ABSTRACT

Jiang, Honghua**.** Age-Dependent Tag Return Models for Estimating Fishing Mortality, Natural Mortality and Selectivity (Under the direction of Kenneth H. Pollock and Cavell Brownie).

In Chapter 1, we extend the instantaneous rates formulation of fisheries tag return models to allow for age-dependence of fishing mortality rates. This is important in many applications where tagged fish vary over a large range of ages (and sizes). We focus on a model based on assuming selectivity by age is constant over years and that above a certain age selectivity is fixed at 1. We show that it is possible to allow natural mortality to vary by age and year, although in many applications we would use a constant natural mortality rate to keep the model as simple as possible to avoid parameter redundancy problems. We allow for incomplete mixing of tagged fish and for fisheries to be pulse, continuous or continuous over part of the year. We focus on the case where all or most age classes are tagged each year. We investigate model identifiability and how well parameters can be estimated using analytic and simulation methods. Results show that some models with the tag reporting rate estimated are singular or near-singular.

We illustrate the methods using multiple age class tag return data on striped bass (*Morone saxatilis*) from the Maryland Department of Natural Resources (MDNR). We found that fishing mortality rates are underestimated in models where these rates are assumed to be age-independent, compared to models where fishing mortality rates are assumed to be age-dependent. Results indicate an increase in fishing mortality after the relaxation of fishing regulations, and an increase in the natural mortality rate beginning in 1999, coinciding with observations of a bacterial disease in the fish. Estimates indicate that selectivity increases

with age as expected and that fish of age 6 years and greater appear to be fully recruited to the fishery. With the assumptions that the reporting rate is 0.43 from a previous reward tagging study, that fishing mortality is constant from 1991 to 1994, and from 1995 to 2003, and that fishing mortality rate for the new releases is different from the others, the estimate of the natural mortality rate for young fish is 0.39 (SE=0.02) from 1991 to 1998, 0.84 (SE=0.06) from 1999 to 2003, respectively, and for adults is 0.13 (SE=0.01) from 1991 to 1998, 0.65 (SE=0.03) from 1999 to 2003, respectively. Estimates of fishing mortality rate range from 0.27 to 0.39.

For a better understanding of the population dynamics of a fishery and for proper fisheries management, scientists have started to apply tag return models to estimate age-specific mortality rates. One challenge of this method is the correct specification of ages for tagged fish. The age-length key method commonly used for age specification may produce substantial errors in converting size to age, especially for the older fish. To reduce such errors, in Chapter 2 we propose two alternative sampling designs to the standard one of tagging all age classes: one where only age 1 fish (fish in the youngest year class that enter the fishery) are tagged, another where both age 1 and age 2 fish (fish in the two youngest year classes that enter the fishery) are tagged. Usually, the younger the fish, the less error there will be in converting size to age.

Model identifiability is assessed by calculating the smallest eigenvalue of the Fisher information matrix. If the smallest eigenvalue is zero, the Fisher information matrix is singular and the model is non-identifiable. For all of the models we consider, the smallest eigenvalues are nonzero, and the models are identifiable. However, in some cases, the smallest eigenvalue is close to zero, indicating that the information matrix is near singular

and that some estimators will perform poorly. Near-singularity and poor estimator performance are noted for models which involve estimation of the reporting rate. Estimator properties are better for the design with tagging the two youngest year-classes than the single year class design, due to the parameter redundancy problems noted by others (Freeman and Morgan, 1992). For models where the tag reporting rate is estimated, estimator properties improve as the tag reporting rate increases.

Simulation studies show similar results to those from analysis of the information matrix. Given the same total number of tagged fish each year, estimator bias and precision are worst for the design where all tagged fish are in age class 1, better when tagged fish are equally spread across age classes 1 and 2, and best when equal numbers are tagged in the 5 age classes.

The two sampling designs are illustrated and compared with a third design involving tagging of 5 age classes using tag return data on striped bass from a study carried out by Maryland Department of Natural Resources from 1991 to 2003. We treat fish of age 3 years as the youngest age class, and fish of age 4 years as the second youngest age class. Unlike the simulations, the total number of striped bass tagged was not the same for the three designs, but numbered 2178 for age class 3 only, 6338 for age classes 3 and 4, and 24356 for all 5 age classes (Table A.1). When both age 3 and age 4 fish are tagged, we obtain precise estimates with the assumption that the tag reporting rate is 0.43 based on information from a previous reward tagging study. The design where only age 3 fish are tagged produces estimates with poor precision whether the tag reporting rate is estimated or treated as known. This is partly because of the smaller number of fish tagged in age class 3 (compared to tagging both ages 3 and 4) and partly because of parameter redundancy issues. Improved precision resulting from

tagging fish in multiple age-classes must be balanced against the bias introduced by errors that occur in aging fish.

Catch-and-release fisheries have become very important to the management of overexploited recreational fish stocks. Tag return studies where the tag is removed regardless of fish disposition have been used to assess the effectiveness of restoration efforts for these catch-and-release fisheries. In Chapter 3, we extend the instantaneous rate formulation of tag return models introduced in Chapter 1 to catch-and-release tagging studies. The key point of our methods is that, given an estimate of the tag reporting rate, the fishing mortality rate is separated into two components: mortality on harvested fish, and mortality on tags of fish released alive (because the tag is removed). Adjusting for hooking mortality suffered by fish released alive, total fishing mortality can be computed. Natural mortality rates can also be estimated. Both age-independent models and age-dependent models are constructed. Methods are illustrated by application to the Maryland striped bass data. By fitting models with limited age- and year- dependence of the natural mortality rate M, our analyses demonstrate a decrease in natural mortality rates as fish age, and, in addition, provide evidence of an increase in natural mortality beginning in about 1999. Results also indicate that fishing mortality is age-dependent, with selectivity increasing with age and up to age 6 years when fish appear to be fully recruited to the fishery.

Age-Dependent Tag Return Models for Estimating Fishing

Mortality, Natural Mortality and Selectivity

by

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DEDICATION

TO MY PARENTS, MY WIFE, AND MY SONS

BIOGRAPHY

Honghua Jiang was born on May 4, 1969 in Yantai, P.R.China. He received his secondary education in 1987 at Qixia First High School, in Yantai, then directly enrolled at Ocean University of China, where he received a B.A. in Fishery management in July, 1991. He worked as an instructor at Fisheries School of Shandong Province after obtaining his B.A degree. He started his graduate study at North Carolina State University in 2001, where he received his Master in Biomathematics in August, 2003 and Ph.D. co-majored in Statistics and Biomathematics in August, 2005.

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Chapter 1

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

1.1 Introduction

The use of tag return methods to obtain separate estimates of fishing and natural mortality rates has received much recent attention in fisheries research (Pollock et al. 1991, Hoenig et al 1998a, 1998b, Hearn et al. 1998 and others). This work was built on the earlier work of Brownie et al. (1985) who focused on estimating only total survival and hence total mortality. Pollock et al. (1991) showed that one can determine both the instantaneous rates of fishing and natural mortality if the tag reporting rate is estimated either by conducting a reward tagging study or by a creel survey or by port sampling. The earlier estimates of total mortality of Brownie et al. (1985) did not require an independent estimate of the tag reporting rate.

Hoenig et al. (1998a) formulated a general theory for the instantaneous rates version of the tag return models. They also incorporated fishing effort into multi-year tag return studies to estimate natural mortality and fishing mortality if the tag reporting and initial retention-survival rates are known. The retention-survival rate was defined as the product of the initial survival caused by tagging and the short-term tag retention rate. They also showed how to estimate the fishing mortality rate, natural mortality rate, and the product of the tag reporting and retention-survival rates, if the reporting and retention-survival rates are not known. In many applications the retention-survival rate is assumed to be 1 so that only the tag reporting rate needs to be considered. In this case they found that although they could estimate the tag reporting rate with the multi-year tag return

data, the estimates were not stable. Therefore effectively one needs to have an external estimate of tag reporting rate.

One assumption of most multi-year tag return studies is that after release, the newly tagged animals are completely mixed with, and have the same survival rates as, previously tagged animals. Hoenig et al. (1998b) built models that allow for incomplete mixing of newly tagged animals leading to estimates of different fishing mortality and natural mortality rates for newly tagged and previously tagged animals. Tag reporting rates were assumed to be known or well estimated from another study.

Hearn et al. (1998) developed pre- and post-season tagging models that allow one to estimate reporting rates and fishing and natural mortality rates. Twice-a-year tagging for multiple years provides more information about the effects of exploitation so that reasonable estimates of tag reporting rates, and also estimates of fishing and natural mortality rates can be obtained. Pollock et al. (1991), and more recently Pollock et al. (2001, 2002) and Hearn et al. (2003), have made a systematic study of methods of estimating the tag reporting rate that are external to the tag return data (high reward tagging, planted tags, observers etc).

All of the previous modeling efforts have assumed that fishing mortality does not vary by age. This is clearly not ideal for fisheries applications where biologists often tag fish of a wide age range with possibly quite different fishing mortality rates. Here we generalize the Hoenig et al. (1998a, b) models to multiple age classes with potentially different fishing mortality rates and also perhaps different natural mortality rates. In the next section we develop the theoretical foundations for our age-dependent models where multiple ages of fish are tagged each year. Hierarchical models with different parameter

structures are presented in Section 1.3 and parameter redundancy issues are addressed. This is followed by a simulation study to evaluate estimators under certain models. In Section 1.5 we consider an example based on a striped bass (*Morone saxatilis*) tagging study from Maryland. We conclude with a discussion and some suggestions for future research.

1.2 Model Structures

1.2.1 Continuous Fishery

We present a likelihood for data from 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 ($k=1,2,...,K$) and released in year i ($i=1,2,...I$). Let R_{ijk} be the number of fish tagged at age k and released in year i, then harvested and reported in year j, for j = *i, i+1, i+2, ..., J*. We assume that the instantaneous fishing mortality rate for fish of age k in year j is

$$F_{jk} = Sel_k \, F_j \, ,$$

where F_j is the instantaneous fishing mortality rate in year j for fully recruited fish, and Sel_k is the selectivity coefficient for age k fish. Selectivity is assumed to be constant over years for each age, and is assumed to be 1 for fish of age K_c and greater ($Sel_k \equiv 1 \; for \; k \geq k_c$).

Also let

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

S_{ijk} be the conditional survival rate in year j for the fish tagged at age k in year i, and

alive at the beginning of year j,

M be the instantaneous natural mortality rate,

λ be 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. It is possible to relax this assumption to construct more general models, and the performance of such models with M and λ age- and/or year- dependent are investigated in sections 1.3 and 1.5.

For a fishery continuous over the whole year, the expected number of fish tagged at age k and released in year i, then harvested and returned in year j, is:

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

where

$$P_{ijk} = \begin{cases} \left(\displaystyle\prod_{v=i}^{j-1} S_{ivk} \right)(1 - S_{ijk}) \dfrac{F_j\, Sel_{k+j-i}}{F_j\, Sel_{k+j-i} + M}\lambda & (when\ j > i) \\[2em] (1 - S_{ijk}) \dfrac{F_j\, Sel_k}{F_j\, Sel_k + M}\lambda & (when\ j = i), \end{cases}$$

$$S_{ijk} = \exp(-F_j\, Sel_{k+j-i} - M).$$

Under the assumption that fish suffer independent fates, the number of fish tagged at age k and released in year i, then harvested and returned in year j follows the multinomial distribution. Therefore the full likelihood function is product multinomial following Hoenig et al. (1998a):

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

We can obtain maximum likelihood estimators (MLEs) to estimate F_j (j=1,2,...,J) , M , and Sel_k, if λ is known, or to estimate F_j (j=1,2,...,J), M , Sel_k and λ, when λ is unknown. In many cases we constrain λ to some known value and only estimate the remaining parameters.

When independent external information about the reporting rate λ is available, we can incorporate this information into the tag return model and obtain a joint likelihood function. For instance, suppose we have information from a planted tag study with m tags planted in the catch from which v tags are reported. Then the likelihood function for the planted tag study is binomial:

$$L_2 = \binom{m}{v} \lambda^v (1 - \lambda)^{m-v} . \quad (2)$$

The joint likelihood for the planted tag data and tag return data is simply the product of the two likelihood functions:

$$L = L_1 \times L_2 .$$

Including external information about λ via the joint likelihood function will result in increased precision of MLEs, compared to estimation when there is no additional information about λ based on results in section 1.4. Including information from a high reward tagging study combined with regular tagging would follow the same principle.

There would be one likelihood for the high reward tag returns and one for the regular tag returns.

1.2.2 Limited Fishery:

In defining mortality and survival rates above, we assume that fishing takes place throughout the year. But in many cases, for a particular fishery, the commercial fishing season is limited to part of the year only. If this is the case, we need to modify the definitions of F_j, S_{ijk} and P_{ijk}, as indicated below, though the model structure is otherwise unchanged. We assume that tagging and release occur at the beginning of the year and that harvest occurs immediately after release of the tagged fish but for only part of the year. Let T ($0 \leq T \leq 1$) be the proportion of year represented by the fishing season. Let F_j^{Δ} be the instantaneous fishing mortality rate during the fishing season for year j. The conditional exploitation rate for age k fish in year j given that they are alive at the beginning of year j is:

$$U_j = \left(1 - e^{-T F_j^{\Delta} Sel_k - T M}\right) \frac{T F_j^{\Delta} Sel_k}{T F_j^{\Delta} Sel_k + T M},$$

and the conditional survival rate is

$$S_j = e^{-T F_j^{\Delta} Sel_k - M}.$$

Now if we let $F_j = T F_j^{\Delta}$, with other parameters as defined previously, we have

$$P_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk} \right)[1 - \exp(-F_j\, Sel_{k+j-i} - T\, M)] \dfrac{F_j\, Sel_{k+j-i}}{F_j\, Sel_{k+j-i} + T\, M}\, \lambda & (when\ j > i) \\ \\ [1 - \exp(-F_j\, Sel_{k+j-i} - T\, M)]\, \dfrac{F_j\, Sel_k}{F_j\, Sel_k + T\ M}\, \lambda & (when\ j = i), \end{cases}$$

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

Note that if $T = 1$, then $T\, F_j^{\Delta} = F_j$, corresponding to a continuous fishery. If $T\, F_j^{\Delta} \to F_j$

as $T \to 0$, we get a pulse fishery (Ricker 1975), and P_{ijk} simplifies to:

$$P_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk} \right)[1 - \exp(-F_j\, Sel_{k+j-i})]\lambda & (when\ j > i) \\ \\ [1 - \exp(-F_j\, Sel_{k+j-i})]\ \lambda & (when\ j = i), \end{cases}$$

$$S_{ijk} = \exp(-F_j\, Sel_{k+j-i} - M).$$

The form of the likelihood function for the limited fishing and pulse fishery models is

exactly the same as the likelihood function (L_1) for the continuous fishery models. The

likelihood function is used to obtain MLEs.

1.2.3 Incomplete Mixing of Newly Tagged Fish:

We also extend the incomplete mixing model of Hoenig et al. (1998b) to the case of

age-dependence. We assume that tagging and release occur at the beginning of the year

and harvest occurs continuously during the year. We let $F_j\, {}^*$ be the fishing mortality for

the newly tagged animals that are fully recruited in year j, and let F_j be the fishing

mortality rate for previously released animals that are fully recruited in year j. The

definitions of other parameters are unchanged. In the general case, if we tag multiple age

fish each year, the expected number of the N_{ik} fish tagged at age k and released in year i,

that are harvested and reported in year j is:

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

where

$$P_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk} \right) (1-S_{ijk}) \dfrac{F_j \, Sel_{k+j-i}}{F_j \, Sel_{k+j-i} + M} \lambda & (when \; j > i) \\[4mm] (1-S_{ijk}) \dfrac{F_j * Sel_k}{F_j * Sel_k + M} \lambda & (when \; j = i), \end{cases}$$

$$S_{ijk} = \begin{cases} \exp(-F_j \, Sel_{k+j-i} - M) & (when \; j > i) \\[4mm] \exp(-F_j * Sel_k - M) & (when \; j = i). \end{cases}$$

 The likelihood function under incomplete mixing is the same as the likelihood function

(L_1) but with P_{ijk} and S_{ijk} as defined above.

Assumptions:

The following assumptions are needed for the likelihood L_1:

(1) There is no tag loss, and tag numbers are correctly reported.

(2) Tagging induced mortality is negligible.

(3) There is no emigration.

