

Age-Dependent Tag Return Models for Estimating Fishing Mortality, Natural Mortality, and Selectivity

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Tag return studies play an important role in providing estimates of mortality rates needed for management of many fisheries, but current methods of estimation do not allow age dependence of instantaneous mortality rates. We present models that allow age-dependent fishing and natural mortality rates, an important advance, because there is often substantial variation in age (and size) of fish at tagging. Age dependence of fishing mortality is modeled by assuming that availability to the fishery, that is, selectivity, depends on age but is constant over years. We assume that all age classes are tagged each year, and allow for incomplete mixing of newly tagged fish and for fisheries that are year-long or limited to a fishing season. We investigate parameter redundancy and estimator performance using analytic and simulation methods, and show that estimator properties are poor if the tag reporting rate is estimated (without auxiliary data such as planted tags). We analyzed multiple age class tag return data from a 13-year study on striped bass (*Morone saxatilis*) and saw clear evidence that selectivity increases with age. Assuming that the tag reporting rate is constant and known, results also demonstrate age dependence of natural mortality rates, and an increase in natural mortality rates from about 1999 coinciding with observation of a bacterial disease in the fish.

Key Words: Instantaneous mortality rates; Near-singularity; Parameter redundancy; Striped bass; Tag reporting rate.

1. INTRODUCTION

Tag return studies play an important role in providing estimates of mortality rates needed for management of many fisheries. Tagged fish are released annually and the tags from harvested fish are returned to the agency in charge by fishers. Typically, the tagged fish vary

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over a large range of ages and sizes. For example, the Maryland Department of Natural Resources (MDNR) carried out a study on the Chesapeake Bay striped bass (*Morone saxatilis*) stock in order to estimate fishing mortality rates. Reliable information is essential for management because this stock supports one of the most important recreational fisheries on the Atlantic coast. A total of 24,533 fish, ranging in age from 2 to 8+ years, were tagged between 1991 and 2002. The releases and tag returns for this study are presented in the Appendix.

Brownie, Anderson, Burnham, and Robson (1985) presented models for tag return data based on annual survival and “reported exploitation” rates. They noted (Brownie et al. 1985, p. 14) that without additional information on the reporting rate, the exploitation rate cannot be estimated. In fisheries, it is important to obtain separate estimates of the two components of mortality, fishing, and natural mortality, and Pollock, Hoenig, and Jones (1991) showed how to estimate both the instantaneous fishing and natural mortality rates if an estimate of the tag reporting rate is available. Hoenig, Barrowman, Hearn, and Pollock (1998a) formulated a general theory for the instantaneous rates version of the tag return models. By analyzing multiple subsets of a dataset on lake trout (*Salvelinus namaycush*), they showed that it is possible to estimate the tag reporting rate in addition to the fishing and natural mortality rates, but that estimates were not stable. Hoenig et al. (1998b) presented models that allowed for incomplete mixing of newly tagged fish. Tag reporting rates were assumed to be known or well estimated from another study.

A limitation of the methods of Pollock et al. (1991) and Hoenig et al. (1998a) is the assumption that fishing mortality does not vary with age. For the striped bass dataset, given the variation in age at tagging, we expect that fishing mortality rates depend on age and an appropriate analysis should allow such age dependence. We therefore developed a generalization of the Hoenig et al. (1998a,b) models to allow multiple age classes with potentially different fishing mortality rates and also possibly different natural mortality rates.

In this article, we present the new age-dependent models for the case where multiple ages of fish are tagged each year. We examine whether the tag reporting rate can be estimated and address parameter redundancy issues for models with different degrees of age and year specificity. We assess performance of estimators under certain models by simulation. The new models are applied to the striped bass dataset and results show evidence of age dependence of both fishing and natural mortality rates.

2. MODEL STRUCTURE

2.1 BASIC MODEL: CONTINUOUS FISHERY

We consider multiple age tagging studies, where tagging and release occur at the beginning of the year and harvest occurs continuously during the entire year. Let N_{ik} be the number of fish tagged at age k and released in year i ($k = 1, 2, \dots, K, i = 1, 2, \dots, I$), and let R_{ijk} be the number of these N_{ik} fish that are subsequently harvested and reported in year j ($j = i, i + 1, \dots, J$). Age dependence of the instantaneous fishing mortality rate

is modeled by allowing recruitment into the fishery to be related to age. Thus, for fish of age a in year j , the instantaneous fishing mortality rate is $F_{ja} = F_j \text{Sel}_a$, where F_j is the instantaneous fishing mortality rate in year j for fully recruited fish, and Sel_a is the selectivity coefficient for age a fish. We assume that the age at which fish are fully recruited, a_c , is known, and that a_c does not exceed the number of age classes tagged. That is, $\text{Sel}_a \equiv 1$ for $a > a_c$, where $a_c \leq K$. Assuming selectivity to be constant over years for each age results in a parsimonious representation of age and year dependence for fishing mortality.

We also let M be the instantaneous natural mortality rate, and λ the tag reporting rate (the probability that the tag is reported, given that a tagged fish is caught). For simplicity, we assume at first that M and λ are constant over year and age. Models with M and λ age and/or year dependent are investigated in Sections 3 and 5.

To present expected numbers of tag returns, and obtain a likelihood, the following assumptions (which extend those in Brownie et al. 1985) are required. We assume there is no tag loss (immediate or long-term), tag numbers are correctly reported, and tagging induced mortality is negligible. If immediate tag loss occurs, the parameter λ is actually a product of the tag retention and tag reporting rates. There is no emigration. Fishing and natural mortality forces are additive, and the instantaneous rates F and M (or more generally, their ratio), are constant within a year. Fish behave independently with respect to their mortality process. Age at tagging is correctly identified, and there is no heterogeneity in mortality among fish within the same age specific release cohort.

