of the year has elapsed. Sometimes, animals must be tagged after the fishing season has begun. In this case, newly tagged animals experience fishing and natural mortality for only a fraction of the year. The partial-year non-mixing model can be modified to account for this situation.

Résumé : Les modèles de Brownie pour les données de marquage permettent d'évaluer le taux de survie totale propre à un âge et à une année ainsi que des paramètres du taux de récupération des marques. Ces derniers peuvent fournir des évaluations du taux d'exploitation lorsqu'on peut estimer les taux de déclaration des marques, de perte des marques et de mortalité induite par les marques. Le fait que dans ces modèles les sujets nouvellement marqués ne peuvent pas avoir des taux de survie différents de ceux des animaux déjà marqués en raison d'un mélange incomplet constitue une limitation. Nous avons élaboré un modèle qui permet un mélange incomplet des animaux, ou un recrutement incomplet, dans la population pendant toute l'année au cours de laquelle ils ont été marqués. L'utilisation de ce modèle comporte un désavantage au niveau de la précision. Afin d'accroître la précision, nous avons également élaboré un modèle dans le cadre duquel on suppose que les poissons sont entièrement mélangés (recrutés) après un certain temps. Les poissons doivent être parfois marqués après le début de la saison de pêche. Dans ce cas, ces poissons nouvellement marqués ne sont exposés à une mortalité par pêche et à une mortalité naturelle que pendant une partie de l'année. Le modèle de non-mélange pendant une partie de l'année peut être modifié pour prendre en compte cette situation.

[Traduit par la Rédaction]

Introduction

Brownie et al. (1978, 1985) developed simple, elegant and generally robust models for data from multiyear tagging studies. These models allow one to estimate year-specific survival rates and rates of tag recovery. The latter were originally viewed as nuisance parameters, because they represented the combined effects of tag-induced mortality, tag shedding, exploitation, and tag reporting. In recent years, it has been recognized that tag-induced mortality and tag shedding could be quantified by holding tagged animals in cages or pens. Also, tag reporting rate could be estimated from planted tags, creel

or port sampling programs, or high-reward tagging studies. Thus, it is possible to determine the exploitation rate from the tag recovery rate (Conroy 1985; Conroy et al. 1989; Pollock et al. 1991, 1994, 1995).

One limitation of the Brownie models, pointed out by Youngs and Robson (1975), is that it is necessary to assume that newly tagged animals have time to mix thoroughly among the previously tagged animals before the fishing season begins and that they are fully recruited. This can be difficult to achieve in practice. Youngs and Robson developed a test for non-mixing but were unable to remedy the problem in the context of Brownie models.

Hoenig et al. (1998) reparameterized the Brownie models in terms of instantaneous rates of fishing and natural mortality. Here, we show that the instantaneous rates formulation makes it possible to allow for non-mixing (and incomplete recruitment) of newly tagged animals. We develop two kinds of models: those in which the newly tagged animals are mixed through the population after 1 year and those in which the animals are mixed after a fraction of the year has passed.

Instantaneous rates formulation of the Brownie models

Consider a tagging study where animals are tagged at the start of each year and animals are recaptured over a number of years

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Table 1. Instantaneous rates formulation for expected number of tag recoveries in a multiyear tagging study.

Year	Expected recoveries in year		
	1	2	3
1	$N_1\phi\lambda u_1(F_1, M)$	$N_1\phi\lambda u_2(F_2, M)e^{-F_1-M}$	$N_1\phi\lambda u_3(F_3, M)e^{-F_1-F_2-2M}$
2	—	$N_2\phi\lambda u_2(F_2, M)$	$N_2\phi\lambda u_3(F_3, M)e^{-F_2-M}$
3	—	—	$N_3\phi\lambda u_3(F_3, M)$

Note: Symbols are as follows: N_i , number tagged and released in year i ; F_j , instantaneous rate of fishing mortality in year j ; M , instantaneous rate of natural mortality; ϕ , probability of surviving being tagged and retaining the tag (in the short term); λ , tag reporting rate; $u_j(F_j, M)$, exploitation rate in year j as defined by eq. 1 (note that u_j is a function of F_j and M and depends on the seasonal pattern of fishing).