(4) All animals behave independently with respect to their mortality process.

(5) Fishing and natural mortality forces are additive, and instantaneous rates are constant within a year (except for the case of a limited fishery where F is constant during the fishery but 0 the rest of the year).

(6) Selectivity for each age is the same for different years and selectivity is one above a certain age class.

(7) Ages of individuals are correctly identified.

(8) There is no heterogeneity in mortality between fish within a group. That is we assume that all fish within the same group (age and year) have the same fishing and natural mortality rates.

1.3 Parameter Identification

The basic model described in Section 1.2 allows instantaneous fishing mortality rates to be year-specific and to depend on age through selectivity, while natural mortality rate, M, is assumed constant. Models which permit age- and year- dependence of M are of considerable biological interest, but raise questions about over parameterization. Whether a statistical model is parameter redundant or not is an important issue in the modeling of recapture data. The model is parameter redundant if it can be rewritten in terms of a smaller set of parameters. Catchpole and Morgan (1997) showed that parameter redundancy is equivalent to singularity of the information matrix for a general class of nonlinear models. Sometimes we may be interested in which and how many parameters can be estimated if the model is parameter redundant (Catchpole et al 1998). Models for mark-recapture and tag return data are usually of product multinomial form. The expected information matrix for a multinomial distribution (N, π_1, π_2, …, π_t), where

π_1, π_2, …, π_t are probabilities that depend on some parameter vector $\theta = (\theta_1, \theta_2, …, \theta_q)^T$, is given by Catchpole and Morgan (1997) as

$$I = D\Pi^{-1}D',$$

where Π is a diagonal matrix whose jth diagonal element is $\mu_j = N\pi_j$ and the (i, j)th element

of D is $d_{ij} = \dfrac{\partial u_j}{\partial \theta_i}$. They also show that rank $I(\theta)$ = rank $D(\theta)$. This general form of I can

be extended to the product-multinomial case in which the mean vector μ contains the mean values for all of the multinomials.

The symbolic algebra package MAPLE (Waterloo Maple Inc., Maple 9) can be used to calculate the derivative matrix D. For some models, especially if the number of parameters is large, it is difficult to determine the rank of D symbolically, and we determine the rank of the derivative matrix D (hence singularity of I) numerically. Figure 1.1 shows whether the information matrices are singular or not for a set of hierarchical models, based on a study with 3 years of tagging, 3 years of recoveries, and 3 age classes. The models are represented by a list of parameters in parentheses. Subscript y indicates that the parameter is year specific, subscript a indicates that the parameter is age specific, and no subscript means that the parameter is constant over ages and years. For example, in the general model (F_y, M_{y+a}, Sel_a, λ_{y+a}), the notation M_{y+a} indicates that natural mortality M is both year specific and age specific. The '+' in the subscript indicates an additive model, with the property that there is a constant relationship between the age-specific M_k no matter which year it is. For instance, we assume $M_2 = bM_1$ and $M_3 = cM_1$, where b and c are constants. Additive models are considered, because they provide a parsimonious way to include both age- and year- dependence.

The general model with F and M both year- and age- specific is identifiable and if λ known. If λ is unknown, and assumed year- and age- specific, the general model is singular (Figure 1.1). All submodels are identifiable if λ is known, and so we show results for two sets of submodels for the case where λ is unknown. We let M and/or λ be year specific but not age specific in one set (left side of Figure 1.1), and M and/or λ be age specific but not year specific in the other set (right side of Figure 1.1). All submodels where M and/or λ are year specific but not age specific are nonsingular. The models *(F, M_a, Sel_a, λ)* and *(F, M, Sel_a, λ_a)*, where M or λ is age specific but not year specific, are singular. Figure 1.1 displays the same phenomenon demonstrated by Catchpole et al. (2001) and Nasution et al. (2004) in that sometimes the more general model is nonsingular but the reduced model is singular. Models *(F_y, M_a, Sel_a, λ)*, *(F_y, M, Sel_a, λ_a)* and (F_y, M_a, Sel_a, λ_a) are nonsingular, but the constant F reduced models *(F, M_a, Sel_a, λ)* and *(F, M, Sel_a, λ_a)* are singular. We call *(F_y, M_a, Sel_a, λ)*, *(F_y, M , Sel_a, λ_a)* and (F_y, M_a, Sel_a, λ_a) near-singular models in this case. Some estimators are expected to have poor precision in near-singular models. The parameters that are poorly estimated in near-singular models can be determined from the coefficients in the eigenvector corresponding to the smallest eigenvalue of $I(\theta)$ (Catchpole et al. 2001, Nasution et al. 2004). We use this approach for some of the models studied in Chapter 2.

Figure 1.1. Singularity determination for a set of hierarchical models for multiple age tag return data. (ns) means nonsingular and (s) means singular.

F, M and λ year and age specific

$(F_y, M_{y+a}, Sel_a, \lambda_{y+a})$
(s)

M and λ year specific

M and λ age specific

$(F_y, M_y, Sel_a, \lambda_y)$
(ns)

$(F_y, M_a, Sel_a, \lambda_a)$
(ns)

$(F_y, M_y, Sel_a, \lambda)$
(ns)

$(F_y, M, Sel_a, \lambda_y)$
(ns)

$(F_y, M_a, Sel_a, \lambda)$
(ns)

$(F_y, M, Sel_a, \lambda_a)$
(ns)

(F, M_y, Sel_a, λ)
(ns)

(F, M, Sel_a, λ_y)
(ns)

(F_y, M, Sel_a, λ)
(ns)

(F, M_a, Sel_a, λ)
(s)

(F, M, Sel_a, λ_a)
(s)

(F, M, Sel_a, λ)
(ns)
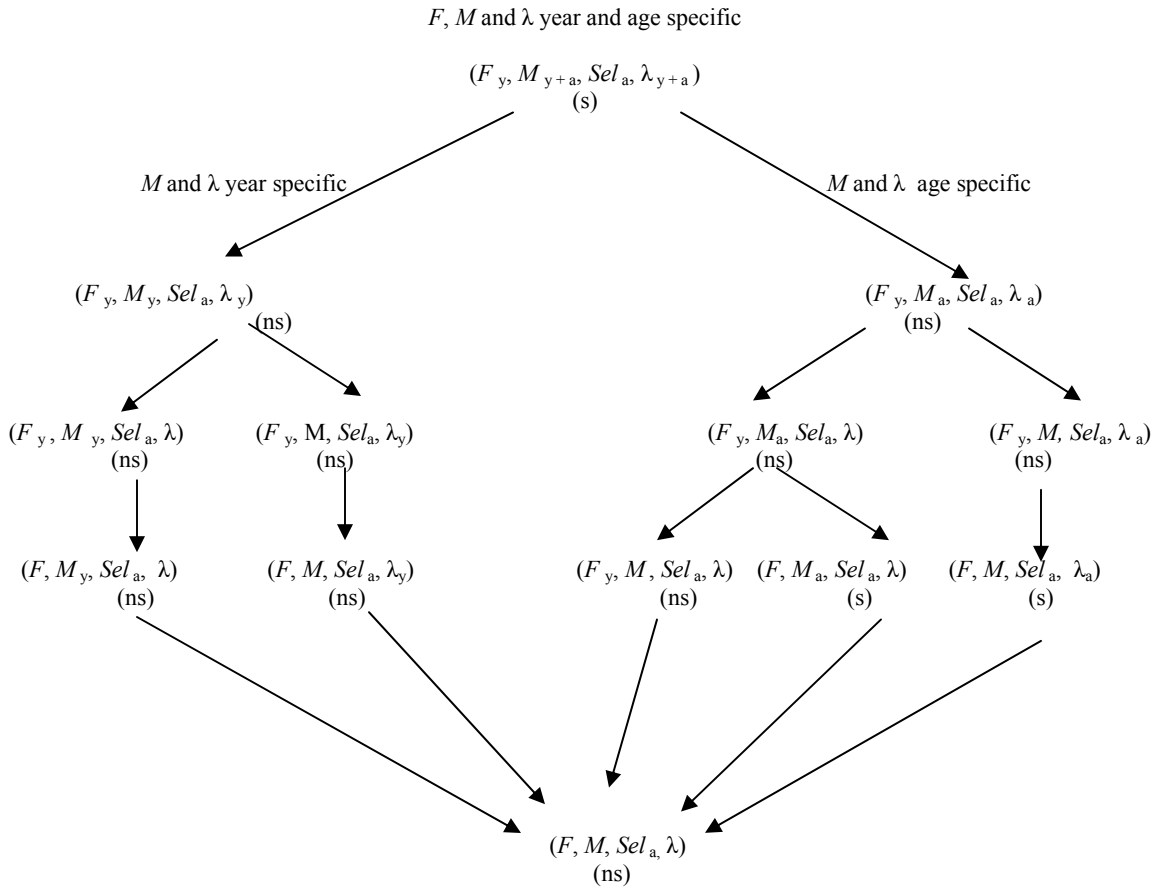
1.4 Simulations

In the previous section we determined that although many models with year- or age- specific natural mortality rates are identifiable, there is evidence of near-singularity for models with λ unknown. Estimators obtained under such models may not have good properties in terms of bias and precision. We therefore carried out a simulation study to investigate the properties of some basic models that are of biological interest. We investigate the models (F_y, M, $Sel_{a1,a2,a3}$, λ) and (F_y, M, $Sel_{a1,a2,a3}$) where we assume that fishing mortality rate, F, is year- specific (because F usually changes over years) and

age- specific through selectivity, and natural mortality rate, M, is constant (fishery biologists often make this assumption), with the reporting rate, λ, estimated or known, respectively.

1.4.1 Methods

We used the new version of the SURVIV program (White 1983) modified by James Hines of Patuxent Wildlife Research Center to conduct simulations. The maximum likelihood method is used in SURVIV to estimate unknown parameters for complex product multinomial likelihoods like those presented in Section 1.2. We assume that 500 or 1000 fish are tagged for each age class in each year in a multiple age tag return study. Fish are tagged at the beginning of 5 consecutive years with 5 or 7 consecutive years of recoveries. We assume there are 4 different age classes: 1, 2, 3, and 4+ years. We generate 500 replicate data sets for each case. We currently consider just one set of conditions where $F_1=0.2$, $F_2=0.5$, $F_3=0.3$, $F_4=0.4$, $F_5=0.6$, $F_6=0.3$, $F_7=0.4$, $M=0.2$, $\lambda=0.3$ and $Sel = 0.6, 0.7, 0.9,$ and 1.0, respectively, for ages 1, 2, 3, and 4+. Here we assume that fish are fully recruited at age 4 and greater. We use the same parameter values mentioned above for both continuous and pulse fishery models. (Note that the definition of F_i in the pulse fishery is different from that for a continuous fishery, and annual fishing mortality is 0.39 for the pulse fishery, and 0.24 for the continuous fishery, given $F=0.3$ and $M=0.2$.) For incomplete mixing models, we let the true parameter values be $F_1{}^*=0.2$, $F_2{}^*=0.6$, $F_3{}^*=0.4$, $F_4{}^*=0.5$, $F_5{}^*=0.7$, while other parameter values are the same as for the continuous and pulse fishery models. Keeping all other parameter values the same, we investigate the properties of model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ and model $(F_y, M, Sel_{a1,a2,a3})$ when the value of $\lambda = 0.1, 0.2, 0.4, 0.5, 0.6, 0.7, 0.8$ and 0.9. We also consider

the effect of adding 50 planted tags to provide an external estimate of the reporting rate (Table 1.2). In all cases, the model used to obtain estimates is the same as the one used to generate the data. In other words, there is no model misspecification.

1.4.2 Results

For continuous fisheries, the average estimates with standard errors in parentheses are included in Table 1.1 for the case where 500 or 1000 fish of each age class are tagged. Standard errors are the standard deviation among estimates from 500 Monte Carlo samples. When 500 fish are tagged, estimators under model $(F_y, M, Sel_{a1,a2,a3})$ have good properties with relative bias less than 2% and relative standard error less than 11%. For model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$, most estimators are unbiased, but the reporting rate estimator has some bias (relative bias = 9.6% for 5 years of recoveries, relative bias = 5.7% for 7 years of recoveries). The precision of the parameter estimators is poor. For example, the relative standard error of $\hat{\lambda}$ is 42% for 5 years of recoveries, and 30% for 7 years of recoveries. The relative bias (RB) and relative standard error (RSE) of the reporting rate estimator, $\hat{\lambda}$ are calculated using the following formulas:

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

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

where $\bar{\hat{\lambda}}$ is the average estimate of the parameter λ, and SE is the standard error of $\hat{\lambda}$ from the 500 Monte Carlo samples. RSE for $\hat{M}$ is similar to RSE for $\hat{\lambda}$, though bias is smaller.

When 1000 fish are tagged, the precision of estimates for both models is much improved compared to that when 500 fish are tagged (relative standard errors of $\hat{\lambda}$ and $\hat{M}$ are 17% and 26%, respectively, compared to 30% and 38%, respectively, for 7 years of recoveries). The bias of the reporting rate estimate is reduced by including two additional years of recoveries (relative bias = 5.3% for 5 years of recoveries, relative bias = 3.3% for 7 years of recoveries). With the two additional years of recovery information, the 7 year tag return study results in better performance of estimators under model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ compared to a study with 5 years of recovery data. The practical implication is that collecting recovery information for several years after tagging has ceased will lead to less biased and more precise parameter estimates. Another finding is that the selectivity estimates are essentially unbiased and precise regardless of whether the reporting rate is known or estimated.

Table 1.1. Average estimates with standard errors in parentheses from fitting models (a) $(F_y, M, Sel_{a1,a2,a3})$ and (b) $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ to simulated data for a continuous complete mixing fishery, and a pulse fishery, assuming a tagging study with 5 years of tagging and either 5 or 7 years of recoveries. In each replicate, N=500 fish, or N=1000 fish are tagged for each of 5 age classes in each of 5 consecutive years. Results are based on 500 replications. True parameter values are 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, M=0.2, λ=0.3, Sel_1=0.6, Sel_2=0.7 and Sel_3=0.9.

