North American Journal of Fisheries Management 27:773–781, 2007

DOI: 10.1577/M06-127.1

[Article]

Estimating Fishing Mortality, Natural Mortality, and Selectivity Using Recoveries from Tagging Young Fish

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Abstract.—Current methods for estimation of age- and year-specific instantaneous mortality rates based on multiyear, multiple-age tagging studies assume that it is feasible to tag fish in a wide range of ages. For some species, however, only the youngest one or two age-classes are readily available for tagging. Given the practical advantages of tagging young fish only, an important question is whether such studies would provide the information needed for estimation of age-dependent mortality rates. We investigated three designs: tagging only the youngest available age-class, tagging the two youngest age-classes, and tagging the first five age-classes. We carried out simulation studies to assess estimator performance under these three designs, in each case assuming the same total number of tagged fish. Data were generated assuming fishing mortality rates to be age and year dependent and natural mortality rates to be constant or with limited age dependence. Estimator performance is best when fish are tagged in five age-classes, and tagging fish in the two youngest age-classes shows substantial improvement compared with tagging one age-class only. External information about the tag-reporting rate is necessary to obtain estimators with reasonable properties, especially in the case of models with age-dependent natural mortality. Such information can be obtained from auxiliary studies by means of high-reward tags or planted tags. Collecting recovery information for several additional years after the last release produces small improvements in precision and bias. If tagging fish in multiple age-classes is impractical, reasonable precision can be obtained by tagging one or preferably two age-classes and obtaining supplemental information on the reporting rate. For illustration, estimates of age-dependent fishing and natural mortality rates were obtained from tag returns on Chesapeake Bay striped bass *Morone saxatilis* tagged at ages 3 and 4 years.

Pollock et al. (1991) and Hoenig et al. (1998a, 1998b) introduced methods for estimation of instantaneous fishing and natural mortality rates from multiyear tag-return studies. These methods involve reparameterization of the Brownie et al. (1985) band recovery models, which provide estimates of total annual mortality and not the separate components. A problem associated with instantaneous rate parameterization is that the tag-return data contain limited information for separately estimating instantaneous mortality and tag-reporting rates, and there have been a number of suggestions for adding information to the tag-return data to improve estimator properties. For example, Pollock et al. (1991) suggested supplementing the tag-return data by conducting a reward tagging study, a creel survey, or port sampling, and Hearn et al. (2003) suggested using planted tags or observers on fishing boats to estimate the tag-reporting rate in commercial fisheries. Hoenig et al. (1998a) incorporated fishing effort into the instantaneous rate models. They found substantial variation among estimates of the tag-reporting rate when different subsets of the same data set for the lake trout *Salvelinus namaycush* were analyzed, indicating that the tag-reporting rate was not estimated reliably.

Tagging studies ideally involve tagging fish from a wide range of ages to obtain more detailed information concerning fish population dynamics. Jiang et al. 2007a) generalized the Hoenig et al. (1998a, 1998b) models to allow age and year dependence of instantaneous fishing and natural mortality rates. The models were applied to data from a study on Chesapeake Bay striped bass *Morone saxatilis* estimated to be 2 through 8 years of age and older (Jiang et al. 2007a). The results indicated that mortality rates were age dependent (Jiang et al. 2007a). The results

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Received April 27, 2006; accepted November 9, 2006
Published online June 25, 2007

also demonstrated problems with parameter redundancy and poor estimator performance, even for models with constant natural mortality and tag-reporting rates, unless supplemental information concerning the tag-reporting rate was available.

Tagging substantial numbers of fish in multiple age-classes can be extremely difficult for some species. For example, the red drum *Sciaenops ocellatus* and pollock *Pollachius virens* are readily caught at 1 or 2 years of age in coastal waters, but then they migrate offshore where they are difficult to tag in large numbers (Latour et al. 2001; Neilson et al. 2003). Similarly, southern bluefin tuna *Thunnus maccoyi* are tagged as juveniles in coastal waters but are harvested at a range of ages in commercial fisheries operating over a wide geographic area (Polacheck et al. 2006). In addition to greater abundance and availability in most cases, another advantage of tagging young fish is that their age can be determined accurately from size at tagging (e.g., Neilson et al. 2003). In contrast, age determination for older fish can be subject to substantial error.

Another approach for creating a tagged subpopulation is the release of hatchery-reared fish. These are typically young fish because of the additional cost and mortality associated with a longer rearing period. The fish may be batch marked with a chemical such as oxytetracycline or individually marked with a tag such as a coded wire tag (Nielsen 1992). For example, more than 40 million hatchery-reared salmon *Oncorhynchus* spp. and steelhead *O. mykiss* with coded wire tags are released annually in Pacific northwestern North America (Johnson 1990).