with the animals being killed upon recapture. Let N_i be the number of animals tagged in year i for $i = 1, 2, \dots, I$, and let r_{ij} be the number of animals tagged in year i and recaptured in year j for $j = i, i + 1, i + 2, \dots, J$. The observed numbers of recaptures r_{ij} are realizations of the random variables R_{ij} whose expected values are shown in Table 1 for a model in which the instantaneous fishing mortality rate, F_j , is year-specific and the instantaneous natural mortality rate, M , is constant over time. In Table 1, ϕ is the probability an animal survives the tagging process with the tag intact, λ is the tag reporting rate (probability the tag is reported given that a tagged fish is caught), and $u_j(F_j, M)$ is the exploitation rate in year j . The expected value of R_{11} can be interpreted as follows: of the N_1 fish tagged in year 1, the fraction ϕ of the fish will survive the tagging with the tag in place; of these, the fraction $u_1(F_1, M)$ will be caught, with a fraction λ of these reported. The expected value of R_{12} has a similar interpretation: $N_1\phi$ fish are available to be caught at the start of year 1, of these the fraction $\exp(-F_1 - M)$ survives the first year and is available to be caught in the second year, and of these the fraction $\lambda u_2(F_2, M)$ is caught and reported during the second year. Expected values for all cells in the table can be constructed in like fashion.

The exploitation rate, $u_j(F_j, M)$, is a function of the fishing and natural mortality rates. It depends on the relative timing of the components of mortality. We will assume that the natural mortality rate occurs with constant intensity over the course of a year. Suppose the fraction of the annual fishing effort in each period k of year j is denoted by ϵ_{jk} , for $k = 1, 2, \dots, K$. We assume that the fraction of the fishing mortality occurring in period k is equal to the fraction of the annual fishing effort occurring in period k (see Hoenig et al. 1998). Let Δt_k be the length of the k th period of the year expressed as a fraction of the year. Then

$$(1) \quad u_j(F_j, M) = \sum_{k=1}^K a_{jk} b_{jk} c_{jk}$$

where a_{jk} is the fraction of the population surviving to the beginning of period k , with $a_{j1} = 1$ and

$$a_{jk} = \exp \left(-M \sum_{h=1}^{k-1} \Delta t_h - F_j \sum_{h=1}^{k-1} \epsilon_{jh} \right), \quad k > 1$$

b_{jk} is the fraction dying in period k

Table 2. Instantaneous rates formulation for expected number of tag recoveries in a multiyear tagging study when newly tagged animals are not fully mixed into the population in the year of tagging.

Year	Expected recoveries in year		
	1	2	3
1	$N_1\phi\lambda u_1(F_1^*, M)$	$N_1\phi\lambda u_2(F_2, M)e^{-F_1^*-M}$	$N_1\phi\lambda u_3(F_3, M)e^{-F_1^*-F_2-2M}$
2	—	$N_2\phi\lambda u_2(F_2^*, M)$	$N_2\phi\lambda u_3(F_3, M)e^{-F_2^*-M}$
3	—	—	$N_3\phi\lambda u_3(F_3^*, M)$

Note: Symbols are as follows: N_j , number tagged and released in year j ; F_j , instantaneous rate of fishing mortality in year j for previously tagged animals; F_j^* , instantaneous rate of fishing mortality in year j for newly tagged animals; M , instantaneous rate of natural mortality; ϕ , probability of surviving being tagged and retaining the tag (in the short term); λ , tag reporting rate; $u_j(F_j, M)$, exploitation rate (for previously tagged animals) in year j as defined by eq. 1 (note that u_j is a function of F_j and M and depends on the seasonal pattern of fishing); $u_j(F_j^*, M)$, exploitation rate for newly tagged animals in year j .