Under these assumptions, the annual survival and recovery rates are obtained from the instantaneous rates using a competing risks approach. Also, the tag returns R_{ijk} , $j = i, \dots, J$, from fish tagged at age k and released in year i , follow a multinomial distribution. The cell expectations are

$$E[R_{ijk}] = N_{ik} P_{ijk},$$

where

P_{ijk} = the probability that a fish tagged at age k and released in year i , is harvested and returned in year j ;

S_{ijk} = the conditional probability of surviving year j , given it is alive at the start of the year, for a fish tagged at age k in year i ;

and, for a fishery continuous over the whole year,

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

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

The full likelihood function is product multinomial:

$$L_1 = \prod_{k=1}^K \prod_{i=1}^I \binom{N_{ik}}{R_{iik}, R_{i+1k}, \dots, R_{iJk}} \left(\prod_{j=i}^J P_{ijk}^{R_{ijk}} \right) \left(1 - \sum_{v=i}^J P_{ivk} \right)^{N_{ik} - \sum_{v=i}^J R_{ivk}} \tag{2.1}$$

Maximum likelihood estimates (MLEs) based on L_1 are obtained numerically using software such as SURVIV (White 1983). We consider models where λ is a known constant, and also models where λ must be estimated in addition to the parameters $F_j, j = 1, \dots, J, \text{Sel}_a, a = 1, \dots, a_c,$ and M . A third case, with important practical implications, occurs when independent, auxiliary data are available to estimate λ . For instance, a study may include use of high reward tags in addition to the regular tags (Pollock, Hoenig, Hearn, and Calingaert 2001). Assuming independence of returns from the two types of tags, the joint likelihood for the two types of returns would be $L_1 \times L_2$ where L_2 , the likelihood for the high reward tags, has the same form as L_1 but with $\lambda = 1$. Or, if a planted tag study has been performed with m tags planted in the catch from which v tags are reported, then the likelihood function for the planted tag data is binomial,

$$L_3 = \binom{m}{v} \lambda^v (1 - \lambda)^{m-v},$$

and assuming independence of the planted and regular tag returns, the joint likelihood is the product $L_1 \times L_3$.

2.2 LIMITED FISHERY

In many fisheries, the fishing season is limited to part of the year only. In this case, the definitions of $F_j, S_{ijk},$ and $P_{ijk},$ are different but the model structure is otherwise unchanged. We present the modifications assuming that harvest occurs during a fraction T of the year ($0 \leq T \leq 1$) immediately following release of the tagged fish. Other more general formulations are possible based on the models in Hoenig et al. (1998a).

We define $F_j = T F_j^\Delta,$ where F_j^Δ is the instantaneous fishing mortality rate during the fishing season in year j . Assuming that the ratio F_j^Δ / M is constant over the fishing season, then

$$P_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk} \right) [1 - \exp(-F_j \text{Sel}_{k+j-i} - TM)] \frac{F_j \text{Sel}_{k+j-i}}{F_j \text{Sel}_{k+j-i} + TM} \lambda & (\text{where } j > i) \\ [1 - \exp(-F_j \text{Sel}_{k+j-i} - TM)] \frac{F_j \text{Sel}_k}{F_j \text{Sel}_k + TM} \lambda & (\text{when } j = i) \end{cases}$$

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

In some situations, the fishing season is compressed into a brief period and natural mortality is assumed to occur after the harvest is taken. For such a pulse fishery (or Type 1 fishery, Ricker 1975), we let $T F_j^\Delta \rightarrow F_j$ as $T \rightarrow 0,$ with P_{ijk} modified accordingly.

The likelihood function for the limited and pulse fishery models is obtained from L_1 in (2.1) by substituting the appropriate expressions for P_{ijk} and $S_{ijk}.$

2.3 INCOMPLETE MIXING OF NEWLY TAGGED FISH

We also extend the incomplete mixing model of Hoenig et al. (1998b) to allow age dependence, assuming a year-long fishery. For fully recruited fish in year j , we let F_j^* represent the instantaneous fishing mortality rate for newly tagged fish, and let F_j be the rate for previously released fish. The definitions of other parameters are unchanged, and the likelihood is given by L_1 with

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

$$S_{ijk} = \begin{cases} \exp(-F_j \text{Sel}_{k+j-i} - M) & (\text{when } j > i) \\ \exp(-F_j^* \text{Sel}_k - M) & (\text{when } j = i) \end{cases}$$

3. PARAMETER REDUNDANCY

In describing the age-independent models, Hoenig et al (1998a) noted that if λ is constant over time, then λ is “estimable in theory.” Similarly, the basic model described in Section 2, with year specific fishing mortality, age-dependent selectivity and constant natural mortality, is full rank whether λ is known or estimated. Other models which permit age and year dependence of M are of considerable biological interest, but raise questions about overparameterization, or parameter redundancy. We therefore used methods outlined by Catchpole and Morgan (1997) to investigate parameter redundancy for a number of models with different degrees of age and year dependence.

Catchpole and Morgan (1997) showed that parameter redundancy is equivalent to singularity of the information matrix $\mathbf{I}(\boldsymbol{\theta})$ for a class of models that includes the product multinomial likelihood L_1 . They also showed how to obtain $\mathbf{I}(\boldsymbol{\theta})$, for a multinomial distribution, in terms of the derivative matrix, $\mathbf{D}(\boldsymbol{\theta})$, which has ij th element $d_{ij} = \frac{\partial \mu_j}{\partial \theta_i}$, where the cell expectations μ_j are functions of the unknown parameters θ_i . Parameter redundancy is demonstrated by showing that $\mathbf{I}(\boldsymbol{\theta})$ is singular or, equivalently, that $\mathbf{D}(\boldsymbol{\theta})$ is rank deficient.

In order to use the computer algebra approach described by Catchpole, Morgan, and Viallefont (2002), we considered a small study with three age classes tagged in each of three years and three years of recovery. We assumed that the number of age-specific Sel, M , and λ parameters was at most three (the number of age classes identified at tagging) and did not attempt to generalize to situations with extended age dependence or additional years of recovery. The models studied here, and in subsequent sections, are represented by a list of parameters in parentheses. A subscript y indicates that the parameter is year specific, a subscript a indicates that the parameter is age specific, and no subscript means that the parameter is constant over ages and years. If the parameter list includes λ , or λ_y , and so on, then the λ 's are unknown and must be estimated. Otherwise, the λ 's are assumed known. For example, the most general model studied is denoted $(F_y, M_{y \bullet a}, \text{Sel}_a, \lambda_{y \bullet a})$, where the notation $M_{y \bullet a}$ indicates that a separable model is used to account for year and age effects on