These practical considerations led us to examine the properties of studies that involve tagging only younger fish. An important question to address is whether age- and year-dependent fishing mortality rates can be estimated from such studies. Also, the commonly made assumption of constant natural mortality rates may not hold for designs that focus on tagging young fish. Thus, a second question of interest is whether age-dependent natural mortality rates can be estimated. We focused on two designs: design I, in which fish in only the youngest available age-class were tagged, and design II, which required tagging fish in the two youngest age-classes. In view of problems related to overparameterization noted for multiple age studies, it is important to evaluate the properties of estimators before these designs can be recommended.

We present the models for tag-return data arising from designs I and II, for the situations in which the tag-reporting rate is known or is estimated from the data. We also investigate the properties of estimators by simulation under models with age-dependent fishing mortality rates and constant or age-dependent natural mortality. In addition, we study the effect of including information from additional years of recovery or additional information on the reporting rate from planted tags. For comparison, the simulations include a design in which the same total number of tagged fish is distributed across five age-classes. As an example, we analyze a subset of data from a multiple-age tagging study on Chesapeake Bay striped bass.

Methods

Model structure.—Under design I, we consider a multiyear tag-return study in which only age-1 fish (fish in the youngest age-class that is available for capture) are tagged and released each year. Under design II, fish in the two youngest age-classes (ages 1 and 2) are tagged and released each year. We assume that tagging and release happen at the beginning of the year and that harvest occurs at a constant rate throughout the year. Similar to Jiang et al. (2007a), we also assume the following: age at tagging is correctly identified, tag shedding and tag-induced mortality are negligible, fish in a given age-specific cohort are subject to the same mortality rates, and tagged fish suffer independent fates.

We use notation similar to that in Jiang et al. (2007a). Let N_{ik} be the number of fish tagged at age k and released in year i ($i = 1, \ldots, I$), where $k = 1$ for design I and $k = 1, 2$ for design II. Also let R_{ijk} be the number of the N_{ik} fish that are subsequently harvested and reported in year j, for $j = i, \ldots, J$. For design I, the release and recovery data are summarized in a single array, and for design II, there are two data arrays, one for each age at tagging. More generally, there is a recovery array for each of the K age-classes identified at tagging (Jiang et al. 2007a).

We focus on models in which the instantaneous fishing mortality rate is year and age dependent and the age dependence is due to selectivity or availability to the fishery. Thus, F_j is the instantaneous fishing mortality rate in year j for fully recruited fish, Sel_a is the selectivity for fish of age a (constant across years), and $F_{ja} = F_j\text{Sel}_a$ is the instantaneous fishing mortality rate for fish of age a in year j. We assume that fish are fully recruited once they reach a known age, K_c. That is, $\text{Sel}_a = 1$ for $a \geq K_c$. Other scenarios for availability to the fishery could be assumed, providing there is a known age range when fish are fully recruited (e.g., $\text{Sel}_a = 1$ for $K_1 \leq a \leq K_2$, where K_1 and K_2 are known).

Other parameters are M_a, the instantaneous natural mortality rate for fish of age a (constant across years), and λ, the tag-reporting rate, or the probability that the tag is reported given that a tagged fish is caught.

To avoid overparameterization (Jiang et al. 2007a), we allow only a limited type of age dependence of M_a, and define M_Y and M_A to be the instantaneous natural mortality rates for young and older fish, respectively. Although other parameterizations are possible, we assume that "young" applies to fish that are not fully recruited (fish of age a, $a < K_c$) and "older" refers to fully recruited fish. Also to avoid overparameterization, the tag-reporting rate is assumed to be independent of age and constant across years.

The model structure is expressed in terms of the expected numbers of tag returns, $E[R_{ijk}] = N_{ik}P_{ijk}$, where P_{ijk} is the probability that a fish tagged at age k and released in year i is harvested and its tag returned in year j, S_{ijk} is the conditional survival rate in year j for fish tagged at age k in year i and alive at the beginning of year j, and

$$P_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk}\right)(1 - S_{ijk})\dfrac{F_j \mathrm{Sel}_{k+j-i}}{F_j \mathrm{Sel}_{k+j-i} + M_{k+j-i}}\lambda & \text{when } j > i \\ (1 - S_{ijk})\dfrac{F_j \mathrm{Sel}_k}{F_j \mathrm{Sel}_k + M_k}\lambda & \text{when } j = i, \end{cases}$$

$$S_{ijk} = \exp(-F_j \mathrm{Sel}_{k+j-i} - M_{k+j-i}).$$

For each release cohort, the tag returns, R_{ijk}, are assumed to follow a multinomial distribution, leading to a product multinomial likelihood (Hoenig et al. 1998a):

$$L = \prod_{k=1}^{K}\prod_{i=1}^{I}\binom{N_{ik}}{R_{iik}, R_{ii+1k}, \ldots, R_{iJk}}\left(\prod_{j=i}^{J} P_{ijk}^{R_{ijk}}\right) \times \left(1 - \sum_{v=i}^{J} P_{ivk}\right)^{N_{ik} - \Sigma_{v=i}^{J} R_{ivk}}.$$

Note that the index k in the outer product represents an age-class at tagging, so that $k = 1$ for design I, $k = 1, 2$ for design II, and $k = 1, 2, \ldots, 5$ for the design with five age-classes. Also, M_{k+j-i} is replaced by M_Y if $(k + j - i) < K_c$, and by M_A otherwise.