$$b_{jk} = 1 - \exp(-M\Delta t_k - F_j \epsilon_{jk})$$

and c_{jk} is the fraction of the deaths in period k due to fishing

$$c_{jk} = \frac{F_j \epsilon_{jk}}{F_j \epsilon_{jk} + M\Delta t_k}$$

When fishing effort and hence fishing mortality are constant over the course of a year (eq. 1) reduces to the familiar relationship (Ricker 1975):

$$u_j(F_j, M) = \frac{F_j}{F_j + M} (1 - \exp(-F_j - M))$$

and when fishing occurs instantaneously at the start of the year $K = 1$, $\Delta t_1 = 0$, $\epsilon_{j1} = 1$, and

$$u_j(F_j) = 1 - \exp(-F_j).$$

The right-hand side of eq. 1 can be substituted for $u_j(F_j, M)$ in the expressions for the expected values. Then the models for the tagging data are parameterized in terms of instantaneous rates of fishing and natural mortality, tag reporting rate, and tag retention-survival (ϕ). Hoenig et al. (1998) discuss how reporting rate and tag retention-survival can be estimated, and they show how the likelihood function can be constructed to obtain maximum likelihood estimates. The models discussed in this paper can be fitted using program SURVIV (White 1983).

Models that allow for non-mixing

Non-mixing in the year of tagging

Now suppose that the newly tagged animals do not mix throughout the tagged population immediately upon release. Then, in general, the newly tagged animals would be expected to experience a different fishing mortality rate than the previously tagged animals. In Table 2 we describe a model in which this is the case.

The expression for the expected value of r_{11} indicates that the newly tagged animals experience fishing mortality F_1^* . Throughout this paper we use an asterisk to indicate parameters referring to newly tagged animals that are not yet fully mixed into the population. We make the assumption that the

relative timing of the fishing and natural mortality on the newly tagged animals is the same as before. However, this is not a critical assumption, because we are not interested in the value of the fishing mortality on newly tagged animals (since it does not reflect what is happening to the population at large), and because the relative timing has a minor effect on the estimates of mortality rates (see Hoenig et al. 1998).

The expected number of recaptures in year 2 from animals tagged in year 1 depends in part on the fishing mortality experienced by the cohort in year 1 and also on the “normal” fishing mortality, F_2 , experienced by fully mixed animals in year 2:

$$E[R_{12}] = N_1 \phi \lambda u_2(F_2, M) e^{-F_1^* - M}$$

In the above, $\exp(-F_1^* - M)$ is the survival rate in year 1 of newly tagged animals, while $u_2(F_2, M)$ is the exploitation rate in year 2 of animals tagged prior to year 2. Note that the recapture of newly tagged animals in year 2 has expected value:

$$E[R_{22}] = N_2 \phi \lambda u_2(F_2^*, M)$$

That is, these animals experience a different fishing mortality rate (F_2^*) than the previously tagged animals (which experience rate F_2).

The tag recoveries from the 2 years of tagging and 3 years of recapture are modelled with six parameters: F_1^* , F_2^* , F_2 , F_3 , M , and the product $\phi\lambda$. If the product $\phi\lambda$ is known from external information, then setting the observed recaptures (r_{11} , r_{12} , r_{13} , r_{22} , r_{23}) equal to their expected values provides five equations in five unknowns, which can be solved simultaneously to obtain moment estimates of the parameters. If a fourth year of recaptures is obtained then there are two more observations (r_{14} and r_{24}) but only one additional parameter (F_4). In this case, it is possible in theory to also estimate F_4 and the product $\phi\lambda$. With additional tag releases or years of recapture it is possible to estimate additional parameters, e.g., letting natural mortality or the product $\phi\lambda$ vary to some extent over time. It is not possible, however, to estimate a separate fishing mortality rate and natural mortality rate for every year (excluding the first year) even if the product $\phi\lambda$ is known.

Although it is theoretically possible to estimate a wide variety of parameters, in practice it is necessary to introduce restrictions such as holding natural mortality constant to obtain stable estimates (see section on simulation results).