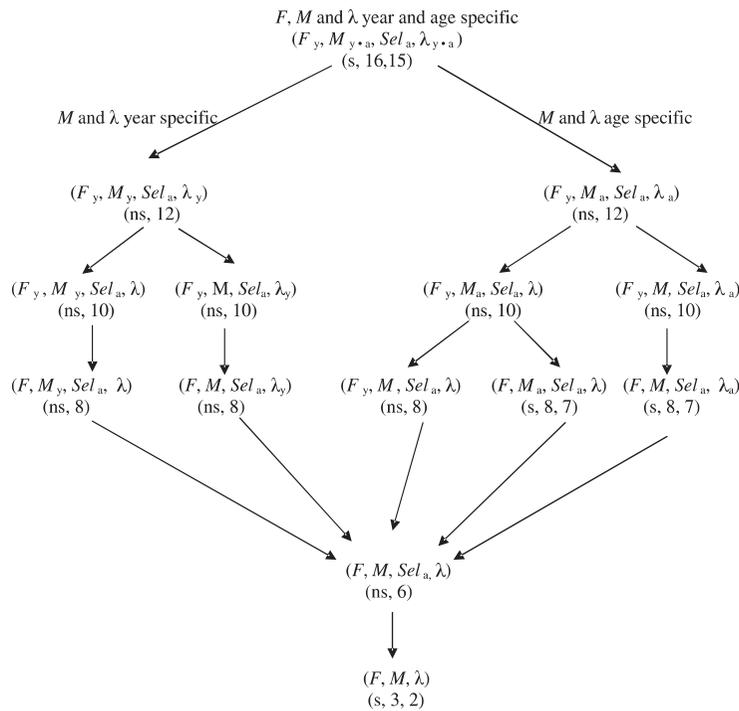


Figure 1. Full rank and rank deficient models, as determined by status of the information matrix, in a set of hierarchical models for multiple age tag return data, based on tagging three age classes for three years, with three years of recoveries: (ns, p) indicates a full rank model with p estimable parameters and (s, p, q) indicates a rank deficient model with p parameters, of which $q < p$ are estimable.

natural mortality M . The age-specific rates for year 1 ($M_{1a}, a = 1, 2, 3+$) are adjusted using year-specific constants for years 2 and 3 ($M_{2a} = bM_{1a}$, and $M_{3a} = cM_{1a}, a = 1, 2, 3+$).

The symbolic algebra package MAPLE (Maplesoft 2003) was used to obtain the matrix $\mathbf{D}(\theta)$, and where possible its rank was obtained using computer algebra. For the more complex models it was necessary to determine the rank of $\mathbf{D}(\theta)$ numerically by specifying the parameter values. Assuming the λ 's are known, the general model (F_y, M_{y+a}, Sel_a) , and all reduced models, are full rank. In contrast, if the λ 's are unknown, both the general model $(F_y, M_{y+a}, Sel_a, \lambda_{y+a})$, and the simplest possible model (F, M, λ) , which assumes $Sel_a = 1, 1 \leq a \leq 5$, are parameter redundant. Various intermediate models are full rank, however, and so we show results in Figure 1 for a number of models where the λ 's are unknown. In one set of reduced models (left side of Figure 1), M and/or λ are year specific but not age specific and in the other set (right side of Figure 1), M and/or λ are age specific but not year specific. All models with M and/or λ year specific but not age specific are full rank. The models (F, M_a, Sel_a, λ) and (F, M, Sel_a, λ_a) , which include two sets of age specific parameters, but no year specificity, are parameter redundant.

To better understand the source of parameter redundancy, we note that the cell probabilities, P_{ijk} , are functions of $\theta = F Sel \lambda$ and $Z = F Sel + M$, with appropriate subscripts to indicate year and age dependence. If for a particular model, the number of F, M, Sel, λ parameters is greater than the number of distinct θ, Z parameters, the model is parameter

redundant. It is easily seen that the simplest model (F, M, λ) is overparameterized, because the P_{ijk} can be written in terms of just two parameters, $\theta = F\lambda$ and $Z = F + M$. For models with F constant, and both Sel, M , or both Sel, λ , age dependent, the number of $F, M, \text{Sel}, \lambda$ parameters exceeds the number of estimable θ, Z parameters. For example, under model $(F, M_a, \text{Sel}_a, \lambda)$, the basic parameters are $\theta_a = F\text{Sel}_a\lambda$, and $Z_a = F\text{Sel}_a + M_a$, fewer than the number of $F, M_a, \text{Sel}_a, \lambda$ parameters. In contrast, when F is year specific, there is a greater number of θ_{ay} and Z_{ay} parameters, and more information for identification of the $F, M, \text{Sel}, \lambda$ parameters.

Parameter redundancy of the simplest model (F, M, λ) suggests that full rank models in Figure 1 will exhibit problems associated with near-singularity (Catchpole, Kgosi, and Morgan 2001; Nasution, Brownie, Pollock, and Powell 2004). Following Catchpole et al. (2001), we therefore evaluated $\mathbf{I}(\theta)$ and its eigenvalues, and examined the eigenvector corresponding to the smallest eigenvalue (EV_{\min}), for various models and parameter values similar to those used in the simulations below. All calculations assumed $N = 1,000$ fish tagged and released annually in each age class. As expected, EV_{\min} was smaller for models with λ estimated compared to the λ known cases, for example, $\text{EV}_{\min} = 4.2$ compared to 23.8 for models $(F_y, M, \text{Sel}_a, \lambda)$ and (F_y, M, Sel_a) , respectively. Near singularity was slightly worse when the number of M parameters increased from 1 to 3 [values of EV_{\min} were 4.2 and 3.4 for models $(F_y, M, \text{Sel}_a, \lambda)$ and $(F_y, M_a, \text{Sel}_a, \lambda)$, respectively]. In the λ known case, reducing the number of Sel parameters by fixing $\text{Sel}_3 = 1$ had a large impact, EV_{\min} increased from 23.8 to 119 for the basic model (F_y, M, Sel_a) and from 8.2 to 61.5 for model (F_y, M_a, Sel_a) . As predicted from the structure of the θ, Z parameters, values of EV_{\min} increased with increasing variation in the values of F_y .