Maximum likelihood estimates (MLEs) must be obtained with specialized software, such as SURVIV (White 1983), which permits coding of the multinomial cell probabilities P_{ijk}. The parameters to be estimated are F_j ($j = 1, 2, \ldots, J$), M_Y, M_A, Sel_a ($a = 1, \ldots, K_c - 1$), and λ, although in some cases λ can be treated as known on the basis of external information (e.g., if tag returns are obtained from observers that examine a known fraction of the catch).

With any of the tagging designs, an auxiliary study can be added to obtain information about λ. One such approach is the use of planted tags, where a known number of specially marked tags is applied to fish in the catch without knowledge of the fishers (Hearn et al. 2003). Given m tags planted in the catch from which v tags are reported, the likelihood function for the planted tag data is binomial,

$$L_p = \binom{m}{v}\lambda^v(1 - \lambda)^{m-v},$$

and the joint likelihood for both types of tag returns is the product $L \times L_p$. We recognize that the planted tags method is of limited use in practice, especially for recreational fisheries, but we include this as a computationally simple way to illustrate the effect on estimator performance of having supplemental information on λ. Similar gains can be obtained with more practical methods, such as the use of high-reward tags that ensure 100% reporting (Nichols et al. 1991; Pollock et al. 2002).

Simulation study.—Jiang et al. (2007a) showed that for multiple-age tagging studies, some parameters of the age-dependent models are close to being confounded if the reporting rate λ is estimated without any supplemental information. We expected the parameter redundancy problem to be worse if only one or two ages were tagged. We also expected parameter redundancy to be worse for models that included two natural mortality rates (M_Y, M_A) compared with models with a single rate ($M_Y = M_A = M$). To obtain information concerning situations where designs I and II provide reliable estimates, we therefore carried out simulation studies under a number of conditions. For comparison with designs I and II, we included a third design, tagging the first five age-classes, corresponding to a multiple-age tagging study. We investigated the effects of adding planted tags, and of increasing the number of years of recovery, and also compared results for estimating two natural mortality rates versus a single rate M.

For each design, we assumed 5 years of tagging, with a total of 2,500 fish tagged and released each year, followed by either 5 or 7 years of recovery. Thus 2,500 age-1 fish were tagged annually under design I, 1,250 fish were tagged annually at each of ages 1 and 2 under design II, and 500 fish were tagged in each of five age-classes each year under the multiple-age design. Data sets were generated using the new version of program SURVIV (White 1983) modified by James Hines of Patuxent Wildlife Research Center. For studies without planted tags, data were generated using the product multinomial likelihood L, and for cases with planted tags, data were generated under the likelihood $L \times L_p$, with $m = 100$ planted tags. We carried out two sets of simulations: the "constant M" models in the first set

TABLE 1.—Bias (RB) and standard error (RSE) of estimators, as percentages of the true parameter values, for designs that differ with respect to the number of age-classes tagged, the number of recovery years, and whether or not planted tags were added. Parameters are as follows: F_n = the fishing mortality rate for age-n fish, λ = the tag-reporting rate, M = the natural mortality rate, and Sel = selectivity. Data were generated assuming a constant M. The RB and RSE are based on 500 simulated data sets, and F_n and Sel are averages of the year- or age-specific results.

Age at tagging and parameter	λ known		λ estimated: No planted tags		λ estimated: 100 planted tags	
	RB	RSE	RB	RSE	RB	RSE
5 years of recovery						
Age 1						
F_1–F_5	6	24	8	39	7	27
λ			15	58	0	12
M	2	14	−3	62	−1	24
Sel	−2	16	−1	16	−1	16
Ages 1–2						
F_1–F_5	1	14	2	34	2	19
λ			11	44	0	11
M	1	11	−1	46	−2	20
Sel	0	11	0	11	0	11
Ages 1–5						
F_1–F_5	−1	7	−1	24	0	13
λ			7	30	0	11
M	0	8	1	37	−2	19
Sel	0	7	0	7	1	8
7 years of recovery						
Age 1						
F_1–F_5	1	13	2	34	2	16
F_6–F_7	2	15	9	47	4	21
λ			16	57	0	12
M	0	8	−2	60	−2	20
Sel	0	10	0	10	0	9
Ages 1–2						
F_1–F_5	0	10	1	26	1	15
F_6–F_7	1	13	5	34	3	20
λ			7	35	0	11
M	0	7	−1	41	−2	19
Sel	0	8	0	8	0	8
Ages 1–5						
F_1–F_5	−1	6	−2	19	0	12
F_6–F_7	0	11	0	28	2	19
λ			5	22	0	10
M	0	7	2	31	−1	18
Sel	1	7	1	7	1	7

assumed M to be age independent, and models in the second set involved two natural mortality rates, M_Y and M_A.