Non-mixing during part of the year of tagging

From the expected values in Table 2, it is clear that the recapture of newly tagged animals provides no information about fishing mortality on previously tagged animals. Thus, the assumption of a non-mixing model results in the loss of a great deal of information. It is therefore of interest to see if some information about fishing mortality rates for previously tagged animals can be obtained from the recapture of newly tagged animals. We do this by assuming that after a portion of the year has passed the animals are fully mixed.

Suppose that fishing effort data are collected by period of the year and, for the first w periods, the newly tagged animals are not mixed into the population. Then for w periods the newly tagged animals will experience an abnormal fishing mortality rate and for $K - w$ periods they will experience the normal fishing mortality rate, i.e., the same rate experienced

by the previously tagged animals. The survival rate, S_j^* , of newly tagged animals in year j can thus be expressed by

$$S_j^* = \exp \left(-F_j^* \sum_{k=1}^w \Delta t_k - F_j \sum_{k=w+1}^K \epsilon_{jk} - M \right)$$

where F_j^* now refers to the fishing mortality on newly tagged animals during the first w periods of year j . (The summation over Δt_k serves only to express F_j^* per year; the summation over ϵ_{jk} applies only a fraction of the normal fishing mortality to the newly tagged animals.) Similarly, the exploitation rate for newly tagged animals in year j can be expressed as

$$(2) \quad u_j^*(F_j^*, F_j, M) = b_j^* c_j^* + \sum_{k=w+1}^K a_{jk}^* b_{jk} c_{jk}$$

For the first part of the year, b_j^* is the fraction dying

$$b_j^* = 1 - \exp \left(-(M + F_j^*) \sum_{k=1}^w \Delta t_k \right)$$

and c_j^* is the fraction of the deaths due to fishing

$$c_j^* = \frac{F_j^*}{F_j^* + M}$$

For the second part of the year (periods $w + 1, 2, \dots, K$), the fraction surviving to the beginning of period k is

$$a_{jk}^* = \begin{cases} \exp \left(-M \sum_{h=1}^{k-1} \Delta t_h - F_j^* \sum_{h=1}^{k-1} \Delta t_h \right), & k = w + 1 \\ \exp \left(-M \sum_{h=1}^{k-1} \Delta t_h - F_j^* \sum_{h=1}^w \Delta t_h - F_j \sum_{h=w+1}^{k-1} \epsilon_{jh} \right), & k > w + 1 \end{cases}$$

This just adds up the natural mortality since the beginning of the year, the abnormal fishing mortality F_j^* , and the portion of the normal fishing mortality that has occurred up to the beginning of the k th period.

In a competing risks model such as this, it is assumed implicitly that the ratio of fishing to natural mortality rate on unmixed animals is constant over the first w periods and within each period after that. Although this assumption is not likely to be met in the first part of the year, the results are not sensitive to the relative timing of the fishing and natural mortalities (see Hoenig et al. 1998).

For the first year of tagging, the above expression for survival (S_1^*) introduces two parameters — F_1 and F_1^* . However, there is little basis for distinguishing between these parameters. Therefore, we model the survival rate in the first year by

$$S_1^* = \exp (-F_1^* - M)$$

to eliminate the parameter F_1 . Similarly, we can eliminate F_1 from the expression for exploitation rate in the first year by replacing eq. 2 with

Table 3. Recapture data from a tagging study of lake trout (*S. namaycush*) described by Youngs and Robson (1975).

Year	No. tagged	No. recaptured in year				
		1	2	3	4	5
1960	1048	72	44	8	9	4
1961	844	—	74	30	20	7
1962	989	—	—	54	48	13
1963	971	—	—	—	74	24
1964	863	—	—	—	—	48

$$u_1^*(F_1^*, M) = \sum_{k=1}^K a_{1k}^* b_{1k}^* c_{1k}^*$$

where the factors are the same as in eq. 1 except that F_1 is replaced by F_1^* . In other words, we treat the data from the first year of the tagging study as if animals are not completely mixed into the population until an entire year has elapsed. In this case, we lose the ability to estimate F_1 , but our ability to do this was poor anyway.