Coefficients in the eigenvector corresponding to EV_{\min} were of similar absolute magnitude for many of the models with small EV_{\min} indicating that all parameters are poorly estimated. An exception to this occurred in models with $\text{Sel}_3 = 1$, where the coefficients corresponding to $\text{Sel}_1, \text{Sel}_2$ indicated better performance for estimators of these parameters. Examining the cell probabilities for direct recoveries, the approximation $x \approx 1 - e^{-x}$, when x is small, gives $P_{iik} = (1 - e^{-(F\text{Sel}_k+M)}) \frac{F\text{Sel}_k}{F\text{Sel}_k+M} \lambda \approx F\text{Sel}_k\lambda$, so that ratios of direct recoveries provide information about ratios of Sel_k . Thus, if $\text{Sel}_a = 1$ for one or more of the age classes tagged (i.e., $K > a_c$), the result is that estimators of Sel_a have good precision even when λ is estimated (see also Myers and Hoenig 1997).

4. SIMULATION STUDY

To further assess the impact of the near-singularity phenomenon, we carried out a simulation study to investigate the properties of estimators under models (F_y, M, Sel_a) and $(F_y, M, \text{Sel}_a, \lambda)$, these being two reasonably parsimonious models that are also of biological interest. Both models allow annual variation in fishing pressure and age-dependent selectivity, but assume a constant natural mortality rate, M . The first model assumes λ is known, while the second requires estimation of λ .

We used the new version of program SURVIV (White 1983), modified by James Hines of Patuxent Wildlife Research Center, to generate data and to obtain MLEs. We assumed

five years of tagging and either five or seven years of recovery, with either 500 or 1,000 fish tagged annually in each of five age classes. Fish were assumed to be fully recruited at age 4 ($\text{Sel}_a = 1$ for $a > 3$). We generated 500 replicate datasets for each case, with parameter values $F_1 = 0.2, F_2 = 0.5, F_3 = 0.3, F_4 = 0.4, F_5 = 0.6, F_6 = 0.3, F_7 = 0.4, \text{Sel}_a = 0.6, 0.7, 0.9$, for $a = 1, 2, 3$, respectively, $M = 0.2$, and $\lambda = 0.3$. We generated data assuming complete mixing for both a continuous fishery and a pulse fishery. For incomplete mixing models, additional parameter values were $F_1^* = 0.2, F_2^* = 0.6, F_3^* = 0.4, F_4^* = 0.5, F_5^* = 0.7$.

Evidence that near-singularity worsens as variation in the F_y decreases led to including an additional case with the same parameter values for Sel_a, M , and λ , but with $F_j = 0.4, j = 1, \dots, 5$. Complete mixing, 500 releases in each age class, and five years of recovery, were assumed. Finally, we carried out simulations to study the impact on estimator performance of adding 50 planted tags. Parameter settings were otherwise the same as for the complete mixing, continuous fishery case. Estimates were obtained using the correct likelihood in all cases (i.e., there was no model misspecification).

Average estimates and standard errors are reported in Table 1 for the case of a continuous fishery with complete mixing, seven years of recovery, and F_y ranging from 0.2 to 0.6. Results for five years of recovery showed the same patterns and are not shown. Similarly, results for the case of a pulse fishery show similar patterns and are not presented here (see Jiang 2005). When 500 fish are tagged in each age class, estimators under model (F_y, M, Sel_a) have good properties with relative bias less than 2% and relative standard error (RSE) less than 11%. Under model $(F_y, M, \text{Sel}_a, \lambda)$, with the exception of $\hat{\lambda}$, estimators again have little bias, but precision is poor. For example, the RSE of $\hat{\lambda}$ is 42% for five years of recoveries, and 30% for seven years of recoveries. RSE for \hat{M} is of similar magnitude. There is a noticeable increase in the precision of estimators when $N = 1,000$ fish of each age class are tagged annually, compared to tagging 500 fish. For example, RSEs of $\hat{\lambda}$ and \hat{M} are 17% and 26%, respectively, with $N = 1,000$, compared to 30% and 38%, respectively, for $N = 500$.

For the case where $F_j = 0.4, j = 1, \dots, 5$, results (not shown) are essentially the same under model (F_y, M, Sel_a) as in the variable F case, but under model $(F_y, M, \text{Sel}_a, \lambda)$ bias of the estimators $\hat{\lambda}$ and \hat{M} is substantially greater in the constant F versus the variable F case. Standard errors of these estimators increase by more than a third for the $F_j = 0.4$ case compared to the variable F case. As noted in Section 3, greater variation in the true F_j leads to cell probabilities that contain more information for estimation of M and λ . In contrast, estimators of selectivity are essentially unbiased and precise, regardless of whether λ is known or estimated, or whether the F_j are variable or constant. This agrees with results in Section 3 that estimators of Sel_a will have good properties under models in which the number of these parameters is smaller than the number of age classes identified at tagging.

Table 1 also shows the effect of augmenting a hypothetical tag return study with a planted tag study with 50 tags planted in the catch to provide an independent estimate of λ . All estimators are essentially unbiased; relative bias of $\hat{\lambda}$ is less than 2%. With the additional information from the planted tags, the precision of some estimators is still poor, but is substantially improved compared to the case where no external information about λ

Table 1. Average Estimates (with standard errors in parentheses), Obtained (a) Under Model (F_y, M, Sel_a) , or (b, c) Under Model (F_y, M, Sel_a, λ) , From Simulated Data for a Continuous Complete Mixing Fishery, Assuming a Study With Five Years of Tagging and Seven years of Recoveries. For each of five age classes, either $N = 500$ fish, or $N = 1,000$, fish are tagged annually. For (c), the study is supplemented with returns from 50 planted tags. Results are based on 500 replications.