	5 Years of recoveries		7 Years of recoveries	
Parameter	(a) λ known	(b) λ estimated	(a) λ known	(b) λ estimated

Continuous complete mixing fishery with N=500

Parameter	(a) λ known	(b) λ estimated	(a) λ known	(b) λ estimated
$F(1)$	0.198 (0.021)	0.197 (0.054)	0.197 (0.021)	0.197 (0.044)
$F(2)$	0.499 (0.033)	0.499 (0.136)	0.499 (0.032)	0.499 (0.109)
$F(3)$	0.298 (0.022)	0.298 (0.084)	0.298 (0.021)	0.298 (0.066)
$F(4)$	0.397 (0.026)	0.398 (0.111)	0.397 (0.024)	0.397 (0.087)
$F(5)$	0.598 (0.044)	0.608 (0.189)	0.598 (0.038)	0.604 (0.148)
$F(6)$			0.299 (0.033)	0.306 (0.091)
$F(7)$			0.404 (0.062)	0.422 (0.149)
M	0.200 (0.017)	0.200 (0.088)	0.200 (0.014)	0.200 (0.075)
λ	0.300	0.329 (0.125)	0.300	0.317 (0.091)
sel_1	0.607 (0.063)	0.607 (0.063)	0.607 (0.061)	0.607 (0.062)
sel_2	0.704 (0.058)	0.704 (0.059)	0.704 (0.053)	0.704 (0.053)
sel_3	0.901 (0.061)	0.901 (0.062)	0.902 (0.055)	0.902 (0.056)

Continuous complete mixing fishery with N=1000

Parameter	(a) λ known	(b) λ estimated	(a) λ known	(b) λ estimated
$F(1)$	0.199 (0.015)	0.196 (0.040)	0.199 (0.015)	0.197 (0.033)
$F(2)$	0.497 (0.024)	0.490 (0.097)	0.497 (0.023)	0.492 (0.076)
$F(3)$	0.299 (0.015)	0.295 (0.058)	0.299 (0.014)	0.296 (0.046)
$F(4)$	0.397 (0.018)	0.392 (0.077)	0.397 (0.017)	0.394 (0.060)
$F(5)$	0.596 (0.032)	0.592 (0.134)	0.596 (0.028)	0.592 (0.102)
$F(6)$			0.299 (0.026)	0.298 (0.060)
$F(7)$			0.401 (0.047)	0.403 (0.098)
M	0.200 (0.013)	0.205 (0.061)	0.200 (0.011)	0.203 (0.051)
λ	0.300	0.316 (0.068)	0.300	0.310 (0.051)
sel_1	0.607 (0.044)	0.607 (0.044)	0.607 (0.042)	0.607 (0.042)
sel_2	0.704 (0.038)	0.705 (0.039)	0.704 (0.035)	0.705 (0.035)
sel_3	0.904 (0.046)	0.904 (0.046)	0.904 (0.041)	0.904 (0.041)

Pulse fishery with N=500

Parameter	(a) λ known	(b) λ estimated	(a) λ known	(b) λ estimated
$F(1)$	0.197 (0.020)	0.196 (0.051)	0.197 (0.020)	0.198 (0.041)
$F(2)$	0.500 (0.031)	0.498 (0.128)	0.500 (0.030)	0.502 (0.101)
$F(3)$	0.297 (0.020)	0.296 (0.078)	0.297 (0.019)	0.298 (0.061)
$F(4)$	0.397 (0.025)	0.397 (0.105)	0.398 (0.022)	0.399 (0.081)
$F(5)$	0.598 (0.039)	0.605 (0.179)	0.599 (0.035)	0.606 (0.137)
$F(6)$			0.300 (0.030)	0.307 (0.084)
$F(7)$			0.402 (0.055)	0.419 (0.137)
M	0.200 (0.019)	0.201 (0.083)	0.200 (0.016)	0.199 (0.069)
λ	0.300	0.322 (0.097)	0.300	0.310 (0.062)
sel_1	0.606 (0.060)	0.607 (0.060)	0.605 (0.057)	0.606 (0.058)
sel_2	0.703 (0.056)	0.703 (0.058)	0.703 (0.052)	0.703 (0.052)
sel_3	0.902 (0.058)	0.902 (0.059)	0.902 (0.052)	0.902 (0.053)

Some results of parameter estimates and standard errors from fitting pulse fishery models $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ and $(F_y, M, Sel_{a1,a2,a3})$ are also presented in Table 1.1 for the situation where a pulse fishery occurs at the start of each year. With the same values for all parameters, the number of tag returns in a pulse fishery is greater than in a continuous fishery, because exploitation is concentrated in a short period immediately following release before any natural mortality occurs. As a result, the precision of fishing mortality and selectivity estimates is better under the pulse fishery models compared to the continuous fishery, and reporting rate estimates from model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ are also somewhat improved in terms of bias and precision (relative bias = 7.3% compared to 9.6% in continuous fishery, RSE= 32% compared to 42% in continuous fishery with 5 years of recoveries; relative bias = 3.3% compared to 5.7% in continuous fishery, RSE=21% compared to 30% in continuous fishery with 7 years of recoveries). However, there is little change in relative standard errors of the estimator, $\hat{M}$, in the pulse fishery compared to those in the continuous fishery.

Table 1.2 provides results on the effect of augmenting the hypothetical tag return study with a planted tag study with 50 tags planted in the catch to provide an independent estimate of the reporting rate. With the additional information about the reporting rate from a planted tag study, all parameter estimates are unbiased. Relative bias of the reporting rate estimate is less than 2% for all cases. Though the precision of some estimators is still poor, it is improved much compared to models without a planted tag study. For instance, the relative standard errors of $\hat{\lambda}$ and $\hat{M}$ are 17% and 29% (compared to 42% and 44%, respectively, if there are no planted tags) with 5 years of recoveries when 500 fish are tagged in each age-class each year, and are 14% and 24%

(compared to 23% and 31%, respectively, if there are no planted tags) with 5 years of recoveries when 1000 fish are tagged in each cohort. This indicates that external information about the reporting rate results in substantial improvement in the performance of model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$.

Table 1.2. Average estimates with standard errors in parentheses from fitting model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ to simulated data for a continuous complete mixing fishery. In each replicate, N=500 fish or N=1000 fish are tagged for each of 5 age classes in each of 5 consecutive years, and there are either 5 or 7 years of recoveries. In addition we assume recoveries are augmented with data from a planted tag study with 50 tags planted in the catch.

	N=500		N=1000	
Parameter	5 Years	7 Years	5 Years	7 Years
F(1)	0.201 (0.041)	0.198 (0.036)	0.200 (0.030)	0.199 (0.027)
F(2)	0.502 (0.091)	0.495 (0.076)	0.502 (0.072)	0.499 (0.063)
F(3)	0.303 (0.059)	0.299 (0.048)	0.301 (0.045)	0.299 (0.039)
F(4)	0.402 (0.076)	0.396 (0.061)	0.402 (0.059)	0.400 (0.051)
F(5)	0.609 (0.135)	0.596 (0.109)	0.607 (0.103)	0.602 (0.086)
F(6)		0.301 (0.069)		0.304 (0.053)
F(7)		0.412 (0.123)		0.410 (0.087)
M	0.195 (0.057)	0.200 (0.051)	0.198 (0.047)	0.199 (0.042)
λ	0.305 (0.052)	0.307 (0.046)	0.303 (0.043)	0.303 (0.038)
sel_1	0.608 (0.066)	0.610 (0.061)	0.605 (0.043)	0.605 (0.041)
sel_2	0.707 (0.058)	0.708 (0.054)	0.704 (0.040)	0.704 (0.037)
sel_3	0.907 (0.061)	0.907 (0.056)	0.907 (0.042)	0.906 (0.038)

Note: Results are based on 500 replications. True parameter values are 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, M=0.2, λ=0.3, Sel_1=0.6, Sel_2=0.7 and Sel_3=0.9.

We have many more parameters to estimate in incomplete mixing models than in continuous and pulse fishery mixed models. However, the simulation results (Table 1.3)

demonstrate that parameter estimates from fitting incomplete mixing models $(F_y, F^*_y, M,$

$Sel_{a1,a2,a3})$ are essentially unbiased and reasonably precise; relative biases for all estimates

are less than 2%, and relative standard errors for most estimates are less than 10%.

However, comparing results for the incomplete and complete mixing cases (Tables 1.1

and 1.3) we see that standard errors for $\hat{F}_i$, $i = 2,...,5$, are considerably larger in the

former case because of the larger number of parameters that are estimated. Model $(F_y,$

$F^*_y, M, Sel_{a1,a2,a3}, \lambda)$ produces essentially unbiased estimates (relative bias less than 5%

for most estimates), but with poor precision, indicating this model is near-singular. For

simulation studies where we allow $F^*_y < F_y$ the precision will be much worse than for

complete mixing models (Hoenig et al. 1998b).

Table 1.3. Average estimates with standard errors in parentheses from fitting incomplete mixing models (a) (F_y, F^*_y, M, $Sel_{a1,a2,a3}$) and (b) (F_y, F^*_y, M, $Sel_{a1,a2,a3}$, λ) using simulations where we assume that 500 fish are tagged for each of 5 age classes in each of 5 consecutive years, and there are either 5 or 7 years of recoveries. Results are based on 500 replications. True parameter values are F_2=0.5, F_3=0.3, F_4=0.4, F_5=0.6, F_6=0.3, F_7=0.4, F_1^*=0.2, F_2^*=0.6, F_3^*=0.4, F_4^*=0.5, F_5^*=0.7, M=0.2, λ=0.3, Sel_1=0.6, Sel_2=0.7 and Sel_3=0.9.

	5 Years of recoveries		7 Years of recoveries	
Parameter	(a) λ known	(b) λ estimated	(a) λ known	(b) λ estimated
F*(1)	0.198 (0.021)	0.194 (0.046)	0.197 (0.021)	0.196 (0.038)
F*(2)	0.596 (0.046)	0.590 (0.146)	0.596 (0.044)	0.593 (0.117)
F*(3)	0.397 (0.036)	0.393 (0.098)	0.397 (0.034)	0.395 (0.078)
F*(4)	0.496 (0.042)	0.492 (0.126)	0.496 (0.039)	0.495 (0.101)
F*(5)	0.698 (0.054)	0.695 (0.187)	0.697 (0.052)	0.698 (0.152)
F(2)	0.500 (0.050)	0.492 (0.116)	0.500 (0.046)	0.496 (0.095)
F(3)	0.297 (0.031)	0.294 (0.075)	0.297 (0.028)	0.295 (0.060)
F(4)	0.398 (0.042)	0.394 (0.104)	0.397 (0.032)	0.395 (0.078)
F(5)	0.600 (0.084)	0.605 (0.191)	0.597 (0.055)	0.599 (0.139)
F(6)			0.300 (0.037)	0.305 (0.085)
F(7)			0.403 (0.068)	0.417 (0.140)
M	0.199 (0.024)	0.203 (0.073)	0.200 (0.016)	0.201 (0.064)
λ	0.300	0.327 (0.114)	0.300	0.314 (0.072)
sel$_1$	0.606 (0.060)	0.607 (0.061)	0.606 (0.058)	0.607 (0.058)
sel$_2$	0.704 (0.058)	0.705 (0.059)	0.705 (0.053)	0.706 (0.053)
sel$_3$	0.901 (0.060)	0.901 (0.060)	0.902 (0.055)	0.902 (0.055)

It is of interest to examine how the performance of model *(F_y, M, $Sel_{1,2,3}$, λ)* depends on the value of the reporting rate λ. As an illustration, we consider the continuous fishery data with 5 years of tagging and either 5 or 7 years of recoveries. Figure 1.2 illustrates how the relative bias (RB) and relative standard error (RSE) of the reporting rate estimate ($\hat{\lambda}$) change as the true value of λ changes. We can see both RB and RSE of $\hat{\lambda}$ drop dramatically as λ increases to about 0.25. Model *(F_y, M, $Sel_{a1,a2,a3}$, λ)*

performs quite well when λ is 0.5 (RB=5.2%, RSE=22%) and greater in 5 years of recoveries data. With 7 years of recovery data, results for model *(F$_y$, M, Sel$_{a1,a2,a3}$, λ)* are acceptable when λ is 0.4 (RB=5.3%, RSE=25%) and greater. Similar trends are noted for estimation of *M*.

Figure 1.2. Relative bias (RB) and Relative standard error (RSE) of the estimator $\hat{\lambda}$ from fitting the complete mixing model (F$_y$, M, Sel$_{a1,a2,a3}$, λ) using simulations where we assume that 500 fish are tagged for each of 5 age classes in each of 5 consecutive years, followed by either 5 or 7 years of recoveries. Results are based on 500 replications. True parameter values are F1=0.2, F2=0.5, F3=0.3, F4=0.4, F5=0.6, F6=0.3, F7=0.4, M=0.2, Sel1=0.6, Sel2=0.7 and Sel3=0.9.
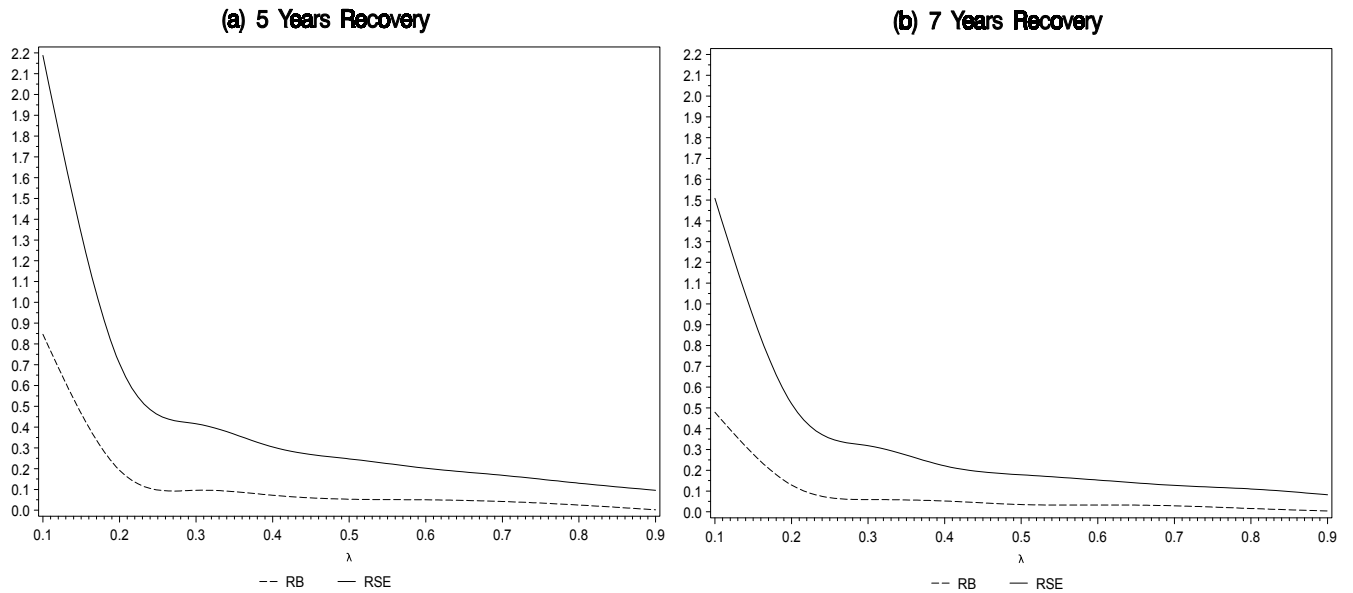
1.5 Example

1.5.1 Study Description

Seven age classes (from age 2 to age 8+ years) of striped bass were tagged and released by Maryland Department of Natural Resources (MDNR) from 1991 to 2002 in the upper Chesapeake Bay to estimate the survival rates. Internal anchor tags were used and the length of each fish was measured. Age groups were classified with the age-length key method (Secor et al. 1995). We obtained this data from Brian Wells. We only analyze the data for fish tagged at age 3 and greater because of the small sample sizes for fish tagged at age 2. We group all ages above age 8 because of small sample sizes. Some recovered fish were harvested and some were released. The numbers of releases and tag returns for the striped bass are listed in Appendix A. Purely for illustration of our methodology, we assume that all recovered fish died which will result in overestimation of fishing mortality. We will present methods to account for live releases in Chapter 3.

Fishery biologists believe that striped bass of age 6 and greater are fully recruited. Thus we assume selectivity for striped bass of age 6 and greater is 1. We let Sel_3, Sel_4 and Sel_5 represent the selectivities for striped bass of age 3, 4 and 5, respectively. We first consider the basic model $(F_y, M, Sel_3, Sel_4, Sel_5)$ with fishing mortality rate, F_{jk}, age-dependent through selectivity, and natural mortality rate, M, constant. We also assume that the newly released fish are able to completely mix with previously released fish in the first year, and that the tag reporting rate, λ, is known and equal to 0.43 (based on a previous reward tagging study, Brian Wells personal communication; Smith et al. 2000). We also fit corresponding model $(F_y, M, Sel_3, Sel_4, Sel_5, \lambda)$ with λ estimated. Due to concerns that newly released fish do not have enough time to mix with others in the first

year, we investigate incomplete mixing models $(F_y, F^*_y, M, Sel_3, Sel_4, Sel_5)$ and $(F_y, F^*_y, M, Sel_3, Sel_4, Sel_5, \lambda)$, allowing the newly released fish to have different fishing mortality rates from those of others. Based on near-singularity of models with M age-dependent (Figure 1.1), the models above make the strong assumption that the natural mortality rate, M, is constant across ages. To investigate this assumption, we consider models with a limited age-dependence of M, models $(F_y, M_{3-5}, M_{6+}, Sel_3, Sel_4, Sel_5)$ and $(F_y, M_{3-5}, M_{6+}, Sel_3, Sel_4, Sel_5, \lambda)$ assuming a complete mixing fishery, and $(F_y, F^*_y, M_{3-5}, M_{6+}, Sel_3, Sel_4, Sel_5)$ and $(F_y, F^*_y, M_{3-5}, M_{6+}, Sel_3, Sel_4, Sel_5, \lambda)$ for the case of incomplete mixing. In these models, natural mortality for young fish (age 3, 4 and 5 years) is allowed to be different from the rate for adults (age 6 years and greater).

Some time in the late 1990s, a bacterial disease known as mycobacteriosis appeared in Chesapeake Bay striped bass (John Hoenig, personal communication). It is characterized by external lesions (open sores on the skin) and internal lesions that look like lumps in the pancreas and kidney. It is caused by bacteria in the genus Mycobacterium. There are about a dozen species of Mycobacteria in the striped bass and it is not known which one or ones are causing the disease or diseases. In late summer, the prevalence of mycobacteriosis in striped bass may be 60% or even higher in the Rappahannock River. To allow for an effect of disease on natural mortality while minimizing parameter redundancy problems, we fit two-period M models where we assume that M is different in years before and after disease effects began to be observed. In addition, we also consider models which incorporate both the limited age- and year-dependence described for M. We also consider reduced models with constant fishing mortality rate before and after the year 1995 to investigate the effects of a relaxation of

harvest regulations which began in 1995 (Richards and Rago, 1999). For models with the assumption that the tag reporting rate is known, we assume $\lambda = 0.43$ (Wells, B.K personal communication; Smith et al. 2000).