Tagging after the fishing season begins

An interesting situation is where animals are tagged after the fishing season has begun. This is not really a non-mixing model, but it can be handled in a fashion similar to that used for non-mixing. Suppose all tagging is done in a short period of time w periods after the season begins, and tagged animals are released throughout the area inhabited by the stock. Then it might be reasonable to assume that animals are thoroughly mixed as soon as they are released. In this case, the fishing and natural mortality rates on newly tagged animals would be 0 during the first w periods of the year and would be the same as for previously tagged animals for all other periods of the year. Thus, the annual survival rate for the newly tagged animals would be

$$S_j^* = \exp \left(-F_j \sum_{k=w+1}^K \epsilon_{jk} - M \sum_{k=w+1}^K \Delta t_k \right), \quad j = 1, 2, \dots, I$$

and the exploitation rate would be

$$u_j^*(F_j, M) = \sum_{k=w+1}^K a_{jk}^{**} b_{jk} c_{jk}, \quad j = 1, 2, \dots, I$$

with all symbols defined as for eq. 1 except $a_{j,w+1}^{**} = 1$ and

$$a_{jk}^{**} = \exp \left(-M \sum_{h=w+1}^{k-1} \Delta t_h - F_j \sum_{h=w+1}^{k-1} \epsilon_{jh} \right), \quad k > w + 1.$$

Tests for non-mixing

We can use a likelihood ratio test to compare the fits of a model assuming complete mixing to one allowing for non-mixing of newly tagged animals. Let Λ_m and Λ_n be the values of the likelihood functions for the models assuming complete mixing and non-mixing, respectively, evaluated at the parameter estimates. (The model assuming non-mixing is the “full” model while the model assuming complete mixing is the “restricted”

Table 4. Two model fits to the data in Table 3.

Parameter	Estimate	SE
Fully mixed model		
F_1	0.58	0.08
F_2	0.69	0.07
F_3	0.42	0.05
F_4	0.65	0.07
F_5	0.40	0.07
M	0.11	0.04
Non-mixed model		
F_1^*	0.59	0.08
F_2^*	0.64	0.09
F_3^*	0.41	0.07
F_4^*	0.63	0.11
F_5^*	0.41	0.08
F_2	0.82	0.18
F_3	0.45	0.10
F_4	0.68	0.16
F_5	0.40	0.14
M	0.11	0.05

Note: The fully mixed model assumes newly tagged animals are fully mixed into the population. Negative log likelihood = 2101.1; χ^2 goodness of fit statistic = 8.13 with 9 df, $p = 0.52$. The non-mixed model assumes a lack of mixing in the year of tagging. Negative log likelihood = 2100.3; χ^2 statistic = 6.54 with 5 df, $p = 0.26$.

model). Then, under the null hypothesis that the fully mixed (restricted) model is true, the expression

$$-2 \log_e \left(\frac{\Lambda_m}{\Lambda_n} \right)$$

has an asymptotic χ^2 distribution with degrees of freedom Δ equal to the difference in the number of parameters estimated under the two models. The fully mixed model is rejected in favor of the non-mixed model if the value of the test statistic exceeds the critical value for a χ^2 variable with Δ degrees of freedom.

Example: lake trout in Cayuga Lake

We consider 5 years of results from a tagging study described by Youngs and Robson (1975) of lake trout (*Salvelinus namaycush*) in Cayuga Lake, New York (Table 3). Youngs (1974) estimated the tag reporting rate, λ , from these data to be 18%. (Actually, the estimate is of the product $\phi\lambda$.) Hoenig et al. (1998) showed that the estimate was not stable. Therefore, for illustrative purposes, we will assume that the product $\phi\lambda$ is known to be 0.18, and we will not try to estimate $\phi\lambda$. The fishing season occurred during the last 6 months of the year, assuming the year begins in October when the animals were tagged (W.D. Youngs, personal communication).