Parameter	Value	(a) λ known	(b) λ estimated no planted tags	(c) λ estimated 50 planted tags
Continuous complete mixing fishery with $N = 500$				
F_1	0.2	0.20 (0.02)	0.20 (0.04)	0.20 (0.04)
F_2	0.5	0.50 (0.03)	0.50 (0.11)	0.50 (0.08)
F_3	0.3	0.30 (0.02)	0.30 (0.07)	0.30 (0.05)
F_4	0.4	0.40 (0.02)	0.40 (0.09)	0.40 (0.06)
F_5	0.6	0.60 (0.04)	0.60 (0.15)	0.60 (0.11)
F_6	0.3	0.30 (0.03)	0.31 (0.09)	0.30 (0.07)
F_7	0.4	0.40 (0.06)	0.42 (0.15)	0.41 (0.12)
M	0.2	0.20 (0.01)	0.20 (0.08)	0.20 (0.05)
λ	0.3	—	0.32 (0.09)	0.31 (0.05)
Sel_1	0.6	0.61 (0.06)	0.61 (0.06)	0.61 (0.06)
Sel_2	0.7	0.70 (0.05)	0.70 (0.05)	0.71 (0.05)
Sel_3	0.9	0.90 (0.06)	0.90 (0.06)	0.91 (0.06)
Continuous complete mixing fishery with $N = 1,000$				
F_1	0.2	0.20 (0.02)	0.20 (0.03)	0.20 (0.03)
F_2	0.5	0.50 (0.02)	0.49 (0.08)	0.50 (0.06)
F_3	0.3	0.30 (0.01)	0.30 (0.05)	0.30 (0.04)
F_4	0.4	0.40 (0.02)	0.39 (0.06)	0.40 (0.05)
F_5	0.6	0.60 (0.03)	0.59 (0.10)	0.60 (0.09)
F_6	0.3	0.30 (0.03)	0.30 (0.06)	0.30 (0.05)
F_7	0.4	0.40 (0.05)	0.40 (0.10)	0.41 (0.09)
M	0.2	0.20 (0.01)	0.20 (0.05)	0.20 (0.04)
λ	0.3	—	0.31 (0.05)	0.30 (0.04)
Sel_1	0.6	0.61 (0.04)	0.61 (0.04)	0.61 (0.04)
Sel_2	0.7	0.70 (0.04)	0.71 (0.04)	0.70 (0.04)
Sel_3	0.9	0.90 (0.04)	0.90 (0.04)	0.91 (0.04)

is available. For instance, the RSEs of $\hat{\lambda}$ and \hat{M} are 15% and 26% (compared to 30% and 38%, respectively, if there are no planted tags) when 500 fish are tagged in each age class each year, and are 13% and 21% (compared to 17% and 26%, respectively, if there are no planted tags) when 1,000 fish are tagged in each cohort.

Simulation results for the incomplete mixing situation (Table 2) demonstrate that estimators under model (F_y, F_y^*, M, Sel_a) are essentially unbiased and reasonably precise; relative biases for all estimators are less than 2%, and RSEs for most estimators are less than 10%. However, comparing results for the complete and incomplete mixing cases (Tables 1 and 2) we see that standard errors for \hat{F}_j , $j = 2, \dots, 5$ are considerably larger in the latter case because of the larger number of parameters that are estimated. Model $(F_y, F_y^*, M, Sel_a, \lambda)$ produces estimators with little bias (relative bias less than 5% for

Table 2. Average Estimates With Standard Errors in Parentheses from Fitting Incomplete Mixing Models (a) (F_y, F_y^*, M, Sel_a) and (b) $(F_y, F_y^*, M, Sel_a, \lambda)$. Five hundred fish are tagged for each of five age classes in each of five consecutive years, with either five or seven years of recoveries. Results are based on 500 replications.

Parameter	Value	Five years of recoveries		Seven years of recoveries	
		(a) known	(b) estimated	(a) known	(b) estimated
F_1^*	0.2	0.20 (0.02)	0.19 (0.05)	0.20 (0.02)	0.20 (0.04)
F_2^*	0.6	0.60 (0.05)	0.59 (0.15)	0.60 (0.04)	0.60 (0.12)
F_3^*	0.4	0.40 (0.04)	0.39 (0.10)	0.40 (0.03)	0.40 (0.08)
F_4^*	0.5	0.50 (0.04)	0.49 (0.13)	0.50 (0.04)	0.50 (0.10)
F_5^*	0.7	0.70 (0.05)	0.70 (0.19)	0.70 (0.05)	0.70 (0.15)
F_2	0.5	0.50 (0.05)	0.49 (0.12)	0.50 (0.05)	0.50 (0.10)
F_3	0.3	0.30 (0.03)	0.29 (0.08)	0.30 (0.03)	0.30 (0.06)
F_4	0.4	0.40 (0.04)	0.39 (0.10)	0.40 (0.03)	0.40 (0.08)
F_5	0.6	0.60 (0.08)	0.61 (0.19)	0.60 (0.06)	0.60 (0.14)
F_6	0.3			0.30 (0.04)	0.31 (0.09)
F_7	0.4			0.40 (0.07)	0.42 (0.14)
M	0.2	0.20 (0.02)	0.20 (0.07)	0.20 (0.02)	0.20 (0.06)
λ	0.3	—	0.33 (0.11)	—	0.31 (0.07)
Sel_1	0.6	0.61 (0.06)	0.61 (0.06)	0.61 (0.06)	0.61 (0.06)
Sel_2	0.7	0.70 (0.06)	0.71 (0.06)	0.71 (0.05)	0.71 (0.05)
Sel_3	0.9	0.90 (0.06)	0.90 (0.06)	0.90 (0.06)	0.90 (0.06)

most estimators), but with poor precision, again demonstrating problems associated with near-singularity when λ is estimated.

5. STRIPED BASS TAG RETURN STUDY

In the MDNR study, striped bass were tagged with internal anchor tags, the length of each fish was determined, and an age class assigned based on the age length key method (Secor, Trice, and Hornick 1995). We grouped data for fish tagged at eight years or older because of small sample sizes in each year class, and omitted the data for fish tagged at age 2 for the same reason (see the Appendix). Some reported tags were from fish that were caught and released but we assume here that all reported tags represent harvested fish, which results in overestimation of fishing mortality. Methods to account for live releases were discussed by Jiang (2005).

Striped bass are thought to be fully recruited at 6 years of age. Thus, we assume $Sel_a = 1$ for $a \geq 6$, and let Sel_3 , Sel_4 , and Sel_5 represent the selectivities for fish of age 3, 4, and 5 years, respectively. The basic model is $(F_y, M, Sel_3, Sel_4, Sel_5)$ with complete mixing of new releases, age- and year-specific fishing mortality, and constant natural mortality. Tag shedding was assumed to be negligible and the tag reporting rate was taken to be $\lambda = 0.43$. This value is based on a high reward tagging study conducted by the Delaware Division of Fish and Wildlife, and is used by the Atlantic States Marine Fisheries Commission Tagging Committee in their stock assessments on striped bass. The corresponding model with λ

estimated is $(F_y, M, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5, \lambda)$.