We use Akaike's information criterion (AIC) to choose between models because this method can compare multiple nested and nonnested models. AIC is a statistic that deals with the tradeoff between reduced bias for a model with more parameters and smaller estimator variance for a model with fewer parameters (Burnham and Anderson 2002). AIC is computed as:

$$AIC = -2\log\left[l(\hat{\underline{\theta}}|y)\right] + 2k,$$

where $\log\left[l(\hat{\underline{\theta}}|y)\right]$ is the log likelihood function evaluated at the MLEs $\hat{\underline{\theta}}$ given the data y, and k is the number of parameters. The model with the minimum AIC value is best.

A correction to AIC, to account for small sample size, yields $AICc$, that is,

$$AICc = AIC + \frac{2k(k+1)}{n-k-1},$$

where n is the sample size (total number of animals tagged).

Overdispersion in the data can result due to a lack of independence of capture and survival events, as fish travel in schools. If overdispersion is the reason for lack of fit in the models, a quasilikehood approach is recommended (Burham et al. 1987; Lebreton et al. 1992; Burnham and Anderson, 2002) to deal with the problem. The corresponding criterion is QAIC, defined as,

$$QAIC = -2\log[l(\hat{\underline{\theta}}|y)]/\hat{c} + 2k,$$

where $\hat{c}$ is a variance inflation factor that can be calculated by,

$$\hat{c} = x^2 / df,$$

where x^2 and df correspond to the goodness-of-fit test of the most general model in the model set.

Again with small sample sizes, the corrected form of $QAIC$, $QAICc$ is considered,

$$QAICc = QAIC + \frac{2k(k+1)}{n-k-1},$$

where n is the sample size, and k is the number of parameters.

1.5.2 Results

Table 1.4 displays the values of AIC, ΔAIC (change in AIC compared to the lowest AIC value) ,QAIC and $\Delta QAIC$ (change in QAIC compared to the lowest QAIC value) for models that assume that the tag reporting rate, λ, is known and equal to 0.43. We do not know exactly when the disease started to affect survival, we therefore tried a series of models, assuming the disease effects began in 1997, or 1998, or 1999, or 2000. Based on AIC and QAIC values (not shown), the models that assume an increase in natural mortality beginning in 1999 are the best ones. The model $(F_{91-94}, F_{95-03}, F^*_{91-94}, F^*_{95-03}, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ (model 2) which assumes F and F^* constant from 1991 to 1994, and from 1995 to 2003, M both age- and period- specific, and incomplete mixing of the newly released fish, and the model $(F_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ (model 3),

which assumes year-specific F and complete mixing of the newly released fish, have the smallest AIC and QAIC values. These models assume that M is different for two age groups, young (from age 3 years to age 5 years) and adult (age 6 years and greater), and for two time periods, before and after the year 1999. Note that the subscript A_91-98 indicates a rate for adult fish during 1991 to 1998, subscript Y_91-98 refers to young fish during 1991 to 1998, and so on. Based on AIC and QAIC values, it is difficult to decide whether there is evidence of incomplete mixing of the new releases though AIC and QAIC values do tend to be lower for models that include F^* (cf., models 2 and 4, 5 and 7, 6 and 8, 10 and 12). Models which assume the fishing mortality rate is age-independent (10 and 12), fit poorly.

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 much smaller than for the corresponding models (F_y, F^*_y, M) and (F_y, M), with age-independent fishing mortality. Estimates of fishing mortality rates obtained under age-independent models are lower than for models with age-dependent fishing mortality, suggesting a negative bias in estimating F due to incorrectly assuming fish of all ages are fully recruited. We should keep in mind that underestimation of fishing mortality rates may lead to implementation of poor fisheries management policies.

Table 1.4. AIC values for models with F and $F*$ age-dependent through selectivity, M

constant over years and ages, and with M age- and/or year- specific to a limited degree,

where we assume $\lambda = 0.43$.

Model	K	*AIC*	ΔAIC	QAIC	ΔQAIC
1	31	2097.94	16.39	1635.37	21.75
2	11	2081.55	0.00	1613.62	0.00
3	20	2087.48	5.93	1622.29	8.67
4	9	2120.87	39.32	1643.09	29.48
5	18	2229.58	148.03	1731.19	117.58
6	17	2383.46	301.91	1849.66	236.04
7	29	2087.75	6.20	1626.59	12.97
8	28	2207.30	125.75	1718.52	104.90
9	18	2228.40	146.85	1730.28	116.67
10	14	2462.71	381.16	1909.54	295.92
11	29	2181.12	99.57	1698.74	85.13
12	25	2311.76	230.21	1797.88	184.27

Note: Values of AICc and QAICc are not presented because they are similar to values of

AIC and QAIC, respectively. $\hat{c} = 1.29$, based on model $(F_y, F*_y, M_{Y\_91-98},$

$M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$. K is the number of parameters.

Models

1: $(F_y, F*_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$

2: $(F_{91-94}, F_{95-03}, F*_{91-94}, F*_{95-03}, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$

3: $(F_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$

4: $(F_{91-94}, F_{95-03}, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$

5: $(F_y, M_{3-5}, M_{6+}, Sel_3, Sel_4, Sel_5)$

6. $(F_y, M, Sel_3, Sel_4, Sel_5)$

7. $(F_y, F*_y, M_{3-5}, M_{6+}, Sel_3, Sel_4, Sel_5)$

8. $(F_y, F*_y, M, Sel_3, Sel_4, Sel_5)$

9. $(F_y, M_{91-98}, M_{99-03,} Sel_3, Sel_4, Sel_5)$

10. (F_y, M)

11. $(F_y, F*_y, M_{91-98}, M_{99-03,} Sel_3, Sel_4, Sel_5)$

12. $(F_y, F*_y, M)$

Estimates and their standard errors from fitting models $(F_{91-94}, F_{95-03}, F*_{91-94}, F*_{95-03}, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ and $(F_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ to the striped bass data are presented in Table 1.5. The estimates of standard errors are produced by SURVIV, based on the information matrix. Both models produce estimates with good precision; relative standard errors for most estimates are less than 10%. Estimates of selectivity have the expected trend under both models, with an estimate equal to 1 for fish of age 5 years. Under model $(F_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$, the estimated natural mortality for young fish is 0.42 (SE=0.02) from 1991 to 1998, which is smaller than that from 1999 to 2003, 0.78 (SE=0.06). The estimated natural mortality for adult fish is 0.15 (SE=0.09) from 1991 to 1998, which is smaller than that from 1999 to 2003, 0.58 (SE=0.04). In both periods, 1991 to 1998, and 1999 to 2003, the estimated natural mortality rate for young striped bass is higher than that for the adults. We note that the estimate of M for adults in 1991 to 1998 agrees well with the value (0.15) assumed for striped bass by Smith et al. (2000). Estimates also indicate that fishing mortality increased after fishing regulations were relaxed in 1995.

Table 1.5. Parameter estimates with standard errors in parentheses from fitting two-age, two-period M models (a) $(F_{91-94}, F_{95-03}, F*_{91-94}, F*_{95-03}, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98},$ $M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ and (b) $(F_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4,$ $Sel_5)$ to the striped bass data. We assume that $\lambda = 0.43$.

Parameter	(a)		(b)	
F(92)	0.299	(0.015)	0.324	(0.021)
F(93)	0.299	(0.015)	0.263	(0.015)
F(94)	0.299	(0.015)	0.296	(0.016)
F(95)	0.296	(0.012)	0.372	(0.018)
F(96)	0.296	(0.012)	0.337	(0.017)
F(97)	0.296	(0.012)	0.356	(0.020)
F(98)	0.296	(0.012)	0.374	(0.024)
F(99)	0.296	(0.012)	0.355	(0.024)
F(00)	0.296	(0.012)	0.405	(0.024)
F(01)	0.296	(0.012)	0.368	(0.025)
F(02)	0.296	(0.012)	0.294	(0.020)
F(03)	0.296	(0.012)	0.177	(0.024)
Sel1	0.491	(0.046)	0.505	(0.047)
Sel2	0.711	(0.043)	0.728	(0.044)
Sel3	1.000	(0.048)	1.000	(0.048)
F*(91)	0.269	(0.012)	0.251	(0.023)
F*(92)	0.269	(0.012)		
F*(93)	0.269	(0.012)		
F*(94)	0.269	(0.012)		
F*(95)	0.388	(0.012)		
F*(96)	0.388	(0.012)		
F*(97)	0.388	(0.012)		
F*(98)	0.388	(0.012)		
F*(99)	0.388	(0.012)		
F*(00)	0.388	(0.012)		
F*(01)	0.388	(0.012)		
F*(02)	0.388	(0.012)		
M_Y_91_98	0.386	(0.022)	0.419	(0.021)
M_Y_99_03	0.837	(0.057)	0.784	(0.061)
M_A_91_98	0.134	(0.009)	0.152	(0.009)
M_A_99_03	0.645	(0.028)	0.580	(0.036)

Models considered above assume that λ is constant and equal to 0.43. If the true value of λ is not 0.43, parameter estimates will be biased. Models with different values of

λ were also fitted, showing that larger values of λ are usually associated with smaller estimates of F and F^*, and larger estimates of M. We also investigated a series of models $(F_y, M_{91-98}, M_{99-03})$ where tag reporting rates were constant from 1991 to 1998 (λ_{91-98}), and constant from 1999 to 2003 (λ_{99-03}). We found that when λ_{91-98}=0.5, and λ_{99-03}=0.2, estimates of M were $\hat{M}_{91-98}$=0.25 and $\hat{M}_{99-03}$=0.25. So an alternative to the conclusion that M increased in later years is that λ decreased in later years with no change in M. However, we do not believe that λ changed that much. These analyses suggest the importance of accurate and year-specific information on the tag reporting rate for obtaining unbiased estimates of mortality rates.

We also investigated models where λ is estimated. Estimates, with their standard errors in parentheses, from fitting models $(F_{91-94}, F_{95-03}, F^*_{91-94}, F^*_{95-03}, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda)$ and $(F_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda)$ to the striped bass data are displayed in Table 1.6. Both models produce poor precision with relatively high estimates of F and F^*, and relatively low estimates of natural mortality compared with estimates obtained under the corresponding models where λ is assumed equal to 0.43. The estimates of M_{A_91-98} are close to 0 and not at all realistic. It is worth noting that estimates of selectivity are reasonable with expected trend and high precision. The poor performance of the models with λ estimated is not surprising given the indication of near-singularity for models in Figure 1.2. Again, we emphasize the importance of using external sources to obtain accurate information for λ (Pollock et al. 1991, 2001, and 2002; Hearn et al. 2003).

Table 1.6. Parameter estimates with standard errors in parentheses from fitting two-age, two-period M models (a) $(F_{91-94}, F_{95-03}, F*_{91-94}, F*_{95-03}, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda)$ (b) $(F_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda)$ to the striped bass data.

Parameter	(a)		(b)	
F(92)	0.435	(0.092)	0.462	(0.097)
F(93)	0.435	(0.092)	0.379	(0.077)
F(94)	0.435	(0.092)	0.419	(0.080)
F(95)	0.439	(0.098)	0.529	(0.099)
F(96)	0.439	(0.098)	0.484	(0.093)
F(97)	0.439	(0.098)	0.514	(0.100)
F(98)	0.439	(0.098)	0.557	(0.117)
F(99)	0.439	(0.098)	0.523	(0.114)
F(00)	0.439	(0.098)	0.599	(0.125)
F(01)	0.439	(0.098)	0.535	(0.111)
F(02)	0.439	(0.098)	0.417	(0.081)
F(03)	0.439	(0.098)	0.230	(0.043)
lambda	0.297	(0.061)	0.297	(0.058)
Sel1	0.482	(0.046)	0.502	(0.047)
Sel2	0.696	(0.044)	0.717	(0.044)
Sel3	1.000	(0.047)	1.000	(0.047)
F*(91)	0.392	(0.084)	0.366	(0.082)
F*(92)	0.392	(0.084)		
F*(93)	0.392	(0.084)		
F*(94)	0.392	(0.084)		
F*(95)	0.572	(0.123)		
F*(96)	0.572	(0.123)		
F*(97)	0.572	(0.123)		
F*(98)	0.572	(0.123)		
F*(99)	0.572	(0.123)		
F*(00)	0.572	(0.123)		
F*(02)	0.572	(0.123)		
M_Y_91_98	0.283	(0.071)	0.305	(0.074)
M_Y_99_03	0.714	(0.099)	0.641	(0.109)
M_A_91_98	0.000	(0.091)	0.010	(0.090)
M_A_99_03	0.489	(0.108)	0.396	(0.121)

1.6 Discussion

In this chapter, we have developed models incorporating age effects for tag return data where age at tagging is determined using length. Previous age-independent tag return models have a strong assumption that all fish have the same fishing mortality rates and the same natural mortality rate no matter what age they are. Our new age-dependent models allow fish of different ages to have different fishing mortality rates, and even different natural mortality rates. Our models can be adapted to allow both a continuous fishery and a pulse fishery. Our models can also allow for newly released fish to have different fishing mortality rates from previously released fish of the same age. Based on AIC, for the striped bass data, models with incomplete mixing tend to be better than models with complete mixing, suggesting that the newly released striped bass did not get well mixed with other tagged fish in the first year. Estimates of annual mortality were, however, similar under the complete mixing models and the incomplete mixing models.

Monte Carlo simulations for models with M and λ constant, and F age- and year-specific demonstrate that with large sample sizes (numbers of fish tagged and released ≥ 500 for each age class annually) and moderate levels of the reporting rate, all estimators have good properties if λ is known. Simulation results (Table 1.2) also indicate that having external information about λ can greatly improve estimator precision. So we recommend incorporating the external information about λ (Pollock et al. 1991, 2001, and 2002; Hearn et al. 2003) into the models on a routine basis. Reliable results are not likely otherwise.

The inclination to obtain as much information as possible from current data drives people to build more and more general models. Examining singularity of expected

information matrix for models with age-specific natural mortality or reporting rates indicates that parameter redundancy problems arise when the tag reporting rates are estimated.

Time variation in the reporting rate is an additional complication and can cause bias as typically we get a reporting rate estimate for one year (e.g. from reward tags) and apply this estimate to all years. Ideally one should get an estimate of the reporting rate every year.

In our age-dependent models we assume that all ages are correctly classified. In practice the age-length key method is the most commonly used method to identify the age of fish. Errors do exist in the process of identification of the ages with this method. We can consider this kind of errors as measurement errors. The effects of measurement error on parameter estimation have received increasing attention (Walters and Ludwig 1981; Stefanski 1985; Stefanski and Cook 1995; Gould et al. 1997). Modification of the age-dependent models to incorporate effects of measurement errors would be an interesting topic for future research. Two sampling designs to reduce such measurement errors for tag return studies: one where only fish in the youngest year class are tagged, another where fish of the two youngest year classes are tagged, will be investigated in Chapter 2.

1.7 References

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Chapter 2

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

2.1 Introduction

Tag-return methods have been widely used to estimate fishing and natural mortality rates (Pollock et al. 1991, Hoenig et al. 1998 a, 1998 b, Hearn et al. 1998, Pollock et al. 2004). Pollock et al.(1991) suggested conducting a reward tagging study or a creel survey or port sampling to first estimate the tag-reporting rate and then to determine the instantaneous fishing and natural mortality rates. Hoenig et al. (1998a) used multiyear tag-return studies to estimate instantaneous rates of fishing and natural mortality and tag-reporting rate by incorporating fishing effort into the models. But they found that the estimates of the tag-reporting rate were not stable. To relax the assumption that the newly tagged fish must have the same fishing rate as previously tagged fish, which is sometimes unrealistic, Hoenig et al. (1998b) developed models to allow for incomplete mixing of newly tagged fish with the previously tagged fish. With more information about the effects of exploitation, Hearn et al. (1998) built pre- and post-season tagging models that allow one to estimate fishing and natural mortality rates and the tag-reporting rate. Pollock et al. (2004) presented models that combine tag-return data and radio-telemetry data to obtain more precise estimates of fishing and natural mortality rates and in addition an unbiased and precise tag reporting rate estimate.