We fitted two models to the data, one which allowed for non-mixing throughout all of the year of tagging (non-mixed model) and one which was based on the assumption that animals were fully mixed throughout all of the year of tagging (fully mixed model). In both models, the fishing mortality was allowed to vary from year to year, natural mortality was held constant, fishing effort was assumed to be of constant intensity

Table 5. Tagging data from Table 3 modified to simulate lack of mixing in the year of tagging.

Year	No. tagged	No. recaptured in year				
		1	2	3	4	5
1960	1048	48	55	10	11	5
1961	844	—	49	39	26	9
1962	989	—	—	36	56	15
1963	971	—	—	—	49	31
1964	863	—	—	—	—	32

Note: Recaptures of newly tagged animals (along the main diagonal) were reduced by one-third to simulate an exploitation rate on newly tagged animals that is two-thirds that of previously tagged animals. Recaptures in subsequent years were increased to reflect the higher survival of animals in their year of tagging (see text for details).

during months 7 to 12 of the year, and the product $\phi\lambda$ was fixed at 0.18.

Both models fit the data well judging by the χ^2 goodness of fit statistics. The estimates from the two models were very similar (Table 4). Both models provided estimates of M of around 0.11-year^{-1} and both models indicated that the fishing mortality rates were quite high. The estimated standard errors for the non-mixed model were noticeably higher than for the fully mixed model.

To see how the models might perform in a case where non-mixing is a problem, we modified the data set to simulate a non-mixing scenario. The numbers of recaptures along the main diagonal of the recapture matrix were multiplied by two-thirds to simulate newly tagged animals having an exploitation rate two-thirds that of previously tagged animals. This meant that the number of recaptures in subsequent years had to be adjusted upwards to account for the higher survival rate in the year of tagging. This adjustment was accomplished as follows. The natural mortality rate and fishing mortality rates estimated from the original data (assuming a fully mixed population) were used to calculate the exploitation rate in the year of tagging for each cohort. We then searched iteratively for the fishing mortality rate F^* that would result in the exploitation rate being reduced to two-thirds of the original value. Every entry in a row to the right of the cell for newly tagged animals was then multiplied by the ratio of the survival rates (new:old), i.e., by $\exp(F_i - F_i^*)$ where F_i is the fishing mortality that occurred on the newly tagged animals from cohort i (in year i) and F_i^* is the fishing mortality that would have resulted in two-thirds the exploitation rate. The results were rounded to the nearest whole number (Table 5).

The fit of the fully mixed model to the data modified to reflect non-mixing was extremely poor (Table 6). The chi-square goodness of fit statistic was highly significant suggesting the model was not appropriate, and there was a clear pattern to the residuals: the residuals were all negative on the main diagonal and positive immediately to the right of the main diagonal. The χ^2 statistic suggests the non-mixed model fit well, and there was no obvious pattern to the residuals (Table 6). The estimated fishing mortality rates for previously tagged animals, and the estimated natural mortality rate, were similar to those obtained when the mixing model was fitted to the original data. Thus, it appears that the non-mixed model successfully handled the non-mixing situation.

Table 6. Model fits to the data in Table 5.

Parameter	Estimate	SE
Fully mixed model		
F_1	0.33	0.05
F_2	0.47	0.05
F_3	0.29	0.04
F_4	0.42	0.06
F_5	0.26	0.05
M	0.05	0.05
Non-mixed model		
F_1^*	0.36	0.06
F_2^*	0.38	0.06
F_3^*	0.25	0.05
F_4^*	0.37	0.07
F_5^*	0.25	0.06
F_2	0.82	0.14
F_3	0.46	0.08
F_4	0.69	0.16
F_5	0.41	0.13
M	0.12	0.05

Note: Data were modified from Table 3 to represent an exploitation rate on newly tagged animals that is two-thirds that of previously tagged animals. For the fully mixed model, negative log likelihood = 1985.3; χ^2 goodness of fit = 34.45, 9 df, $p < 0.0001$. For the non-mixed model, negative log likelihood = 1972.7; $\chi^2 = 7.62$, 5 df, $p = 0.18$.