In all cases, fish were assumed to be fully recruited at age 4. The parameter values used in the constant M cases were $F_1 = 0.2$, $F_2 = 0.5$, $F_3 = 0.3$, $F_4 = 0.4$, $F_5 = 0.6$, $M = 0.2$, $\lambda = 0.4$, $\text{Sel}_1 = 0.6$, $\text{Sel}_2 = 0.7$, and $\text{Sel}_3 = 0.9$ for 5 years of recoveries, plus $F_6 = 0.3$ and $F_7 = 0.4$ for 7 years of recovery. In the second set of "M_Y, M_A" cases, natural mortality rates were $M_Y = 0.40$ for ages 1–3 years and $M_A = 0.15$ for ages ≥4 years; otherwise, parameter values were the same as for the constant M simulations. These values were based roughly on estimates obtained for the striped bass data set described in the Example. For each study design, we generated 500 tag-return data sets and obtained MLEs of parameters. Estimates were constrained to be in the interval 0–1 by means of the bounds option in SURVIV.

For the constant M cases, estimates were obtained under three scenarios: (1) with the value of λ assumed known, (2) with λ estimated without supplemental information, and (3) with λ estimated given supplemental information from $m = 100$ planted tags. In the M_Y, M_A cases, estimates were obtained either assuming λ known or with λ estimated given supplemental information from $m = 100$ planted tags. Assuming that the value of λ is known exactly is not realistic in practice, but represents the best possible situation for estimation of the other parameters.

Mean estimates and standard errors were calculated for each parameter from the 500 simulated data sets for each scenario and estimation method. Results are reported in terms of relative bias and relative standard error, both expressed as a percentage of the true parameter value. For example, for the reporting rate estimator, $\hat{\lambda}$, relative bias (RB) and relative standard error (RSE) are calculated as

$$\text{RB}(\hat{\lambda}) = \frac{\overline{\hat{\lambda}} - \lambda}{\lambda} \times 100\%,$$

$$\text{RSE}(\hat{\lambda}) = \frac{\text{SE}(\hat{\lambda})}{\lambda} \times 100\%,$$

where $\overline{\hat{\lambda}}$ is the average estimate of the parameter λ, and $\text{SE}(\hat{\lambda})$ is the standard error of $\hat{\lambda}$, from the 500 Monte Carlo samples. To simplify results, and with little loss of information, values of RB and RSE were averaged for the parameter subsets (F_1, F_2, F_3, F_4, F_5), (F_6, F_7), and (Sel_1, Sel_2, Sel_3), and the averages presented in Tables 1 and 2 denoted as F_1–F_5, F_6–F_7, and Sel, respectively.

Results

Constant M

Results for the data sets generated assuming constant M (Table 1) show that auxiliary information about λ is essential for deriving reliable estimates. Except for the estimators of Sel, compared with the ideal situation when λ is known, the RSE is generally at least twofold greater if λ is estimated from the data without any supplemental information. When there is no supplemental information from planted tags, the RB is largest for the estimator $\hat{\lambda}$, and the RSE is large for both $\hat{M}$ and $\hat{\lambda}$, although performance improves somewhat as more age-classes are tagged. For estimators of λ and of F_1 –

TABLE 2.—Bias (RB) and standard error (RSE) of estimators as percentages of the true parameter values for designs that differ with respect to the number of age-classes tagged and the number of recovery years. Data were generated assuming different natural mortality rates, (M_Y and M_A) for young and fully recruited fish. See Table 1 for additional details.