One limitation of these models is that they assume all tagged fish are fully recruited and hence fishing mortality does not vary by age. But in many tagging studies fisheries biologists tag fish from a wide range of ages that might have very different

fishing mortality rates. Brownie et al. (1985) built a series of models for a multiyear tagging study to estimate age- and year- specific survival rates and tag recovery rates. Even though the methodology was primarily developed in the context of bird-banding studies, it is also applicable to fisheries tagging studies. But under Brownie models, only the finite total annual mortality rates are estimated instead of the separate components of mortality corresponding to exploitation and natural causes.

Chapter 1 re-parameterized the Brownie models and generalized the Hoenig et al. (1998a, b) models to estimate age- and year- specific instantaneous fishing mortality rates, age-specific instantaneous natural mortality rates and the tag-reporting rate. One challenge of this method is the correct specification of ages of tagged fish. One common approach that fisheries biologists use for age specification is the age-length key method (Secor et al. 1995). But there may be substantial errors in determining the ages by this age-length key approach.

In general, the older the fish is, the more error in converting its size to its age (LeCren 1974, Lai and Gunderson 1987). To reduce errors for age specification from the age-length key method we propose two sampling designs for tag return studies: i) Only fish in the youngest age class are tagged; ii) Fish in the two youngest age classes are tagged. These designs also have the practical advantage that often fish in the younger age classes are caught in greater numbers and are more available for tagging than older fish. In Section 2.2 we describe the Brownie et al. (1985) models for two age classes and the detailed model structure for the two new sampling designs.

One big concern of these new designs where only one or two age classes are tagged is model identifiability. With considerably less information for these new designs,

the question is whether the parameters of interest (age- and year- specific fishing mortality rates, natural mortality rate and tag-reporting rate) are still estimable. Catchpole and Morgan (1997, 2001) and Catchpole et al. (1996, 1998, 2001) presented methods for investigating model identifiability for tagging studies. They noted that the most obvious cause of non-identifiability is overparameterization, or parameter redundancy. For a general class of nonlinear models, they showed that parameter redundancy is equivalent to singularity of the information matrix of the corresponding likelihood, and also equivalent to rank-deficiency of the derivative matrix. In Section 2.3 we investigate parameter redundancy of different models for the new designs.

Section 2.4 describes the simulations conducted to compare the accuracy and precision of parameter estimation from different sampling designs. Section 2.5 illustrates the application of the different sampling designs using Chesapeake Bay striped bass (*Morone saxatilis*) data. A general discussion and suggestions for future research complete the paper.

2.2 Model Structures

2.2.1 The Brownie Models: 2 Age Classes, Young and Adults

In this section we briefly present the Brownie et al. (1985) formulation for a two age class model. First we present the notation and then the model structure.

Notation:

f_i: finite recovery rate for adults in year i.

S_i: survival rate for adults in year i.

f_i': finite recovery rate in year i for animals tagged and released as young in year i.

S_i': survival rate for year i for animals tagged and released as young in year i.

Table 2.1. Expected and observed number of tag recoveries for 3 years of release and 4 years of recoveries when animals are recorded as young or adult at tagging, using the Brownie et al. (1985) formulation.

Year	No. tagged	Year of recovery 1	2	3	4
Expected recoveries (Tagged as Adult)					
1	N_1	$N_1 f_1$	$N_1 S_1 f_2$	$N_1 S_1 S_2 f_3$	$N_1 S_1 S_2 S_3 f_4$
2	N_2		$N_2 f_2$	$N_2 S_2 f_3$	$N_2 S_2 S_3 f_4$
3	N_3			$N_3 f_3$	$N_3 S_3 f_4$
Observed recoveries (Tagged as Adult)					
1	N_1	r_{11}	r_{12}	r_{13}	r_{14}
2	N_2		r_{22}	r_{23}	r_{24}
3	N_3			r_{33}	r_{34}
Expected recoveries (Tagged as Young)					
1	N_1'	$N_1' f_1'$	$N_1' S_1' f_2$	$N_1' S_1' S_2 f_3$	$N_1' S_1' S_2 S_3 f_4$
2	N_2'		$N_2' f_2'$	$N_2' S_2' f_3$	$N_2' S_2' S_3 f_4$
3	N_3'			$N_3' f_3'$	$N_3' S_3' f_4$
Observed recoveries (Tagged as Young)					
1	N_1'	r_{11}'	r_{12}'	r_{13}'	r_{14}'
2	N_2'		r_{22}'	r_{23}'	r_{24}'
3	N_3'			r_{33}'	r_{34}'

Note that "young" means "young of the year" or the 1-year age class, "adult" means all ages greater than young of the year. Assuming that young animals have different survival rates from adults, Brownie et al. (1985) developed models that incorporate different survival rates for these two age classes (young and adult). Suppose N_i adults and N_i' young animals (Table 2.1) are tagged in year i ($i=1, 2, ..., I$). From these r_{ij} adults and r_{ij}' young animals are harvested and their tags reported in year j ($j=i, i+1, ..., J$). The expected number of recovered tags from animals tagged as adults is:

$$E[r_{ij}] = N_i \, P_{ij},$$

where

$$P_{ij} = \begin{cases} f_j & (j=i) \\ \left(\prod_{k=i}^{j-1} S_k \right) f_j & (j>i) \end{cases}$$

and

P_{ij} is the probability that an adult tagged and released in year i, is then harvested and reported in year j.

We assume that the number of animals harvested and reported for each cohort follows the multinomial distribution, and each cohort is independent of other cohorts. The likelihood function for animals tagged as adults is product multinomial:

$$L_a = \prod_{i=1}^{I} \binom{N_i}{r_{ii}, r_{ii+1}, \ldots, r_{iJ}, N_i - \sum_{v=i}^{J} r_{iv}} \left(\prod_{j=i}^{J} P_{ij}^{r_{ij}} \right) \left(1 - \sum_{v=i}^{J} P_{iv} \right)^{N_i - \sum_{v=i}^{J} r_{iv}}.$$

For young animals:

$$E[r_{ij}'] = N_i' P_{ij}',$$

where

$$P_{ij}' = \begin{cases} f_i' & (j=i) \\ S_i' f_{i+1} & (j=i+1) \\ S_i' \left(\prod_{k=i+1}^{j-1} S_k \right) f_j & (j>i+1), \end{cases}$$

and

P_{ij}' is the probability that a young animal tagged and released in year i, is then harvested and returned in year j. Notice that after the first year, surviving animals are adults and hence subject to adult rates.

The likelihood function for animals tagged as young is product multinomial:

$$L_y = \prod_{i=1}^{I} \binom{N_i\,'}{r_{ii}\,',r_{i\,i+1}\,',\ldots,r_{iJ}\,',N_i\,'-\sum_{v=i}^{J} r_{iv}\,'} \left(\prod_{j=i}^{J} P_{ij}\,'^{\,r_{ij}\,'}\right)\left(1-\sum_{v=i}^{J} P_{iv}\,'\right)^{N_i\,'-\sum_{v=i}^{J} r_{iv}\,'}.$$

Under the assumption that animals tagged as young act independently from animals tagged as adult, we have a joint likelihood for a tagging study with two age classes:

$$L = L_a \times L_y\,.$$

Exact expressions for maximum likelihood estimators based on the joint likelihood function are presented in Brownie et al. (1985, p. 60-61).

2.2.2 Models for Tagging Age 1 Fish Only

Chapter 1 presented a general model structure for multiple age tagging studies that are appropriate for a continuous fishery, limited continuous fishery, pulse fishery and incomplete mixing fishery models, with the assumption that all age classes were tagged. Here, for simplicity, we only consider the continuous fishery, and focus on the design where only age 1 fish (fish in the youngest year class that enter the fishery) are tagged. Previous research (Brownie et al. 1985; Anderson et al. 1985) showed that with the finite mortality rates parameterization, it is impossible to estimate age- and year-specific survival rates for the young if only young are tagged. So sampling designs with only young animals tagged are generally considered impractical. However, with the instantaneous mortality rate parameterization, estimation of young and adult survival is possible when only young are tagged if certain rates are assumed constant across years; that is, if additional structure is imposed on the parameters. Accordingly, we assume a constant natural mortality rate, M, a constant tag reporting rate, λ, and multiplicative time- and age- dependent fishing mortality rates, F ($F_{jk} = Sel_k\,F_j$).

Following the structure of the likelihood of Chapter 1, we let N_i be the number of fish tagged at age 1 and released in year i ($i =1,2,...I$), and let R_{ij} be the number of fish tagged at age 1 and released in year i, then harvested and reported in year j, for $j = i, i+1, i+2, ..., J$. We assume that tagging and release happen at the beginning of the year and harvest occurs during the whole year.

Also let

P_{ij} be the probability that a fish tagged at age 1 and released in year i, is harvested and its tag returned in year j,

S_{ij} be the conditional survival rate in year j for fish tagged at age 1 in year i and alive at the beginning of year j (Each year fish are a year older and that has to be taken into account),

F_j be the instantaneous fishing mortality rate in year j for fully recruited fish,

M be the instantaneous annual natural mortality rate,

λ be tag-reporting rate, the probability that the tag is reported, given that a tagged fish is caught,

Sel_k be the selectivity for age k fish. Here we assume that all fish of age K_c and greater are fully recruited ($Sel_k =1$ for all $K \geq K_c$). Selectivity is assumed to be constant over years for each age. Therefore the fishing mortality rate for fish of age k in year j is:

$$F_{jk} = Sel_k F_j .$$

We assume M and λ are year and age independent to achieve parsimony. Models with M and λ dependent on year or age are discussed earlier in Chapter 1.

The expected number of fish tagged at age 1 and released in year i, then harvested and returned in year j is:

$$E[R_{ij}] = N_i P_{ij},$$

where

$$P_{ij} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{iv}\right)(1-S_{ij})\dfrac{F_j\, Sel_{1+j-i}}{F_j\, Sel_{1+j-i} + M}\, \lambda & \\[6pt] & (when\ \ j > i) \\[12pt] (1-S_{ij})\dfrac{F_j\, Sel_1}{F_j\, Sel_1 + M}\, \lambda & (when\ j = i) \end{cases} \qquad (2.2.1)$$

$$S_{ij} = \exp(-F_j\, Sel_{1+j-i} - M),$$

The number of fish tagged at age 1 and released in year i, then harvested and returned in year j follows a multinomial distribution. Therefore the likelihood function is product multinomial, following Hoenig et al. (1998a):

$$L_1 = \prod_{i=1}^{I} \binom{N_i}{R_{ii}, R_{ii+1}, \ldots, R_{iJ}, N_i - \sum_{v=i}^{J} R_{iv}} \left(\prod_{j=i}^{J} P_{ij}^{R_{ij}}\right)\left(1 - \sum_{v=i}^{J} P_{iv}\right)^{N_i - \sum_{v=i}^{J} R_{iv}}.$$

Maximum likelihood estimators (MLEs) do not have closed forms. We use the computer software SURVIV (White 1983) to estimate F_j (j=1,2,...,J) , M , and Sel_k (k=1, 2,...,K$_c$), if λ is known, or to estimate F_j , M , Sel_k and λ, when λ is unknown.

2.2.3 Models for Tagging Age 1 and Age 2 Fish

Now we consider the case where age 1 and age 2 fish (fish in the youngest and second youngest year classes that enter the fishery) are tagged. Following the structure of the likelihood of Chapter 1, we let N_i and N_i' be the number of fish tagged at age 1 and age 2, respectively, and released in year i ($i = 1,2,...I$). Then R_{ij} and R_{ij}' are the numbers of the N_i and N_i' fish, respectively, that are subsequently harvested and reported in year j, for $j = i, i+1, i+2, ..., J$. Let P_{ij} and S_{ij} be as defined in section 2.2.2 for fish tagged at age 1. Also let P_{ij}' and S_{ij}' be defined as indicated below for fish tagged at age 2. We assume that tagging and release occur at the beginning of the year and that harvest occurs continuously in the whole year.

Let

P_{ij}' be the probability of fish tagged at age 2 and released in year i, then harvested and returned in year j.

S_{ij}' be the conditional survival rate in year j for the fish tagged at age 2 in year i, and alive at the beginning of year j.

For a fishery continuous over the whole year, the expected number of the N_i' fish tagged at age 2 and released in year i, that are harvested and returned in year j is:

$$E[R_{ij}'] = N_i' \, P_{ij}',$$

where

$$P_{ij}' = \begin{cases} \left(\prod_{v=i}^{j-1} S_{iv}'\right)(1 - S_{ij}')\dfrac{F_j\, Sel_{2+j-i}}{F_j\, Sel_{2+j-i} + M}\lambda & (when \ \ j > i) \\[3em] (1 - S_{ij}')\dfrac{F_j\, Sel_2}{F_j\, Sel_2 + M}\lambda & (when \ j = i), \end{cases} \qquad (2.2.2)$$

$$S_{ij}' = \exp(-F_j\, Sel_{2+j-i} - M).$$

The likelihood function for the number of fish tagged at age 2 and released in year i, then harvested and returned in year j, has a multinomial form:

$$L_2 = \prod_{i=1}^{I}\binom{N_i'}{R_{ii}', R_{ii+1}',\dots,R_{iJ}', N_i' - \sum_{v=i}^{J} R_{iv}'}\left(\prod_{j=i}^{J} P_{ij}'^{R_{ij}'}\right)\left(1 - \sum_{v=i}^{J} P_{iv}'\right)^{N_i' - \sum_{v=i}^{J} R_{iv}'}.$$

The component of the likelihood for fish tagged at age 1 is exactly the same as L_1 in section 2.2.2. Assuming that fish tagged at age 1 act independently from fish tagged at age 2, the joint likelihood function for the two-age-class tagging study is:

$$L = L_1 \times L_2.$$

Using this joint likelihood we can obtain MLEs of F_j (j=1,2,…,I), M, and Sel_k, if λ is known, or of F_j (j=1,2,…,I), M, Sel_k and λ, when λ is unknown.

2.3 Parameter Redundancy

Catchpole and Morgan (1997) described a method to determine parameter redundancy by checking the singularity of the information matrix for product multinomial models with complex cell probabilities, when it is impossible to check

parameter redundancy by inspection. For counts y_i (i=1,...,n) from a multinomial distribution ($N, p_1,..., p_n$), where $p_1,..., p_n$ are functions of parameter vector $\theta=(\theta_1,\ldots,\theta_k)$, let $\mu_j=E(y_j)=Np_j$, $\mu=(\mu_{1,...,} \mu_n)$, the model is parameter redundant if we can express μ in terms of a smaller parameter vector $\beta = (\beta_1,..., \beta_q)$, where q < k. They showed that the information matrix can be written as

$$I = D\,\Pi^{-1}\,D^T, \tag{2.3.1}$$

where Π is a diagonal matrix whose jth diagonal element is equal to $\mu_j = N\,p_j$. D is the derivative matrix with elements

$$D_{ij} = \partial\mu_j / \partial\theta_i \quad (j=1,...,n;\ i=1,...,k).$$

For a simpler test of parameter redundancy, Catchpole and Morgan (1997) proved that rank $I(\theta)$ = rank $D(\theta)$. So we can more easily check parameter redundancy by checking rank-deficiency of the derivative matrix.

Even if a model does not have parameter redundancy, estimators may still behave poorly. Catchpole et al. (2001) demonstrated that I (θ) may be non-singular for a given model, but if the smallest eigenvalue of I (θ) is close to 0, estimators may perform poorly. The parameters that are poorly estimated can be determined by checking the magnitudes of the coefficients of parameters in the eigenvector corresponding to the smallest eigenvalue of the information matrix. Generally, the bigger the absolute value of the coefficient of a parameter in the eigenvector, the lower the precision of the estimator.