Simulation studies

We conducted a simulation study of a tagging program with 3 years of tagging and 3 years of recaptures to see how well models assuming complete mixing and assuming non-mixing in the first year performed under a variety of situations. In particular, we wished to see how great is the penalty for having to assume a non-mixed model. This is important inasmuch as the extent of non-mixing problems may be controlled by the choice of time for tagging.

We simulated the following conditions:

- (1) a type I (pulse) or type II (continuous) fishery;
- (2) number tagged per year was 500 or 1000;
- (3) $\phi = 1$ and reporting rate (λ) was 1.0 or 0.50, assumed known;
- (4) fishing mortality for fully mixed animals was constant at either $F = 0.2\text{-year}^{-1}$ or $F = 0.4\text{-year}^{-1}$;
- (5) natural mortality rate was constant at either 0.2-year^{-1} or 0.4-year^{-1} ; and
- (6) fishing mortality on newly tagged animals (F^*) was either (i) the same as for previously tagged animals, (ii) 0.1 when $F = 0.2$, or (iii) 0.3 when $F = 0.4$.

We fitted models that either assumed constant fishing and natural mortality rates or just constant natural mortality. We fitted non-mixed models to data generated with non-mixing, and we fitted fully mixed models to data generated as fully mixed.

For each set of conditions, we generated 1000 data sets. Results for each estimated parameter were summarized by computing the bias and the relative standard error. The bias is defined to be the average of the 1000 estimates minus the true value of the parameter. For a parameter θ , estimated by $\hat{\theta}$, the bias is $\text{bias}(\hat{\theta}) = \bar{\theta} - \theta$, where $\bar{\theta}$ is the average of the

Table 7. Results of simulations to determine relative standard errors (%) of estimated mortality rates.

Parameter	$F = 0.2$				$F = 0.4$			
	$M = 0.2$		$M = 0.4$		$M = 0.2$		$M = 0.4$	
	$F^* = F$, mixed	$F^* = 0.1$, non-mixed	$F^* = F$, mixed	$F^* = 0.1$, non-mixed	$F^* = F$, mixed	$F^* = 0.3$, non-mixed	$F^* = F$, mixed	$F^* = 0.3$, non-mixed
Year-specific mortality assumed								
F_1^*	—	10.19	—	10.19	—	6.19	—	6.19
F_2^*	—	10.15	—	10.14	—	6.18	—	6.18
F_3^*	—	10.20	—	10.20	—	6.20	—	6.20
F_1	7.40	—	7.40	—	5.50	—	5.50	—
F_2	6.10	14.47	6.31	16.89	4.67	11.02	4.81	12.94
F_3	6.59	18.66	6.72	21.65	4.99	14.44	5.10	17.04
M	24.84	52.65	14.15	31.66	18.00	35.61	10.62	22.03
Constant mortality assumed								
F^*	—	5.88	—	5.88	—	3.57	—	3.57
F	4.10	14.45	4.15	16.88	3.06	10.95	3.09	12.90
M	22.50	46.59	13.08	28.26	16.67	31.63	10.00	19.61

Note: Animals were tagged for 3 years and recaptured for 3 years. Mortality rates were held constant over time. Estimates were made separately under two assumptions, either that (i) natural mortality is constant over time but fishing mortalities vary over time (top), or (ii) mortality rates are constant over time (bottom). In half of the simulations, newly tagged animals have the same fishing mortality as previously tagged animals while, in the other half, the fishing mortality on newly tagged animals is less than that on previously tagged ones. Non-mixed models were fitted to data sets in which newly and previously tagged animals had different mortality rates. Type 1 (pulse) fishery ($N=1000$ tagged/year; $\phi\lambda=100\%$).

1000 estimates. The relative standard error is defined to be the standard error of $\hat{\theta}$ divided by θ . It is computed as

$$\text{Relative SE}(\hat{\theta}) = \frac{\left(\frac{\sum_{i=1}^{1000} (\hat{\theta}_i - \bar{\theta})^2}{999} \right)^{1/2}}{\theta}$$

where $\hat{\theta}_i$ is the parameter estimate for the i th simulated data set.