Age at tagging and parameter	λ known		λ estimated[a]	
	RB	RSE	RB	RSE
5 years of recovery				
Age 1				
F_1–F_5	8	38	8	39
F_6–F_7				
λ			0	12
M_Y	−1	20	−1	23
M_A	−19	79	−19	79
Sel	2	24	2	25
Ages 1–2				
F_1–F_5	1	19	2	23
F_6–F_7				
λ			0	11
M_Y	0	12	−1	14
M_A	−2	55	−5	61
Sel	1	14	1	14
Ages 1–5				
F_1–F_5	−1	7	1	15
F_6–F_7				
λ			0	11
M_Y	0	7	−1	10
M_A	0	12	−3	31
Sel	1	8	1	8
7 years of recovery				
Age 1				
F_1–F_5	4	35	4	35
F_6–F_7	5	39	6	40
λ			0	12
M_Y	−2	19	−3	22
M_A	−8	102	−8	102
Sel	3	23	3	23
Ages 1–2				
F_1–F_5	1	17	2	21
F_6–F_7	2	22	5	29
λ			0	11
M_Y	0	10	−1	13
M_A	0	44	−3	55
Sel	0	12	0	12
Ages 1–5				
F_1–F_5	−1	6	1	14
F_6–F_7	1	13	4	24
λ			0	11
M_Y	0	6	−1	10
M_A	0	10	−3	29
Sel	1	7	1	7

[a] 100 planted tags.

F_5, the additional information provided by 100 planted tags leads to dramatic improvement in performance compared with having no supplemental information. Even so, the RSE for estimators of $F_1 - F_5$ is still about 1.5 times greater than in the λ known case. Figure 1 illustrates results for $\hat{M}$, showing that bias is generally less than 5% but that bias and RSE are greatest when only age-1 fish are tagged and λ is estimated without supplemental information. Even with 100 planted tags, the RSE for $\hat{M}$ is 2–3 times that in the λ known case.

Tagging both age-1 and age-2 fish results in improved performance compared with tagging age-1 fish only. Distributing the same total number of tagged fish across five age-classes leads to additional gains in efficiency, although these gains are smaller than those produced by the supplemental information from 100 planted tags. Increasing the number of years of recovery from 5 to 7 produces small improvements in the properties of estimators of $F_1 - F_5$, M, and λ.

Age-Dependent M

The simulations with age-dependent M show that, even with λ assumed known, the natural mortality rate for fully recruited fish, M_A, is poorly estimated if only young fish are tagged (Table 2). In contrast, estimators of M_Y behave reasonably well. The poor results for estimation of M_A are due to overparameterization (Jiang et al. 2007a). Other parameters, such as the Fs and selectivities, are also poorly estimated for designs I and II, in comparison to the constant M cases, because of confounding of parameters (Jiang et al. 2007a). Similar to the constant M cases, estimator performance improves if age-1 and age-2 fish are tagged compared with tagging age-1 fish only, and small gains are associated with 7 compared with 5 years of recovery.

In summary, for both the constant M and the age-dependent M cases, even under the ideal "λ known" situation, the RSE is greater than 20% for estimators of $F_1 - F_5$ under design I with 2,500 age-1 fish tagged annually for 5 years and 5 years of recovery. Given the rate parameters assumed, tagging fish in two age-classes results in more reasonable estimator performance compared with design I. In the more realistic situation where λ must be estimated, and especially under the models with age-dependent M, with design II it is clear that supplemental information on λ must be obtained to achieve RB $<$ 5% and RSE $<$ 25% for parameters of interest (with the exception of M_A). To achieve reasonable precision for estimation of M_A, it is necessary that fully recruited fish be tagged. Although tagging 500 fish in each of five age-classes produces estimators with superior properties, reasonable performance can be obtained with design II provided supplemental information is available for the estimation of λ.

Example

We utilize data from a multiyear, multiple-age tagging study on Chesapeake Bay striped bass, carried out by the Maryland Department of Natural Resources, to illustrate the use of data from tagging one or two age-classes to estimate instantaneous mortality rates. The complete (1991–2003) data set is analyzed in Jiang et al. (2007b), and we use a subset here, ignoring the