Several modifications of the basic models were fit to the data to investigate specific questions of interest. The incomplete mixing models $(F_y, F_y^*, M, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$ and $(F_y, F_y^*, M, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5, \lambda)$, were fit to assess whether newly released fish have different fishing mortality rates from previously released fish. To investigate the assumption that M is independent of age, we fit models $(F_y, M_Y, M_A, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$ and $(F_y, M_Y, M_A, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5, \lambda)$ which assume complete mixing, and $(F_y, F_y^*, M_Y, M_A, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$ and $(F_y, F_y^*, M_Y, M_A, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5, \lambda)$ for the case of incomplete mixing. In these models, M_Y and M_A represent the natural mortality rates for young (3 to 5 years) and adult (≥ 6 years) fish, respectively.

Beginning in the late 1990s, mycobacteriosis, a disease caused by bacteria in the genus *Mycobacterium*, was observed in Chesapeake Bay striped bass (Cardinal 2001). The disease is characterized by external lesions (open sores on the skin) and internal lesions that look like lumps in the pancreas and kidney. To allow for a possible effect of disease on natural mortality in a parsimonious manner, we assumed that M was constant within each of two periods corresponding to the years before and after the disease appeared. As we do not know when survival may have been affected by the disease, we fit four such models, with the change in M assumed to begin in 1997, 1998, 1999, or 2000. Models which incorporate both age and year dependence of M were also considered. To investigate the effects of a relaxation of harvest regulations which began in 1995 (Richards and Rago 1999), we fit reduced models with constant fishing mortality rates before and after the year 1995. For most models, we fit two versions, one with $\lambda = 0.43$ and the other with λ estimated. SURVIV was used for all computations, and all of the models that we fit to the striped bass data were full rank.

We used Akaike's information criterion (AIC) to compare multiple nested and nonnested models (Burnham and Anderson 2002). A correction to AIC for small sample sizes made little difference and is not reported. To account for possible overdispersion in the data, due to a lack of independence among fish of capture and survival events, we also implemented the quasi-likelihood approach recommended by Burnham and Anderson (2002). The corresponding criterion is QAIC, defined as,

$$\text{QAIC} = -2\log \left[l(\hat{\theta}|y) \right] / \hat{c} + 2p,$$

where $l(\hat{\theta}|y)$ is the likelihood evaluated at the MLE $\hat{\theta}$, p is the number of parameters, and the variance inflation factor, \hat{c} , is calculated as $\hat{c} = \chi^2/df$, with χ^2 and df based on the goodness-of-fit test of the most general model in the model set.

Table 3 displays the values of AIC, ΔAIC (the change in AIC compared to the smallest AIC value), QAIC, and ΔQAIC (the change in QAIC compared to the smallest QAIC value) for models that assume $\lambda = 0.43$. The QAIC values were obtained using $\hat{c} = 1.18$ based on the value of the goodness-of-fit statistic for Model 1 from SURVIV. With regard to the year when a change in natural mortality may have occurred, AIC and QAIC values (not shown) suggested a change in M beginning in 1999. Of the models investigated, the smallest AIC and QAIC values were obtained with the most general model

Table 3. Values of Model Selection Criteria for a Series of Models Applied to the MDNR Striped Bass Dataset. All models assume $\lambda = 0.43$.

Model	p	AIC	Δ AIC	QAIC	Δ QAIC
1	31	2038.24	0.00	1743.60	0.00
2	11	2071.81	33.57	1766.20	22.60
3	20	2074.46	36.22	1771.14	27.54
4	9	2110.17	71.93	1798.25	54.65
5	18	2229.58	191.34	1894.97	151.37
6	17	2348.45	310.21	2003.38	259.78
7	29	2087.75	49.51	1778.13	34.53
8	28	2180.42	142.18	1863.69	120.09
9	18	2200.93	162.69	1878.16	134.56
10	14	2380.42	342.18	2029.69	286.09
11	29	2148.06	109.82	1836.45	92.85
12	25	2234.18	195.94	1908.54	164.94

Note: Description of Models

1. $(F_y, F_y^*, M_{Y_{91-98}}, M_{Y_{99-03}}, M_{A_{91-98}}, M_{A_{99-03}}, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
2. $(F_{91-94}, F_{95-03}, F_{91-94}^*, F_{95-03}^*, M_{Y_{91-08}}, M_{Y_{99-03}}, M_{A_{91-98}}, M_{A_{99-03}}, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
3. $(F_y, M_{Y_{91-98}}, M_{Y_{99-03}}, M_{A_{91-98}}, M_{A_{99-03}}, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
4. $(F_{91-94}, F_{95-03}, M_{Y_{91-98}}, M_{Y_{99-03}}, M_{A_{91-98}}, M_{A_{99-03}}, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
5. $(F_y, M_Y, M_A, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
6. $(F_y, M, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
7. $(F_y, F_y^*, M_Y, M_A, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
8. $(F_y, F_y^*, M, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
9. $(F_y, M_{91-98}, M_{99-03}, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
10. (F_y, M)
11. $(F_y, F_y^*, M_{91-98}, M_{99-03}, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$
12. (F_y, F_y^*, M)

$\hat{c} = 1.18$, based on Model 1, and p is the number of parameters.

$(F_y, F_y^*, M_{Y_{91-98}}, M_{Y_{99-03}}, M_{A_{91-98}}, M_{A_{99-03}}, \text{Sel}_3, \text{Sel}_4, \text{Sel}_5)$ which assumes year specific F and F^* , M both age and period specific, and incomplete mixing of the newly released fish. The next best model differed in that F and F^* were constant within the two periods 1991–1994 and 1995–2003 (Model 2 in Table 3). The three models with the best AIC and QAIC values each involved age and period specific M , where the subscript A_{91-98} indicates a rate for adult fish during 1991 to 1998, Y_{91-98} refers to young fish during 1991 to 1998, and so on. Models with age-dependent M have better AIC values than those with age-independent M (compare Model 5 with 6, and 7 with 8). Comparing each model that includes F^* with the corresponding complete mixing model (Models 2 and 4, 5 and 7, 6 and 8, 10 and 12) provides evidence of incomplete mixing because in each case the AIC and QAIC values are better for the version that includes F^* .