We are interested in evaluating the performance of models *(F_y, M, $Sel_{a1,a2,a3}$, λ)* and *(F_y, M, $Sel_{a1,a2,a3}$)* for two designs, the first where only age 1 fish are tagged, and the second where both age 1 and age 2 fish are tagged. From Chapter 1, we know that when all age classes are tagged, this model performs well if the reporting rate is known. The

model *(F_y, M, Sel_{a1,a2,a3}, λ)* assumes that fishing mortality rates (F_j Sel_k) are year specific

and also age specific (because of the dependence on Sel_k), that selectivity is 1 for fish of

age 4 and greater, and that both the natural mortality rate (*M*) and tag reporting rate (*λ*)

are constant over years and ages. The model *(F_y, M, Sel_{a1,a2,a3})* is the same as model *(F_y,*

M, Sel_{a1,a2,a3}, λ) except that *λ* is assumed known from external sources without error. For

illustration, we consider 5 years of tagging and releases with either 5 or 7 years of

recoveries. When only age 1 fish are tagged, we assume that 2500 fish are tagged and

released at the beginning of each year for 5 consecutive years. The true parameter values

we chose are *F_1=0.2, F_2=0.5, F_3=0.3, F_4=0.4, F_5=0.6, M =0.2, λ =0.3, Sel_1=0.6, Sel_2=0.7*

and *Sel_3=0.9* for 5 years of recoveries. For 7 years of recoveries, the parameter values are

the same as for 5 years of recoveries except that we let *F_6=0.3, F_7=0.4*. When both age 1

and age 2 fish are tagged, for comparison, we assume that 1250 age 1 fish and 1250 age 2

fish are tagged and released each year for 5 consecutive years. The true parameter values

are the same as when only age 1 fish are tagged. The numbers of fish tagged here are

large to ensure that variance calculation based on $I(\theta)^{-1}$ is accurate. Problems with

estimator performance due to parameter redundancy will be worse when smaller numbers

of fish are tagged.

The information matrix $I(\theta)$ is calculated using equation (2.3.1). The

eigenvalues of $I(\theta)$ and their eigenvectors, large-sample variance-covariance matrix

$\Sigma = I(\theta)^{-1}$ and correlation matrix ρ are computed using program Maple (Waterloo

Maple Inc., Maple 9). The correlation matrix ρ is calculated with the following formula:

$$\rho = \left(V^{1/2}\right)^{-1} \Sigma \left(V^{1/2}\right)^{-1},$$

where V is a diagonal matrix with each of its elements equal to the corresponding diagonal element of the variance-covariance matrix Σ.

The condition number, $K(I(\theta))$, is used to provide a measure of the near-singularity problem (Belsley, Kuh, and Welsh, 1980). It is defined as:

$$K(I(\theta)) = \left(\frac{\lambda_{max}}{\lambda_{min}} \right)^{1/2} ,$$

where λ_{max} and λ_{min} are the largest and smallest eigenvalues of the information matrix $I(\theta)$ respectively. A condition number around 10 indicates weak near-singularity and possible problems with estimator properties, a condition number of 30 to 100 indicates moderate to strong near-singularity problems, and a condition number larger than 100 indicates serious near-singularity problems (Belsley, Kuh, and Welsh, 1980). The condition number, $K(I(\theta))$, of the information matrix, selected relative standard error (RSE) and correlations for models $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ and $(F_y, M, Sel_{a1,a2,a3})$ when only age 1 fish are tagged and when both age 1 and age 2 fish are tagged are displayed in Table 2.2. We let $V(\hat{\theta})$ be the variance of estimator $\hat{\theta}$, $r(\hat{\theta}_1, \hat{\theta}_2) = \dfrac{cov(\hat{\theta}_1, \hat{\theta}_2)}{\sqrt{V(\hat{\theta}_1)V(\hat{\theta}_2)}}$ be the correlation between $\hat{\theta}_1$ and $\hat{\theta}_2$, where $cov(\hat{\theta}_1, \hat{\theta}_2)$ is the covariance of $\hat{\theta}_1$ and $\hat{\theta}_2$, and RSE($\hat{\theta}$) be relative standard error for $\hat{\theta}$, $RSE(\hat{\theta}) = \dfrac{SE(\hat{\theta})}{\theta}$.

For model $(F_y, M, Sel_{a1,a2,a3})$, where λ is assumed to be known without error, when only age 1 fish are tagged with 5 years of recoveries the condition number of the information matrix is larger than 30 and correlations between estimators $\hat{M}$, $\hat{F}_1$ and $\hat{F}_2$ are high. All estimators are poorly behaved in this case. In contrast, with 7 years of

recoveries the condition number of the information matrix is smaller than 30, the correlations between estimators $\hat{M}$, $\hat{F}_1$ and $\hat{F}_2$ reduce to a moderate level, and the relative standard error of $\hat{F}_2$ is much smaller than the value with 5 years of recoveries, indicating improved performance of the estimators in this case. The practical implication is that we should collect additional years of recoveries information beyond the last release of tagged fish. When both age 1 and age 2 fish are tagged, the condition numbers are all smaller than 30, relative standard errors of $\hat{F}_2$ are small and correlations between estimators $\hat{M}$, $\hat{F}_1$ and $\hat{F}_2$ are moderate ($0.34 < r < 0.76$) for both 5 and 7 years of recoveries. Assuming λ known, the design with tagging two age classes produces estimators with better properties than tagging age 1 fish only.

For model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$, when only age 1 fish are tagged the condition numbers of the information matrix are larger than 100, relative standard errors of $\hat{F}_2$ and $\hat{\lambda}$ are large and correlations between estimators $\hat{M}$, $\hat{\lambda}$, $\hat{F}_1$ and $\hat{F}_2$ are strong ($|r| > 0.67$) for both 5 years of recoveries and 7 years of recoveries (Table 2.2). When both age 1 and age 2 fish are tagged the condition numbers are smaller than 100 and relative standard errors of estimators $\hat{F}_2$ and $\hat{\lambda}$ are smaller than their counterparts when only age 1 fish are tagged (RSE($\hat{\lambda}$)=0.37 compared to RSE($\hat{\lambda}$)=0.59 for 5 years of recoveries, RSE($\hat{\lambda}$)=0.28 compared to RSE($\hat{\lambda}$)=0.53 for 7 years of recoveries). When λ must be estimated, tagging age 1 and age 2 fish, compared to age 1 fish only, produces some improvement in estimator properties, but RSE($\hat{\lambda}$) and RSE($\hat{F}_2$) are large under both designs. We emphasize that these results are based on tagging a total of 2500 fish each year and therefore give an optimistic view of estimator performance for studies with

smaller sample sizes. If λ must be estimated, estimator properties will be poor under either design, for sample sizes likely to be met in practice.

Table 2.2. The condition number (K), relative standard error (RSE) and correlations (r) of estimators under the models (a) (F_y, M, $Sel_{a1,a2,a3}$) and (b) (F_y, M, $Sel_{a1,a2,a3}$, λ) for studies where 2500 age 1 fish, or 1250 age 1 and age 2 fish, are tagged and released for 5 years, followed by 5 or 7 years of recoveries. Parameter values assumed are given in Section 2.3.

Recovery	(a) λ known			(b) λ estimated					
	Only age 1 fish are tagged								
	K	RSE($\hat{F}_2$)	r($\hat{M},\hat{F}_1$)	r($\hat{M},\hat{F}_2$)	K	RSE($\hat{F}_2$)	RSE($\hat{\lambda}$)	r($\hat{M},\hat{F}_1$)	r($\hat{M},\hat{F}_2$)	r($\hat{M},\hat{\lambda}$)
5 years	38.3	0.33	0.859	0.902	116.0	0.62	0.59	-0.678	-0.695	0.970
7 years	24.2	0.11	0.460	0.562	120.1	0.44	0.53	-0.879	-0.909	0.994
	Both age 1 and age 2 fish are tagged								
5 years	20.6	0.17	0.639	0.756	84.6	0.41	0.37	-0.786	-0.809	0.970
7 years	17.3	0.11	0.339	0.481	77.0	0.28	0.28	-0.816	-0.870	0.985

According to methods of Catchpole et al. (2001), checking the coefficients of parameters in the eigenvector corresponding to the smallest eigenvalue of I (θ) can provide us important information about which parameters are nearly confounded and hence poorly estimated. As an example, for model *(F_y, M, $Sel_{a1,a2,a3}$, λ)*, when *λ=0.3* with tagging age 1 fish only for 5 years, and with 7 years of recoveries, the smallest eigenvalue is 3.3, with eigenvector (0.212, 0.549, 0.333, 0.435, 0.731, 0.411, 0.574, -

0.386, 0.085, 0.010, -0.044, -0.388), corresponding to parameters (F_1, F_2, F_3, F_4, F_5, F_6, F_7, M, Sel_1, Sel_2, Sel_3, λ). Sel_1, Sel_2 and Sel_3 have the lowest weights, reflecting their relatively high precision. Other parameters have high weights, indicating confounding and poor precision of estimators.

It is of interest to see how parameter values affect the condition number of I (θ). For an illustration, we consider a study with 5 years of tagging and 7 years of recoveries as λ changes (Figure 2.1), keeping other parameter values as stated above. For model *(F_y, M, $Sel_{a1,a2,a3}$)*, whether both age 1 and age 2 fish are tagged, or only age 1 fish are tagged, the condition numbers are quite stable as λ increases, with the condition numbers around 17.3 when both age 1 and age 2 fish are tagged, around 24.2 when only age 1 fish are tagged, indicating weak near-singularity problems for this model (Figure 2.1b). For model *(F_y, M, $Sel_{a1,a2,a3}$, λ)*, the condition numbers decrease dramatically at the beginning as λ increases and then become stable at values of about 90 when only age 1 fish are tagged, and about 54 when both age 1 and age 2 fish are tagged, indicating near-singularity problems for all plausible values of λ (Figure 2.1a). Again, these calculations are based on tagging 2500 fish annually, and suggest serious problems relating to parameter redundancy for more feasible tagging numbers.

Figure 2.1. The condition number of the information matrix versus λ, (a) for model (F_y, M, $Sel_{a1,a2,a3}$, λ), and (b) for model (F_y, M, $Sel_{a1,a2,a3}$), with 5 years of tagging and 7 years of recoveries. Solid lines are for the design where both age 1 and age 2 fish are tagged, dashed lines are for the design where only age 1 fish are tagged.

(a) Model (F_y, M, $Sel_{a1,a2,a3}$, λ)
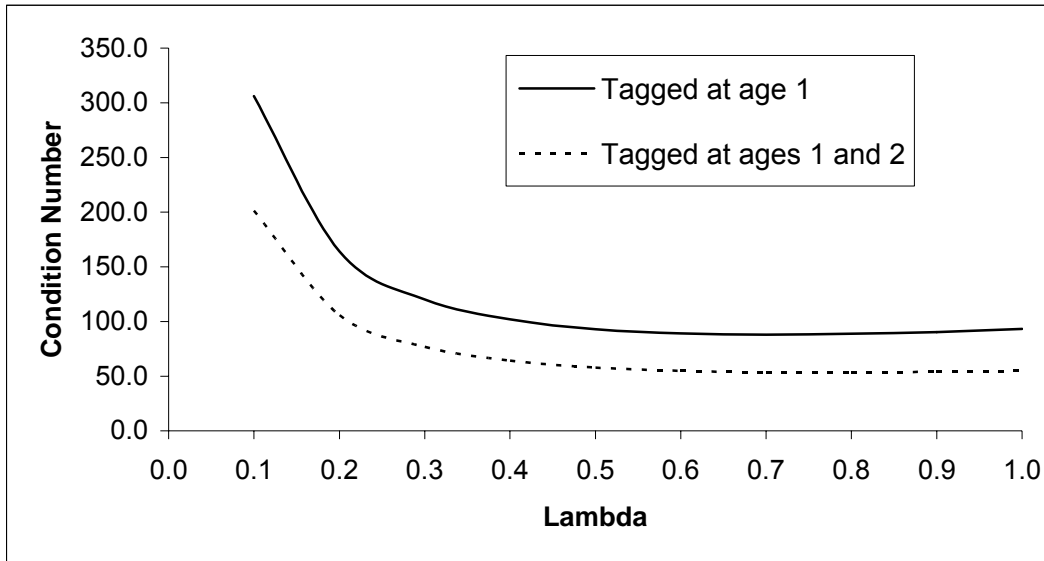
(b) Model (F_y, M, $Sel_{a1,a2,a3}$)
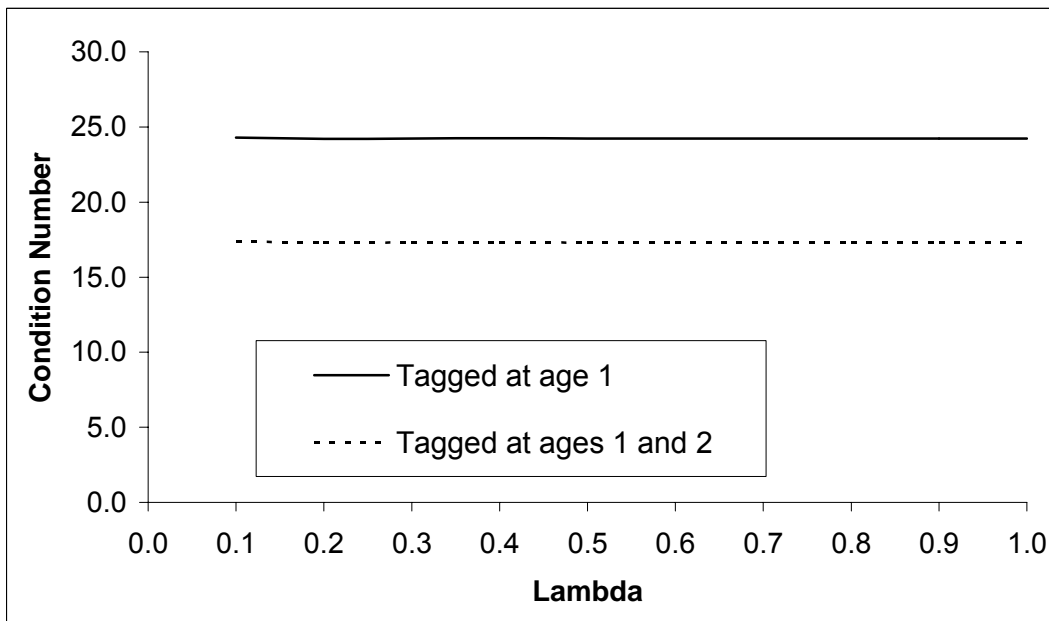
2.4 Simulations

2.4.1 Methods

We carried out Monte Carlo simulations to further investigate the performance of estimators under models $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ and $(F_y, M, Sel_{a1,a2,a3})$. We use maximum likelihood to estimate parameters of interest and obtain standard errors, using the new version of program SURVIV (White 1983) modified by James Hines of Patuxent Wildlife Research Center. We assume that the numbers of tag returns for each cohort follow a multinomial distribution. The cell probability for each cohort is calculated using equations (2.2.1) or (2.2.2), and cohorts are assumed to be mutually independent. For comparison we consider the same data structure as described in section 2.3. We assume 2500 fish are tagged and released in each cohort when only age 1 fish are tagged, while 1250 fish of each age are tagged and released when both age 1 and age 2 fish are tagged. Fish are tagged and released at the beginning of 5 consecutive years with 5 or 7 consecutive years of recoveries. The true parameter values are the same as specified for calculating the information matrix in Section 2.3. We carry out simulations using 500 replicates for each run. We calculate relative bias and relative standard error of $\hat{\lambda}$ using

the follow formulas: $RB(\hat{\lambda}) = \dfrac{\bar{\hat{\lambda}} - \lambda}{\lambda} \times 100\%, \quad RSE(\hat{\lambda}) = \dfrac{SE(\hat{\lambda})}{\lambda} \times 100\%$.

2.4.2 Results

Estimator means and standard errors are presented in Table 2.3 for designs where only age 1 fish are tagged, and where both age 1 and age 2 fish are tagged. Results from Chapter 1 for tagging 500 fish in each of 5 age classes are included for comparison. Standard errors are the standard deviation for estimates from 500 Monte Carlo samples. When only age 1 fish are tagged, model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ produces poor results with 5

years of tagging and 5 or 7 years of recoveries (Table 2.3). The estimator $\hat{\lambda}$ is highly

biased and has poor precision. Relative bias (RB) of $\hat{\lambda}$ is 31% for 5 years of recoveries

and 27% for 7 years of recoveries. Relative standard error (RSE) of $\hat{\lambda}$ is 88% for 5 years

of recoveries and 83% for 7 years of recoveries. Estimators under model $(F_y, M,$

$Sel_{a1,a2,a3})$ behave better than for model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$. With 5 years of tagging and

5 years of recoveries, estimators exhibit some bias and moderate precision (RB($\hat{F}_2$)=7%,

RSE($\hat{F}_2$)=27%), but with 7 years of recoveries, under model $(F_y, M, Sel_{a1,a2,a3})$ all

estimators are essentially unbiased and all relative standard errors are less than 18%. The

improvement in estimator performance when λ is known, compared to when λ is

estimated, agrees with results based on the information matrix in section 2.3.