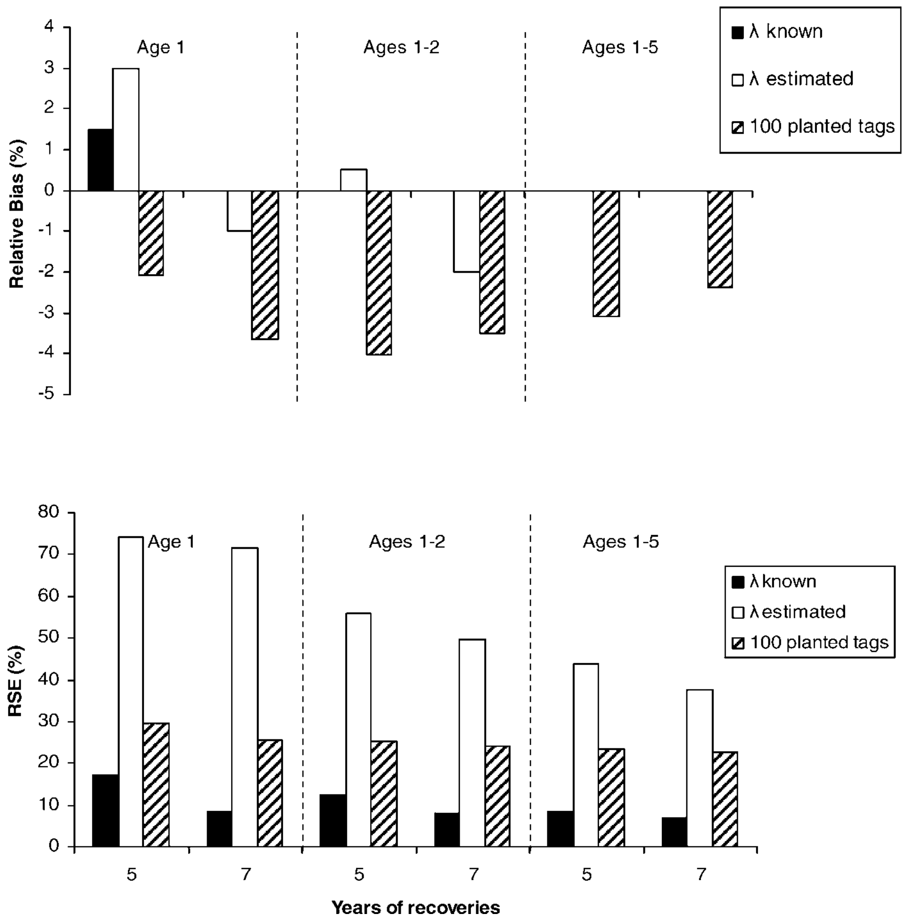

FIGURE 1.—Bias and standard error of the estimator $\hat{M}$ as a percentage of the true value $M = 0.2$, for designs with tagging a total of 2,500 fish, distributed among one, two, or five age-classes, with 5 or 7 years of recovery, and with or without auxiliary information from planted tags. Estimates are based on 500 simulated data sets and are obtained with λ assumed known or with λ estimated when returns are included from 0 or 100 planted tags.

catch-and-release aspect of the data, for purposes of illustration.

Between 1991 and 1998, 14,209 striped bass, age 3 years and older, were tagged and released. Most of the releases were older fish (ages 5, 6, 7, and 8 years and older); just 1,695 and 2,489 were tagged in the two youngest age-classes (3 and 4 years of age, respectively). For illustration, we compare estimates obtained from three subsets of the data: just the 1,695 fish tagged at age 3, the 4,184 fish tagged at ages 3 and 4 years, and all 14,209 releases. This comparison is different from the situation in our simulation study because the average number of fish tagged annually is substantially greater in the multiple-age design (1,776) than in the one- and two-age-class designs (212 and 523, respectively), although lower than the 2,500 assumed in the simulations.

Based on Jiang et al. (2007b), we assumed fish were fully recruited at age 6 years and that the value of the tag-reporting rate was known to be $\lambda = 0.43$. We estimated two natural mortality rate parameters: M_Y for fish of age 3, 4, and 5 years, and M_A for fish of age 6 years and greater. Results in Table 3 indicate that estimates from fish tagged at age 3 only are highly imprecise compared with results for tagging at ages 3–4 and ages 3–8 and older. Based on our simulations, part of the improvement in precision for the multiple-age design compared with the age-3–age-4 design is due to tagging a wider range of ages, but a large part of the improvement is due to the greater total number of fish tagged. Estimates of instantaneous fishing mortality at age 3 (year-specific $F \times \mathrm{Sel}_3$) were relatively similar for the three designs, although the estimates of the F and Sel components differed. It appears likely

TABLE 3.—Estimates of fishing mortality, natural mortality, and selectivity based on 1991–1998 tag returns from Chesapeake Bay striped bass, assuming a known reporting rate of 0.43. Estimates are based on the analysis of returns from fish tagged at age 3, ages 3–4, and all ages (3–8 and older).

	Age 3		Ages 3–4		Ages 3–8 and older	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
F_{1991}	0.72	0.99	0.41	0.14	0.25	0.02
F_{1992}	0.50	0.69	0.40	0.13	0.34	0.02
F_{1993}	0.31	0.42	0.25	0.08	0.28	0.02
F_{1994}	0.44	0.57	0.34	0.10	0.30	0.02
F_{1995}	0.57	0.71	0.39	0.12	0.38	0.02
F_{1996}	0.63	0.82	0.44	0.14	0.35	0.02
F_{1997}	0.65	0.88	0.37	0.12	0.38	0.03
F_{1998}	0.59	0.84	0.36	0.12	0.39	0.03
Sel_3	0.30	0.36	0.41	0.12	0.49	0.06
Sel_4	0.46	0.42	0.54	0.13	0.58	0.05
Sel_5	1.00	0.47	1.00	0.16	0.98	0.06
M_Y	0.48	0.25	0.40	0.08	0.38	0.02
M_A	0.00	0.70	0.17	0.11	0.18	0.01

that the Fs for fully selected fish are overestimated, and the age-3 selectivity is underestimated, for the age-3 design compared with the other two designs. All three designs suggested a difference in natural mortality between young and older fish, although the estimate of adult M is not plausible for the case of tagging only age-3 fish. Both estimates of natural mortality were similar for tagging at ages 3–4 only versus all ages.