Table 4. Estimates, With Standard Errors in Parentheses, for the MDNR Striped Bass Data, (a) with $\lambda = 0.43$, and (b) for the case when λ is estimated, under the model ($F_y, F_y^*, M_{Y.91-98}, M_{Y.99-03}, M_{A.91-98}, M_{A.99-03}, Sel_3, Sel_4, Sel_5$), that is, Model 1 in Table 3.

Parameter	(a) $\lambda = 0.43$	(b) λ estimated	Parameter	(a) $\lambda = 0.43$	(b) λ estimated
			F_{91}^*	0.25 (0.02)	0.26 (0.12)
F_{92}	0.34 (0.03)	0.36 (0.16)	F_{92}^*	0.32 (0.03)	0.34 (0.16)
F_{93}	0.29 (0.02)	0.31 (0.14)	F_{93}^*	0.24 (0.02)	0.25 (0.12)
F_{94}	0.30 (0.02)	0.31 (0.14)	F_{94}^*	0.27 (0.02)	0.29 (0.13)
F_{95}	0.35 (0.02)	0.37 (0.17)	F_{95}^*	0.35 (0.03)	0.37 (0.18)
F_{96}	0.28 (0.02)	0.30 (0.14)	F_{96}^*	0.36 (0.03)	0.38 (0.18)
F_{97}	0.31 (0.02)	0.33 (0.16)	F_{97}^*	0.38 (0.04)	0.40 (0.20)
F_{98}	0.31 (0.03)	0.33 (0.17)	F_{98}^*	0.38 (0.04)	0.40 (0.20)
F_{99}	0.24 (0.02)	0.25 (0.13)	F_{99}^*	0.44 (0.04)	0.46 (0.23)
F_{00}	0.25 (0.03)	0.27 (0.14)	F_{00}^*	0.41 (0.03)	0.43 (0.21)
F_{01}	0.22 (0.03)	0.23 (0.12)	F_{01}^*	0.39 (0.03)	0.41 (0.20)
F_{02}	0.21 (0.04)	0.22 (0.11)	F_{02}^*	0.28 (0.02)	0.29 (0.13)
F_{03}	0.13 (0.02)	0.14 (0.06)			
Sel_3	0.59 (0.06)	0.59 (0.06)			
Sel_4	0.71 (0.04)	0.71 (0.05)			
Sel_5	1.00 (0.05)	1.00 (0.05)			
$M_{Y.91-98}$	0.39 (0.02)	0.38 (0.11)			
$M_{Y.99-03}$	0.63 (0.08)	0.62 (0.14)			
$M_{A.91-98}$	0.14 (0.01)	0.13 (0.14)			
$M_{A.99-03}$	0.48 (0.05)	0.46 (0.15)			
λ		0.41 (0.18)			

Evidence that fishing mortality is age dependent is based on noting that the AIC and QAIC values for the age-dependent models ($F_y, F_y^*, M, Sel_3, Sel_4, Sel_5$) and ($F_y, M, Sel_3, Sel_4, Sel_5$) are substantially smaller than for the corresponding age-independent models (F_y, F_y^*, M) and (F_y, M) (compare Model 8 with 12, and 6 with 10, in Table 3). Likelihood ratio tests also convincingly reject age independence.

Estimates and their standard errors for the striped bass data under model ($F_y, F_y^*, M_{Y.91-98}, M_{Y.99-03}, M_{A.91-98}, M_{A.99-03}, Sel_3, Sel_4, Sel_5$) with $\lambda = 0.43$, and for the corresponding model with λ estimated, are presented in Table 4. Standard error properties agree well with patterns seen in the simulations. When we assume $\lambda = 0.43$, the precision of estimates is reasonable (most estimated RSEs $< 10\%$) but, except for estimates of selectivity, standard errors are substantially larger when λ is estimated.

Point estimates are remarkably similar between the two models, no doubt because $\hat{\lambda} = 0.41$ is close to the assumed value of 0.43. Estimates of selectivity show an increase with age as expected, with an estimate equal to 1 for fish of age 5 years. There is evidence that natural mortality is higher for young fish compared to older fish (0.39 ± 0.02 compared to 0.14 ± 0.01 from 1991 to 1998, and 0.63 ± 0.08 compared to 0.48 ± 0.05 from 1999 to 2003, with $\lambda = 0.43$). These estimates also reflect an increase in natural mortality for the years 1999 to 2003, compared to the earlier years, coinciding with the observation of

mycobacteriosis in striped bass. Estimates of fishing mortality, F , do not reflect an increase after relaxation of fishing regulations in 1995.

To explore the sensitivity of estimates to the assumption that λ is constant and equal to 0.43, we fit a series of models with different values of λ . Results showed that larger values of λ are associated with smaller estimates of F and F^* , and with larger estimates of M . We also investigated a series of models with two λ values, λ_{91-98} and λ_{99-03} , and found that different (λ_{91-98} , λ_{99-03}) combinations would result in estimates of M that were similar in the two periods. In other words, without good information about λ , it is difficult to distinguish which of λ or M is period specific. These sensitivity analyses emphasize the importance of having accurate and year specific information on the tag reporting rate for obtaining unbiased estimates of mortality rates.

6. DISCUSSION

Analysis of the striped bass data demonstrates the potential importance of our age dependent models for multiple age, tag return datasets. We have shown that both fishing mortality and natural mortality rates are age dependent, and that it is possible to estimate these age dependent rates. Models that include a functional relationship between either Sel or M and age would be interesting but are not considered here. Extensions that account for live releases (Jiang 2005) are also of considerable practical importance.

Estimators have good properties under models that include year and age dependence of F , and limited year and age dependence of M , provided that λ is known. When λ must be estimated, even the basic model with M constant and F year and age dependent shows indications of near-singularity, and estimators have poor precision when as many as 1,000 fish are tagged annually in each class. Design options that will lead to better precision include increasing the tag reporting rate (e.g., by using reward tags) or tagging substantially larger numbers of fish. Another option is to include tagging of fish one year younger than that of the first harvest with selectivity assumed to be 0 for this age class (Latour, Hoenig, Hepworth, and Frusher 2003). Our simulation results show that precision can also be improved by obtaining supplemental information about λ . Thus, we support the recommendations of Pollock et al. (1991, 2001, 2002) and Hearn, Hoenig, Pollock, and Hepworth (2003), that such information should be obtained (e.g., from high-reward tagging, observed catches, planted tags) and incorporated into the analysis on a routine basis. Time variation in the tag reporting rate is an additional complication that we have largely ignored, but ideally supplemental information on λ should be obtained on a yearly basis.