When both age 1 and age 2 fish are tagged, model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ performs

better (Table 2.4) than when only age 1 fish are tagged. However, estimator $\hat{\lambda}$ is still

biased with low precision. Relative bias (RB) of $\hat{\lambda}$ is 21% for 5 years of recoveries and

10% for 7 years of recoveries. Relative standard error of $\hat{\lambda}$ is 66% for 5 years of

recoveries and 46% for 7 years of recoveries. Estimators under model $(F_y, M, Sel_{a1,a2,a3})$

perform well for both 5 and 7 years of recoveries when both age 1 and age 2 fish are

tagged. This agrees with the results from section 2.3. Model $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ produces

biased estimators with low precision, especially for the tag reporting rate estimation.

Comparing results for the three tagging designs, we see that, with respect to

precision, it is most efficient to tag 500 fish in each of the 5 age classes, and least

efficient to tag 2500 fish in age class 1. For example, from the first column of Table 2.3,

SE($\hat{M}$) is 147% and 200% greater for designs with tagging 2 age classes and 1 age class,

respectively, compared to tagging 500 in each of the 5 age classes. The greater theoretical efficiency of the multi-age class design must, however, be balanced against the practical difficulties associated with obtaining substantial numbers of older fish for tagging, and the unknown biases that may be introduced by incorrectly aging older fish.

Table 2.3. Average estimates with standard errors in parentheses from fitting the models (a) $(F_y, M, Sel_{a1,a2,a3})$ and (b) $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ to simulated data for three tagging designs: 2500 age 1 fish, or 1250 age 1 and 2 fish, or 500 fish of all 5 ages, tagged in each of 5 consecutive years, followed by either 5 or 7 years of recoveries. True parameter values are $F_1=0.2$, $F_2=0.5$, $F_3=0.3$, $F_4=0.4$, $F_5=0.6$, $F_6=0.3$, $F_7=0.4$, $M=0.2$, $\lambda=0.3$, $Sel_1=0.6$, $Sel_2=0.7$ and $Sel_3=0.9$. Results are based on 500 replicates in each case.

Parameter	5 Years of recoveries		7 Years of recoveries	
	(a) λ known	(b) λ estimated	(a) λ known	(b) λ estimated
	Only age 1 fish tagged			
F(1)	0.212 (0.060)	0.207 (0.086)	0.200 (0.036)	0.199 (0.078)
F(2)	0.537 (0.136)	0.527 (0.213)	0.506 (0.072)	0.506 (0.194)
F(3)	0.320 (0.078)	0.315 (0.128)	0.302 (0.041)	0.303 (0.118)
F(4)	0.425 (0.102)	0.419 (0.168)	0.402 (0.051)	0.403 (0.153)
F(5)	0.643 (0.161)	0.646 (0.278)	0.605 (0.079)	0.621 (0.259)
F(6)			0.302 (0.046)	0.322 (0.151)
F(7)			0.408 (0.070)	0.454 (0.231)
M	0.203 (0.034)	0.206 (0.148)	0.200 (0.017)	0.198 (0.143)
λ		0.392 (0.253)		0.386 (0.248)
sel_1	0.593 (0.132)	0.595 (0.141)	0.604 (0.074)	0.605 (0.088)
sel_2	0.688 (0.127)	0.689 (0.130)	0.702 (0.076)	0.703 (0.078)
sel_3	0.878 (0.112)	0.881 (0.112)	0.898 (0.076)	0.898 (0.075)
	Both age 1 and age 2 fish tagged			
F(1)	0.200 (0.036)	0.198 (0.076)	0.199 (0.030)	0.201 (0.059)
F(2)	0.506 (0.079)	0.503 (0.188)	0.502 (0.055)	0.507 (0.146)
F(3)	0.303 (0.046)	0.302 (0.115)	0.301 (0.032)	0.305 (0.089)
F(4)	0.401 (0.059)	0.400 (0.148)	0.399 (0.038)	0.403 (0.114)
F(5)	0.607 (0.096)	0.616 (0.250)	0.602 (0.058)	0.616 (0.191)
F(6)			0.300 (0.039)	0.314 (0.112)
F(7)			0.407 (0.065)	0.435 (0.173)
M	0.200 (0.025)	0.201 (0.112)	0.200 (0.016)	0.196 (0.099)
λ		0.363 (0.199)		0.331 (0.138)
sel_1	0.607 (0.088)	0.608 (0.088)	0.604 (0.063)	0.606 (0.067)
sel_2	0.705 (0.089)	0.707 (0.089)	0.703 (0.062)	0.704 (0.063)
sel_3	0.900 (0.084)	0.902 (0.084)	0.901 (0.064)	0.901 (0.064)
	fish of all 5 ages tagged			
F(1)	0.198 (0.021)	0.197 (0.054)	0.197 (0.021)	0.197 (0.044)
F(2)	0.499 (0.033)	0.499 (0.136)	0.499 (0.032)	0.499 (0.109)
F(3)	0.298 (0.022)	0.298 (0.084)	0.298 (0.021)	0.298 (0.066)
F(4)	0.397 (0.026)	0.398 (0.111)	0.397 (0.024)	0.397 (0.087)
F(5)	0.598 (0.044)	0.608 (0.189)	0.598 (0.038)	0.604 (0.148)
F(6)			0.299 (0.033)	0.306 (0.091)
F(7)			0.404 (0.062)	0.422 (0.149)
M	0.200 (0.017)	0.200 (0.088)	0.200 (0.014)	0.200 (0.075)
λ		0.329 (0.125)		0.317 (0.091)
sel_1	0.607 (0.063)	0.607 (0.063)	0.607 (0.061)	0.607 (0.062)
sel_2	0.704 (0.058)	0.704 (0.059)	0.704 (0.053)	0.704 (0.053)
sel_3	0.901 (0.061)	0.901 (0.062)	0.902 (0.055)	0.902 (0.056)

2.5 Striped Bass Example

2.5.1 Study Description

Striped bass is one of the most important recreational fisheries along the Atlantic Coast (Field 1997). The Roanoke, Delaware, Hudson rivers and the tributaries of the Chesapeake Bay are major producers. To estimate the fishing mortality rates of striped bass on the Chesapeake Bay stock, Maryland Department of Natural Resources (MDNR) tagged spawning fish from 1991 to 2002 in the upper Chesapeake Bay. The length of fish was measured to the nearest mm. An internal anchor tag was used. For better mixing with untagged fish, tagged fish were at large for more than one week. Reported tags were cut off from the recovered fish. Some of the recovered fish were harvested, some released. Here we assume that all recoveries are dead. If hooking mortality is known, we can correct the estimate of fishing mortality to allow for live releases. We will not consider catch-and-release fishing further here, but leave this to Chapter 3.

An otolith-based age-length key was used to identify the ages of tagged striped bass (Secor et al. 1995). Seven age groups (from age 2 years to age 8+ years) were classified using the age-length key method. Since sample sizes for age 2 years are small, we consider fish of 3 years of age as the youngest age class and 4 years as the second youngest age class. The numbers of releases and tag returns for age 3 and age 4 fish are listed in Table 2.5. Fishery biologists generally believe striped bass of 6 to 8+ years are fully recruited while ages 3, 4, and 5 are not. So we assume selectivity for age 6 and greater is 1. Age classes 3, 4 and 5 are partially recruited with selectivity Sel_1, Sel_2 and Sel_3, respectively, to be estimated. For model $(F_y, M, Sel_{a1,a2,a3})$ we let $\lambda = 0.43$ (previous reward tagging study. Wells, B.K personal communication). This reporting rate was used

by the Atlantic States Marine Fisheries Commission. Also, Smith et al. (2000) obtained year-specific estimates of λ ranging from 0.38 to 0.48 for 1991-1998 in Chesapeake Bay for fully recruited fish.

Table 2.4. Release and tag return data for fish tagged at age 3 and 4 from a study on striped bass carried out from 1991-2003 by Maryland Department of Natural Resources.

Age 3

Year of release	Number Tagged	Number recaptured												
		1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
1991	288	20	8	11	6	3	3	2	1	0	0	0	0	0
1992	380		21	5	12	6	6	1	2	0	0	0	0	0
1993	159			5	6	7	1	2	0	0	0	0	0	0
1994	92				3	6	3	0	0	0	0	0	0	0
1995	221					11	11	7	7	1	1	0	0	0
1996	393						23	23	14	5	1	2	0	0
1997	31							2	0	0	1	0	0	0
1998	131								6	1	0	0	1	0
1999	178									21	5	1	2	0
2000	116										10	2	2	0
2001	116											11	3	1
2002	73												4	4

Age 4

Year of release	Number Tagged	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
1991	202	11	15	2	5	2	1	2	0	0	0	0	0	0
1992	325		24	19	13	6	4	2	1	0	0	0	0	0
1993	721			32	41	27	14	9	4	3	0	0	0	0
1994	333				18	22	11	3	4	0	0	1	0	0
1995	112					7	5	5	4	0	2	0	0	0
1996	352						36	18	8	1	2	0	0	0
1997	372							18	22	0	7	2	1	0
1998	72								4	0	0	0	0	0
1999	221									15	7	4	3	0
2000	596										57	14	6	2
2001	412											39	13	4
2002	442												39	3

2.5.2 Results

Parameter estimates, with standard errors in parentheses, from fitting the models

(a) $(F_y, M, Sel_{a1,a2,a3})$ and (b) $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ to different subsets of the striped bass

data corresponding to designs where fish are tagged at age 3 years only, or at age 3 and 4

years, or at all 5 ages, are presented in Table 2.5. Estimates of standard errors obtained

with the program SURVIV are based on the estimated information matrix. Model $(F_y, M,$

$Sel_{a1,a2,a3}, \lambda)$ produces poor results with an unrealistically small estimate of M and large

estimates of F when one or two age classes are tagged . Model $(F_y, M, Sel_{a1,a2,a3})$ applied

to data from only the fish tagged at age 3 years produces estimates with poor precision.

For instance, the relative standard error (RSE) of fishing mortality rate in 1992 is 34%.

When this model is applied to data from fish tagged at both age 3 and age 4,

precision improves (e.g., $RSE(\hat{F}_{92}) = 19\%$). The parameter estimates from fitting model

$(F_y, M, Sel_{a1,a2,a3})$ to striped bass data when only fish tagged at age 3 are considered, and

when fish tagged at both age 3 and age 4 are considered, are quite similar (Table 2.5).

Given the relatively small sample sizes (numbers of fish tagged, Table 2.4), model $(F_y,$

$M, Sel_{a1,a2,a3})$ produces good results for the striped bass data. Compared with the results

when fish of all age classes are analyzed (Table 2.5), the parameter estimates obtained

under model $(F_y, M, Sel_{a1,a2,a3})$ are very similar, but the precision is lower when fish of

only age 3 years and age 4 years are analyzed. An interesting finding is that the estimate

of M decreases as fish of more age classes are tagged, suggesting an age-dependence in

M. This confirms results in Chapter 1 on age-dependence of M. If λ is estimated, results

are not reliable under all three designs which agrees with the indications of parameter

redundancy obtained from analyses of the information matrix in Section 2.3.

Table 2.5. Parameter estimates with standard errors in parentheses from fitting the models (a) (F_y, M, $Sel_{a1,a2,a3}$) and (b) (F_y, M, $Sel_{a1,a2,a3}$, λ) to subsets of the striped bass data created by using fish tagged at age 3 years, or fish tagged at both age 3 and 4 years, or fish of all age are considered.

Parameter	Tagged at age 3 years	Tagged at age 3 and 4 years	Tagged at all 5 ages
	Model (a)		
F(91)	0.308 (0.118)	0.229 (0.055)	0.234 (0.022)
F(92)	0.242 (0.085)	0.239 (0.046)	0.305 (0.020)
F(93)	0.178 (0.065)	0.165 (0.030)	0.247 (0.015)
F(94)	0.268 (0.087)	0.255 (0.041)	0.278 (0.015)
F(95)	0.313 (0.095)	0.306 (0.047)	0.356 (0.018)
F(96)	0.343 (0.105)	0.328 (0.052)	0.338 (0.017)
F(97)	0.458 (0.150)	0.310 (0.053)	0.376 (0.021)
F(98)	0.456 (0.153)	0.389 (0.069)	0.423 (0.025)
F(99)	0.436 (0.147)	0.234 (0.046)	0.355 (0.023)
F(00)	0.315 (0.121)	0.315 (0.056)	0.321 (0.018)
F(01)	0.270 (0.105)	0.239 (0.044)	0.236 (0.014)
F(02)	0.229 (0.095)	0.218 (0.039)	0.175 (0.010)
F(03)	0.145 (0.079)	0.063 (0.019)	0.065 (0.007)
M	0.398 (0.035)	0.368 (0.021)	0.256 (0.007)
Sel_3	0.637 (0.180)	0.727 (0.115)	0.517 (0.048)
Sel_4	0.645 (0.173)	0.851 (0.115)	0.750 (0.043)
Sel_5	0.969 (0.237)	1.000 (0.122)	0.994 (0.044)
	Model (b)		
F(91)	0.519 (0.216)	0.468 (0.134)	0.123 (0.050)
F(92)	0.467 (0.175)	0.516 (0.125)	0.161 (0.065)
F(93)	0.341 (0.127)	0.353 (0.079)	0.129 (0.051)
F(94)	0.509 (0.163)	0.523 (0.100)	0.145 (0.057)
F(95)	0.558 (0.160)	0.606 (0.106)	0.180 (0.071)
F(96)	0.583 (0.155)	0.666 (0.112)	0.166 (0.067)
F(97)	0.813 (0.216)	0.712 (0.119)	0.179 (0.073)
F(98)	1.000 (0.270)	1.000 (0.172)	0.189 (0.079)
F(99)	1.000 (0.295)	0.744 (0.146)	0.152 (0.063)
F(00)	0.996 (0.358)	1.000 (0.202)	0.140 (0.057)
F(01)	0.816 (0.365)	0.787 (0.194)	0.111 (0.044)
F(02)	0.662 (0.375)	0.672 (0.190)	0.087 (0.033)
F(03)	0.452 (0.368)	0.182 (0.072)	0.035 (0.013)
M	0.017 (0.129)	0.000 (0.089)	0.421 (0.060)
lambda	0.157 (0.038)	0.164 (0.026)	0.915 (0.364)
Sel_3	0.866 (0.161)	0.864 (0.105)	0.479 (0.045)
Sel_4	0.797 (0.159)	0.894 (0.091)	0.693 (0.041)
Sel_5	1.000 (0.209)	1.000 (0.105)	0.921 (0.041)

2.6 Discussion

We have proposed two important sampling designs for age-dependent tag return models for estimating fishing and natural mortality rates and selectivities: i) Tagging only age 1 fish; ii) Tagging both age 1 and age 2 fish, and compared them to tagging all age classes. The age-length key method is a commonly used approach to classify the age of tagged fish, and there could be substantial errors in determining the age of fish using this method. Converting size to age usually has the fewest errors for the age 1 and age 2 fish. These two sampling designs have the advantage of reducing classification errors and for some species such as red drum (*Sciaenops ocellatus*) and pollock (*Pollachius virens*) are easier to accomplish, with less harm to the fish and with lower cost, than designs that require aging and tagging fish from a large number of age classes (Latour et al. 2001, Neilson et al. 2003), given that the youngest age classes are usually caught in greatest numbers. In this chapter we assume that the age of individuals is correctly determined. Although in our sampling designs, tagging only age 1 and age 2 fish will reduce the measurement errors to some degree, this kind of measurement error may still exist. Incorporating the measurement errors into the models is an important and interesting topic for future research.

Some important assumptions are required by the models and theoretical analyses used here for the age-structured tag return data. They are: 1) the sample is representative of the target population; 2) age of individuals is correctly determined; 3) there is no tag loss; 4) tagging induced mortality is negligible; 5) the year of tag recovery is correctly tabulated; 6) all individuals behave independently; 7) all tagged fish of an identifiable age class have the same annual survival and recovery rates; 8) selectivity for each age class is

the same for different years; 9) natural mortality rate is constant over ages and years; 10) the tag reporting rate does not vary by age and year; and 11) tagging and release occur at the beginning of the year, and *Sel, F* and *M* are constant within each year. Any violation of these assumptions may invalidate the calculations and analyses carried out.