Discussion

In tagging studies on birds, there are also strong practical reasons to band or ring only juveniles, often as nestlings. The basic parameters of the Brownie et al. (1985) band return models for such data are finite annual survival rates (S) and band recovery rates (f). Brownie et al. (1985) and Anderson et al. (1985) showed that banding studies where only young animals are tagged cannot be used to estimate age-dependent survival rates in the band recovery model parameterization. If both S and f are age dependent, there is confounding of parameters even when all rates are constant across years, and additional constraints must be imposed for parameters to be estimable. For example, a common life table method assumes that S and f depend on age only and that the ratio $f/(1-S)$ is constant across ages and years (Brownie et al. 1985), while Seber (1971) assumes constant f and age-specific S, plus an additional constraint such as equality of survival rates for the two oldest ages. Freeman and Morgan (1992) investigated models with year-specific first-year survival, constant adult survival and year-specific reporting rates. Our results indicate that parameter redundancy problems also occur with the instantaneous rates parameterization when mortality is year and age dependent and only young are tagged. These problems can be obviated to some extent in designs with tagging the first one or two age-classes if independent information for estimation of the tag-reporting rate is available.

In our simulations, we compared a release of age-1 fish (design I) with ages 1–2 (design II) and ages 1–5 and older. Design I is at an obvious disadvantage in estimating rates (such as selectivity) for older fish, in that the first tagged fish do not reach age 5 until the fifth year of the tagging program. Thus, there is an obvious advantage in extending the length of the study for designs I and II, unless parameters assumed to be constant (such as natural mortality or selectivity) are thought to be changing markedly with time. Another practical issue is the declining sample size at older ages under designs I and II. This loss of information can be partly offset by increasing the number of released tags, but there is still less information under designs I and II because the number of tagged fish at older ages is not known but is instead an estimated product of survival rates in prior years.

In the estimation of instantaneous mortality rates from tag-return studies on fish, it is typical to assume that the natural mortality rate is constant across ages and years. If age-and year-specific estimates of natural mortality are warranted, then a multiyear, multiple-age tagging study would be necessary, along with highly precise estimates of reporting rates (Jiang et al. 2007a). If only young fish are tagged, we have shown that a model with limited age dependence of M can be fitted if additional information on the tag-reporting rate is available. Another parsimonious, and possibly more realistic, approach to allow age dependence of M is to model M as a parametric function (e.g., a logistic function) of age.

We included planted tags in our simulations as a simple way to demonstrate the effect on estimator properties of independent information on λ. Other methods have been proposed for estimating λ from external sources (Pollock et al. 1991, 2001, 2002; Hearn et al. 2003) and may be easier to implement in the field. Any method that provides information about λ can lead to gains in precision similar to those illustrated for planted tags.

The general recommendations made for tagging one or two age-classes can be applied in designing studies where catch-and-release fishing will occur. The analysis of tag returns from harvested fish and fish that are released after tag removal is more complicated (Jiang et al. 2007b), but similar design considerations will hold.

Multiple-age tagging studies make the strong assumption that age at tagging can be reliably determined, either by examining some hard structure, such as a scale, or by using an age–length key (Secor et al. 1995). Either approach will result in some level of misclassification, and use of the age–length key may produce substantial errors for older fish because of overlapping frequency distributions (Le Cren 1974; Beamish and McFarlane 1995). If mortality rates are strongly age dependent, such aging errors could result in biased estimates and reduced precision. Our simulations have assumed that the age of individuals is correctly determined, giving an advantage to the five-age-class design, because aging errors would be more frequent than in designs with tagging young fish. Assessing the impact of age misspecification is an interesting topic but beyond the scope of this paper.

Acknowledgments

Support for this work was provided by Wallop Breaux funds from the U.S. Fish and Wildlife Service under contract F-77–19 and by Anadromous Fish Conservation Act program funds from the National Oceanic and Atmospheric Administration/National Marine Fisheries Service (NOAA/NMFS) under grant NA05NMF4051116. Additional funds were provided by the Virginia Marine Resources Commission Recreational Fishing Advisory Board fund. We thank Brian Wells, NOAA/NMFS, for permission to use the data for striped bass and anonymous reviewers for comments that led to improving the paper.

References

Anderson, D. R., K. P. Burnham, and G. C. White. 1985. Problems in estimating age- specific survival rates from recovery data of birds ringed as young. Journal of Animal Ecology 54:89–98.