In all cases, the biases were small so we restricted our attention to the relative standard errors. Results for the pulse fishery case with $N = 1000$ animals tagged per year and $\phi\lambda = 100\%$ are shown in Table 7. Qualitatively, the results in this table are the same as for all other simulated conditions: there is a significant penalty for having to assume a non-mixed model. Typically, the standard error for a parameter estimated under a non-mixed model is greater than that for the corresponding parameter under a fully mixed model by a factor of two to three. The effect of halving the number of animals tagged is approximately the same as halving the reporting rate. Both serve to reduce the expected number of tag returns and to increase the relative standard errors by approximately 50%. If a continuous (type II) fishery is simulated, the estimated fishing mortalities have slightly higher relative standard errors, and the estimated natural mortality rate(s) has (have) slightly lower relative standard error(s), than if a pulse (type I) fishery is simulated; however, these differences are so small as to be of little practical significance.

Discussion

It is reasonable to assume that the lake trout data considered in the example represent a case where the newly tagged animals are fully mixed into the population when the fishery begins each year. This is because tagging takes place approximately

6 months before the fishery begins. Analysis of the data reveals that a model based on the assumption of complete mixing fits the data very well. Fitting a non-mixed model to these data results in similar estimates to those obtained under the fully mixed model. However, the standard errors are noticeably larger for the non-mixed model.

When we modified the data to simulate a non-mixed situation with abnormally low fishing mortality on the newly tagged animals, the model assuming full mixing performed extremely poorly (low χ^2 goodness of fit statistic, pattern to the residuals, and estimated mortality rates substantially different than those estimated from the original data). In contrast, the non-mixed model performed very well. The model fit the data well judging by the χ^2 statistic and the lack of pattern to the residuals. Furthermore, the estimated natural mortality rates and the fishing mortality rates on previously tagged animals were close to those estimated from the original data.

The simulation results confirm that there is a substantial penalty for having to use a non-mixed model. Insofar as possible, the person designing a tagging program should endeavor to minimize the non-mixing problem by choice of suitable times and locations for the tagging. Apart from that, the options for dealing with non-mixing are to increase the number of recaptures by increasing the number of animals tagged, increase the number of recaptures by increasing the tag reporting rate (e.g., by increasing the reward for returning a tag), or use a model that assumes the period of non-mixing lasts for less than a whole year.

This is the first paper to propose a solution to the non-mixing problem. Brownie et al. (1978, 1985) proposed a model (model 0), which allows for newly tagged animals to have a different tag reporting rate than previously tagged animals but the same exploitation rate and survival rate. They pointed out that if newly tagged animals have a different exploitation rate (and hence different survival rate) than previously tagged animals, the model would be indistinguishable

from their model 0. However, the parameters that can be estimated with model 0 do not include the annual survival rates. That is, the survival rates are confounded with the tag recovery rate parameters so that one can only estimate products of parameters that are not interesting. Our models allow one to estimate fishing and natural mortality rate and thus annual survival rate.

It appears feasible, if expensive, to deal with non-mixing. Further analytical efforts in this area may result in further gains. For example, Hearn et al. (1998) recently described a tagging study design in which animals are tagged before and after the fishery. This provides direct estimates of natural mortality that can be compared with the natural mortality estimated from the kind of data considered here; significant non-mixing would cause a discrepancy in the estimates.

In this paper, we consider the case where there is one count of recaptures per cohort per year. In some cases, it may be possible to apportion the total recaptures from a cohort to subannual periods. For example, it may be possible to determine how many of the recaptures occurred in the first half of the year and how many in the second half by using follow-up interviews of the fishers. This would provide a class of models intermediate between the Brownie-like models and exact time of recapture models (see Hearn 1986; Hearn et al. 1987). The likelihood would still be multinomial, but there would be two cells per year. As before, one would determine an expression for the expected value for each cell of the recovery matrix and raise the expected value to the observed number in the cell. In addition to increasing the precision of the estimates, this type of model would also enable one to estimate the fishing mortality (F_1) in the first year of the study.

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