Our age-dependent models assume that age at tagging is determined without error. In reality, the age length key method commonly used to assign ages results in many fish being incorrectly classified. The effects of such misclassification errors on model performance are beyond the scope of this article, but one way to avoid such errors is to tag mainly young fish for which aging errors tend to be less frequent. Sampling designs involving tagging fish in the youngest year classes are studied in Jiang (2005).

Table A.1. Continued

Year of release	Number tagged	Number recaptured												
		Tagged at Age 7												
		1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
1991	310	28	21	14	7	8	3	4	1	0	1	0	0	0
1992	328		39	20	10	8	2	3	1	1	0	0	0	0
1993	331			31	24	17	8	5	3	2	0	0	0	0
1994	189				19	11	5	7	3	6	1	1	0	0
1995	273					41	15	8	5	2	3	0	2	0
1996	397						52	29	13	5	4	2	0	0
1997	75							10	3	2	0	0	0	0
1998	67								9	1	4	0	1	0
1999	94									12	7	0	0	0
2000	413										55	10	4	1
2001	316											34	5	2
2002	507												50	7

		Tagged at Age 8+												
		1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
1991	365	35	24	17	6	6	3	2	1	0	3	0	0	0
1992	384		39	23	15	14	8	9	6	4	2	0	0	0
1993	568			49	33	29	15	15	7	4	1	2	1	0
1994	371				32	24	19	9	13	8	2	2	0	1
1995	374					39	18	19	14	6	4	2	0	4
1996	719						85	43	35	13	6	5	1	1
1997	350							48	27	13	1	2	1	0
1998	280								34	14	3	5	2	1
1999	221									27	8	10	2	0
2000	368										39	15	6	2
2001	551											44	17	7
2002	598												36	15

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REFERENCES

- Brownie, C., Anderson, D. R., Burnham, K. P., and Robson, D. S. (1985), *Statistical Inference from Band Recovery Data: A Handbook*, U.S. Fish and Wildlife Service Resources Publ. No. 156.
- Burnham, K. P., and Anderson, D. R. (2002), *Model Selection and Inference: A Practical Information-Theoretic Approach* (2nd ed.), New York: Springer-Verlag.
- Cardinal, J. L. (2001), "Mycobacteriosis in striped bass, *Morone saxatilis*, from Virginia waters of Chesapeake Bay," unpublished Master's Thesis, Virginia Institute of Marine Science, School of Marine Science.
- Catchpole, E. A., Kgosi, P. M., and Morgan, B. J. T. (2001), "On the Near-Singularity of Models For Animal Recovery Data," *Biometrics*, 57, 720–726.
- Catchpole, E. A., and Morgan, B. J. T. (1997), "Detecting Parameter Redundancy," *Biometrika*, 84, 187–196.
- Catchpole, E. A., Morgan, B. J. T., and Viallefont, A. (2002), "Solving Problems in Parameter Redundancy Using Computer Algebra," *Journal of Applied Statistics*, 29, 625–636.
- Hearn, W. S., Hoenig, J. M., Pollock, K. H., and Hepworth, D. A. (2003), "Tag-reporting Rate Estimation: III. Use of Planted Tags in One Component of a Multi-Component Fishery," *Journal of Fisheries Management*, 23, 66–77.
- Hoenig, J. M., Barrowman, N. J., Hearn, W. S., and Pollock, K. H. (1998a), "Multiyear Tagging Studies Incorporating Fishing Effort Data," *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 1466–1476.
- Hoenig, J. M., Barrowman, N. J., Pollock, K. H., Brooks, E. N., Hearn, W. S., and Polacheck, T. (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. (2005), "Age-Dependent Tag Return Models for Estimating Fishing Mortality, Natural Mortality and Selectivity," unpublished doctoral dissertation, North Carolina State University at Raleigh, Dept. of Statistics.
- Latour, R. J., Hoenig, J. M., Hepworth, D. A., and Frusher, S. D. (2003), "A Novel Tagging Model With Two Size Classes for Estimating Fishing and Natural Mortality, With Application to Southern Rock Lobster (*Jasus edwardsii*) in Tasmania, Australia," *ICES Journal of Marine Science*, 60, 1075–1085.
- Maplesoft, a division of Waterloo Maple Inc. (2003), *Getting Started Guide*, Maple 9, Waterloo, Ontario, Canada.
- Myers, R. A., and Hoenig, J. M. (1997), "Direct Estimates of Gear Selectivity from Multiple Tagging Experiments," *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1–9.
- Nasution, M.D., Brownie, C., Pollock, K. H., and Powell, R. A. (2004), "The Effect on Model Identifiability of Allowing Different Relocation Rates for Live and Dead Animals in the Combined Analysis of Telemetry and Harvest Data," *Journal of Agricultural, Biological, and Environmental Statistics*, 9, 27–41.
- Pollock, K. H., Hoenig, J. M., and Jones, C. M. (1991), "Estimation of Fishing and Natural Mortality When a Tagging Study is Combined With a Creel Survey or Port Sampling," *American Fisheries Society Symposium*, 12, 423–434.
- Pollock, K. H., Hoenig, J. M., Hearn, W. S., and Calingaert, B. (2001), "Tag Reporting Rate Estimation: 1. An Evaluation of the High Reward Tagging Method," *North American Journal of Fisheries Management*, 21, 521–532.
- (2002), "Tag Reporting Rate Estimation: 2. Use of High Reward Tagging and Observers in Multi-component Fisheries," *North American Journal of Fisheries Management*, 22, 727–736.
- Richards, R. A., and Rago, P. J. (1999), "A Case History of Effective Fishery Management: Chesapeake Bay Striped Bass," *North American Journal of Fisheries Management*, 19, 356–375.
- Ricker, W. E. (1975), "Computation and Interpretation of Biological Statistics of Fish Populations," *Fisheries Research Board of Canada Bulletin*, 191.
- Secor, D. H., Trice, T. M., and Hornick, H. T. (1995), "Validation of Otolith-Based Aging and a Comparison of Otolith and Scale-based Aging in Mark-Harvested Chesapeake Bay Striped Bass, *Morone saxatilis*," *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.