Beamish, R. J., and G. A. McFarlane. 1995. A discussion of the importance of aging errors, and an application to walleye pollock: the world's largest fishery. Pages 81–95 *in* D. H. Secor, J. M. Dean, and S. E. Campana, editors. Recent developments in fish otolith research. Belle W Baruch Library in Marine Science 19.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data: a handbook. U.S. Fish and Wildlife Service Resource Publication 156.

Freeman, S. N., and B. J. T. Morgan. 1992. A modeling strategy for recovery data from birds ringed as nestlings. Biometrics 48:217–236.

Hearn, W. S., J. M. Hoenig, K. H. Pollock, and D. A. Hepworth. 2003. Tag reporting rate estimation, III. Use of planted tags in one component of a multiple-component fishery. North American Journal of Fisheries Management 23:66–77.

Hoenig, J. M., N. J. Barrowman, W. S. Hearn, and K. H. Pollock. 1998a. Multiyear tagging studies incorporating fishing effort data. Canadian Journal of Fisheries and Aquatic Sciences 55:1466–1476.

Hoenig, J. M., N. J. Barrowman, K. H. Pollock, E. N. Brooks, W. S. Hearn, and T. Polacheck. 1998b. Models for tagging data that allow for incomplete mixing of newly tagged animals. Canadian Journal of Fisheries and Aquatic Sciences 55:1477–1483.

Jiang, H., K. H. Pollock, C. Brownie, J. E. Hightower, J. M. Hoenig, and W. S. Hearn. 2007a. Age-dependent tag return models for estimating fishing mortality, natural mortality, and selectivity. Journal of Agricultural Biological and Environmental Statistics 12:177–194.

Jiang, H., K. H. Pollock, C. Brownie, J. M. Hoenig, R. J. Latour, B. K. Wells, J. E. Hightower, and W. S. Hearn. 2007b. Tag return models for catch-and-release fisheries: striped bass natural mortality estimates change with age and calendar year. North American Journal of Fisheries Management 27:387–396.

Johnson, J. K. 1990. Regional overview of coded wire tagging of anadromous salmon and steelhead in northwest America. Pages 782–816 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Latour, R. J., K. H. Pollock, C. A. Wenner, and J. M. Hoenig. 2001. Estimates of fishing and natural mortality for subadult red drum in South Carolina waters. North American Journal of Fisheries Management 21:733–744.

Le Cren, E. D. 1974. The effects of errors in ageing in production studies. Pages 221–224 *in* T. B. Bagenal, editor. Ageing of fish. Unwin Brothers, Surrey, UK.

Neilson, J. D., W. T. Stobo, and P. Perley. 2003. Age and growth of Canadian East Coast pollock: comparison of results from otolith examination and mark–recapture studies. Transactions of the American Fisheries Society 132:536–545.

Nichols, J. D., R. J. Blohm, R. E. Reynolds, R. E. Trost, J. E. Hines, and J. P. Bladen. 1991. Band reporting rates for mallards with reward bands of different dollar values. Journal of Wildlife Management 55:119–126.

Nielsen, L. A. 1992. Methods of marking fish and shellfish. American Fisheries Society, Special Publication 23, Bethesda, Maryland.

Polacheck, T., J. P. Eveson, G. M. Laslett, K. H. Pollock, and W. S. Hearn. 2006. Integrating catch-at-age and multiyear tagging data: a combined Brownie and Petersen estimation approach in a fishery context. Canadian Journal of Fisheries and Aquatic Sciences 63:534–548.

Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation, 1. An evaluation of the high-reward tagging method. North American Journal of Fisheries Management 21:521–532.

Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2002. Tag reporting rate estimation, 2. Use of high-reward tagging and observers in multiple-component fisheries. North American Journal of Fisheries Management 22:727–736.

Pollock, K. H., J. M. Hoenig, and C. M. Jones. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Pages 423–434 *in* D. Guthrie, J. M. Hoenig, M. Holliday, C. M. Jones, M. J. Mills, S. A. Moberly, K. H. Pollock, and D. R. Talhelm, editors. Creel and angler surveys in fisheries management. American Fisheries Society, Symposium 12, Bethesda, Maryland.

Seber, G. A. F. 1971. Estimating age-specific survival rates from bird-band returns when the reporting rate is constant. Biometrika 58:491–497.

Secor, D. H., T. M. Trice, and H. T. Hornick. 1995. Validation of otolith-based ageing and a comparison of otolith and scale-based ageing in mark-harvested Chesapeake Bay striped bass, *Morone saxatilis*. U.S. National Marine Fisheries Service Fishery Bulletin 93:186–190.

White, G. C. 1983. Numerical estimation of survival rates from band recovery and biotelemetry data. Journal of Wildlife Management 47:716–728.