Sampling designs where only young animals are tagged are generally considered ineffective (Brownie et al. 1985; Anderson et al. 1985). However, with the instantaneous mortality rate parameterization, and assuming constant natural mortality, as in our model structure, estimation of young and adult survival is possible when only young are tagged, provided that the reporting rate is known. For studies where only young-of-the year are tagged, others have obtained identifiability of annual rates by imposing other constraints (e.g. Seber 1981; Freeman and Morgan 1992). Seber (1981) built models which assume that the reporting rate is constant over years and that the probability of survival depends on the age of the bird rather than on the calendar year for analyzing recovery data from birds banded as nestlings. Freeman and Morgan (1992) investigated models which assumed either a constant reporting rate or constant first-year survival or constant adult survival.

For the situation where λ is unknown, using methods of Catchpole et al. (2001) , we have found that model *(F_y, M, Sel$_{a1,a2,a3}$, λ)* has strong near-singularity problems when only age 1 fish are tagged, and moderate near-singularity problems when both age 1 and age 2 fish are tagged. So when λ must be estimated from the tag returns, we recommend tagging both age 1 and age 2 fish in order to obtain estimators with reasonable properties. But we recommend estimating λ from external sources (Pollock et al. 1991, 2001, and

2002; Hearn et al. 2003) whenever possible, because of the large increase in precision that is achieved.

These results were supported by Monte Carlo simulations to investigate the performance of models $(F_y, M, Sel_{a1,a2,a3}, \lambda)$ and $(F_y, M, Sel_{a1,a2,a3})$. For a given sample size and true parameter values we can use Monte Carlo simulations to determine which parameter estimates are poor. This also provides us important information to determine the sample size for designing a study. An area for further research is to use the condition number of the expected information matrix to determine the sample size needed for our study design.

In our striped bass example, some recovered fish were harvested and some were released alive. We have assumed that all the recovered fish are dead. This assumption causes upwardly biased estimates for fishing mortality rates. In Chapter 3 we consider using an estimate of the hooking mortality rate to correct this bias.

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Chapter 3

Tag Return Models for Catch-and-Release Fisheries

3.1 Introduction

In traditional tag return studies (e.g. Hoenig et al. 1998a, b), it is assumed that all caught fish are kept (harvested). In catch-and-release fisheries, only a fraction of the captured fish are harvested while the remainder are released alive. The goal is to provide fishing recreation, while conserving the stock. Catch-and-release fisheries have become very important to the management of overexploited recreational fish stocks. However, there has been little work done on how to estimate population demographic parameters (like fishing and natural mortality) for catch-and-release fisheries using tagging studies. Without these tagging studies on fish stocks subject to catch-and-release there will be no way to assess the effectiveness of restoration efforts.

For the released fish, there will be a probability of the tag being reported, which may possibly differ from the probability of the tag from harvested fish being reported. In some studies, the tag will be removed from the fish and then reported (the tag returned to the agency) while in other studies, the tag number will be recorded and reported to the agency without the tag being removed. There are advantages and disadvantages to both approaches. If the tag is removed and returned to the agency, there should be few errors in recording tag numbers. However, no additional data can be obtained on that fish as it is now unmarked. If the tag number is recorded and the fish released with the tag intact, then the chance of recording errors could be substantial. On the other hand, the fish is still marked and could be recaptured multiple times, thus providing additional information on

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survival. This can be viewed as a generalized type of Jolly-Seber model (Williams et al. 2002).

The method used to estimate the tag reporting rate may also affect the decision to remove the tag before releasing a fish. If a high reward tagging approach is used to estimate the regular tag reporting rate (Pollock et al. 2001), then we suspect that the high-reward tags would need to be removed and returned because agencies would require the tag in hand in order to pay the reward. On the other hand, if the angler survey method is used to estimate the regular tag reporting rate (Pollock et al. 1991), then tags could either be cut off or left on the fish provided the agent got to see the tags. In this chapter, we focus on the situation where the tag is removed on capture whether the fish is kept or released, as this approach has been used in several studies on Atlantic striped bass (*Morone saxatilis*).

Smith et al. (2000) presented a method of accounting for catch-and-release fishing in the estimation of total and fishing mortality. Their likelihood was based on finite recovery and survival rates, in which the survival rate for tags was represented as survival for fish with an adjustment for catch-and-release fishing. This adjustment involved parameters for the short-term mortality after release (or hooking mortality) and the tag reporting rate λ. Assuming known values for the instantaneous natural mortality (M=0.15) and for hooking mortality (0.09), an iterative process was used to obtain $\hat{\lambda}$ and to get estimates of fishing mortality and survival that accounted for catch-and-release fishing. We develop an alternative probability model and likelihood for the tag return data, and use the methodology developed to analyze data from a tagging study carried out by Maryland Department of Natural Resources.

3.2 Age-Independent Models

3.2.1 Model Structure

The key point in modeling the tag returns from catch-and-release fishing is to note that removing tags from fish that are caught-and-released leads to an additional force of mortality on the tags that is not necessarily experienced by the fish. We assume that tag returns are recorded separately for fish that are harvested, and for fish that are caught-and-released, and develop a generalization of the Hoenig et al. (1998a) instantaneous rates models for these data. We first consider the situation where tagged fish are assumed to be fully recruited and all rates can be considered age-independent.

We define the following parameters:

N_i is the number of adult fish tagged and released in year i $(i=1,2,...I.)$,

R_{ij} is the number of these N_i fish that are subsequently harvested and reported in year j,

for $j = i, i+1, i+2, ..., J$,

R_{ij}' is the number of these N_i fish that are caught, released (without a tag), and reported

in year j.

F_j is the instantaneous rate of fishing mortality on harvested fish in year j,

F_j' is the instantaneous rate of fishing mortality in year j on the tags taken from fish

that are caught and released,

M is the instantaneous rate of natural mortality,

P_{ij} is the probability that a fish tagged and released in year i, is harvested and

its tag reported in year j,

P_{ij}' is the probability that a fish tagged and released in year i, is caught and released, and its tag reported, in year j,

S_j is the conditional survival rate in year j for tags on fish alive at the beginning of year j,

λ is the tag-reporting rate (the probability that the tag is reported), given that a tagged fish is harvested,

λ' is the tag-reporting rate (the probability that the tag is reported), given that a tagged fish is recaptured and released alive.

To avoid possible problems of non-identifiability (Chapter 1), we assume that the tag reporting rates λ and λ' are equal and constant over years. Similarly, in the basic model, the natural mortality rate M is assumed to be constant over years. Motivated by observations from fishery biologists, we also consider models where M is year-dependent to a limited extent. As noted above all parameters are age-independent, though extensions to multi-age models are presented in section 3.3.

The expected number of tag returns from fish tagged and released in year i, then harvested in year j, is:

$$E[R_{ij}] = N_i \, P_{ij} ,$$

where

$$P_{ij} = \begin{cases} \left(\prod\limits_{v=i}^{j-1} S_v \right) (1-S_j) \dfrac{F_j}{F_j + F_j{}' + M} \lambda & (when \ j > i) \\[4ex] (1-S_j) \dfrac{F_j}{F_j + F_j{}' + M} \lambda & (when \ j = i) \end{cases} \qquad (1)$$

$$S_j = \exp(-F_j - F_j{}' - M).$$

The expected number of tag returns from fish tagged and released in year i, then recaptured and released (without a tag) in year j, is:

$$E[R_{ij}{}'] = N_i \, P_{ij}{}',$$

where

$$P_{ij}{}' = \begin{cases} \left(\prod\limits_{v=i}^{j-1} S_v \right) (1-S_j) \dfrac{F_j{}'}{F_j + F_j{}' + M} \lambda' & (when \ j > i) \\[4ex] (1-S_j) \dfrac{F_j{}'}{F_j + F_j{}' + M} \lambda' & (when \ j = i) \end{cases} \qquad (2)$$

$$S_j = \exp(-F_j - F_j{}' - M).$$

For the batch of N_i fish, tagged and released in year i, assuming independent fates, the tag returns in subsequent years, R_{ij} and $R_{ij}{}'$, follow a multinomial distribution. Therefore the full likelihood function is product multinomial following Hoenig et al. (1998a):

$$L = \prod_{i=1}^{I} \binom{N_i}{R_{ii}, R_{ii+1}, \dots R_{iJ}, R_{ii}', R_{ii+1}', \dots R_{iJ}', N_i - \sum_{j=i}^{J}(R_{ij} + R_{ij}')} \times$$

$$\left(\prod_{j=i}^{J} P_{ij}^{R_{ij}} P_{ij}'^{R_{ij}'} \right) \left(1 - \sum_{v=i}^{J}(P_{iv} + P_{iv}') \right)^{N_i - \sum_{v=i}^{J}(R_{iv} + R_{iv}')} . \quad (3)$$

Maximum likelihood estimators of the instantaneous rates F_j , F_j' ($j=1,2,...,J$), and M, and the tag reporting rates λ and λ' can be obtained from this likelihood using software such as program SURVIV (White 1983). If reliable values of the tag reporting rates λ and λ' are available from other sources such as a reward tagging study, then these parameters are treated as known, and estimates are obtained for F_j , F_j' ($j=1,2,...,J$) , and M. If data for estimating the reporting rate are available (e.g. from a reward tagging study), then an additional component can be included in the likelihood and all parameters, including λ and λ' can be estimated. Estimates of the instantaneous rates are then used to compute the total annual mortality rates for fish.

From (2), the total instantaneous mortality for tags, and the annual survival rate for tags, in year j, are:

$$Z_{j,tags} = F_j + F_j' + M$$

$$S_{j,tags} = \exp(-F_j - F_j' - M).$$

Following the approach in Brooks et al. (1998), the total annual exploitation rate for tags, $U_{j,tags}$, has two components depending upon whether the fish is kept (*i.e*, harvested) or released. Thus

$$U_{j,tags} = U_{j,tags}(kept) + U_{j,tags}(rels), \text{ where}$$

$$U_{j,tags}(kept) = \frac{F_j}{F_j + F_j' + M}\left[1 - \exp\{-(F_j + F_j' + M)\}\right],$$

and

$$U_{j,tags}(rels) = \frac{F_j'}{F_j + F_j' + M}\left[1 - \exp\{-(F_j + F_j' + M)\}\right].$$

To obtain the corresponding rates for fish, we must know whether fish that are caught and released are subject to hooking mortality δ (the mortality immediately following release due to hooking and other handling stresses). To account for hooking mortality on the fish, we let $\delta F'$ represent the instantaneous force of mortality on catch-and-release fish, where $0 \leq \delta \leq 1$, and the annual survival rate and total instantaneous mortality of fish are then:

$$S_{j, \text{ fish}} = \exp\{-(F_j + \delta F_j' + M)\}$$

$$Z_{j, \text{ fish}} = F_j + \delta F_j' + M.$$

If all the released fish die after release because of hooking mortality, then $\delta = 1$, and survival and mortality rates for fish are the same as for tags:

$$S_{j, \text{ fish}} = \exp\{-(F_j + F_j' + M)\}$$

$$Z_{j, \text{ fish}} = F_j + F_j' + M.$$

At the other extreme, assuming none of the released fish die, then $\delta = 0$, and

$$S_{j, \text{ fish}} = \exp\{-(F_j + M)\}$$

$$Z_{j, \text{ fish}} = F_j + M.$$

Diodati and Richards (1996) conducted an experiment to estimate hooking mortality on striped bass. They found that many factors influence the hooking mortality,

including hook penetration, gear type, and angler experiences. The water temperatures in their study did not exceed $25°C$ and dissolved oxygen was above critical levels, so that they did not find significant effects of temperature on the hooking mortality. They reported that the estimated hooking mortality over about 2 months for the entire experimental group was 9% (SE =2%). This estimate of hooking mortality, $\hat{\delta}'$, is a finite rate, but it can be used as an approximation to the hooking mortality rate, δ, in our instantaneous rates formulation. The proof for this approximation is as follows.

The annual exploitation rate for the fish, $U_{fish}(rels)$, should be approximately equal to $\delta'U_{tags}(rels)$, where δ' is the short-term finite hooking mortality rate. So we have,

$$\delta'U_{tags}(rels) \simeq U_{fish}(rels) \Rightarrow$$
$$\delta'\frac{F'}{F+F'+M}\left(1-\exp(-F-F'-M)\right) \simeq \frac{\delta F'}{F+\delta F'+M}\left(1-\exp(-F-\delta F'-M)\right).$$

Making use of the approximation, $1-\exp(x) \simeq x$ if x is small, we get $\delta'F' \simeq \delta F' \Rightarrow \delta' \simeq \delta$. We therefore take $\hat{\delta}$ =0.09 to obtain adjusted total mortality rates and annual survival rates for the striped bass data.

3.2.2 Example

3.2.2.1 Study Description

Maryland Department of Natural Resources (MDNR) carried out a tag-return study from 1991 to 2002. Over 24533 striped bass were marked with an internal anchor tag and released in the upper Chesapeake Bay. An otolith-based age-length key method was used to identify the ages of the tagged fish (Secor et al. 1995), resulting in seven age groups (from age 2 years to age 8+ years). Fishery biologists generally consider striped

bass of ages 6 years and greater as fully recruited. Of the total of 24533 tagged striped bass, 12901 were classified as age 6 years and greater, and the age-independent models developed in section 3.2.1 were applied to the data from these fish. There were 2770 (21%) recaptures, with tags cut off before reporting the tag number to the U.S. Fish and Wildlife Service. 1874 (68%) of the 2770 reported recaptures were harvested (killed) and 896 (32%) were released alive after removing the tags.

A summary of the release and tag-recovery data is presented in Appendix A. A series of models, with different assumptions about year-specificity of F, F', and M was fit to the data. In describing the parameters used in different models, a parameter with a subscript y indicates that the parameter is year specific, and no subscript means that the parameter is constant. If the parameter list does not include λ and λ' then these are assumed known. In this chapter, we assume a complete mixing fishery in our analysis to avoid parameter redundancy problems.

A bacterial disease known as mycobacteriosis, caused by bacteria in the genus Mycobacterium, appeared in Chesapeake Bay striped bass in the late 1990s (John Hoenig personal communication). Symptoms include external lesions (open sores on the skin) and internal lesions that look like lumps in the pancreas and kidney. There are about a dozen species of Mycobacteria in the striped bass and it is not known which species cause the disease or diseases. The prevalence of mycobacteriosis in striped bass may be 60% or even higher in the Rappahannock River in late summer (John Hoenig personal communication). To allow for change in natural mortality due to this disease, we fit models with a limited degree of year-specificity in M, represented as $(F_y, F'_y, M_{early}, M_{later})$, and $(F_y, F'_y, M_{early}, M_{later}, \lambda, \lambda')$, where M_{early} and

M_{later} represent the natural mortality rates in years before and after the disease started to affect survival. Harvest regulations were relaxed from 1995 (Richards and Rago 1999). We also fit reduced models with F and F' constant before, and after 1995, to investigate the effects of the change of harvest regulations. For models with the assumption that tag reporting rates are known, we assume $\lambda=\lambda'=0.43$ (based on earlier reward tagging studies. Wells, B.K personal communication; Smith et al. 2000), though additional models were fit to examine sensitivity to this assumption.

Results for models with the tag reporting rates assumed equal to 0.43 are discussed first. We use Akaike's information criterion (AIC) to choose between models because this method is able to compare multiple nested and nonnested models. AIC is a statistic that deals with the tradeoff between reduced bias associated with more parameters and smaller estimator variance associated with fewer parameters (Burnham and Anderson 2002). AIC can be computed as:

$$AIC = -2\log\left[l(\hat{\underline{\theta}}|y)\right] + 2k,$$

where $\log\left[l(\hat{\underline{\theta}}|y)\right]$ is the log likelihood function evaluated at the MLEs $\hat{\underline{\theta}}$ given the data y, and k is the number of parameters. The model with the minimum AIC value is selected.

Overdispersion in the data can result due to a lack of independence of capture and survival events, as fish travel in schools. If overdispersion is the reason for lack of fit in the models, a quasilikehood approach is recommended (Burham et al. 1987; Lebreton et al. 1992; Burnham and Anderson, 2002) to deal with the problem. The corresponding criterion is QAIC, defined as,

$$QAIC = -2\log[l(\underline{\hat{\theta}}|y)]/\hat{c} + 2k,$$

where $\hat{c}$ is a variance inflation factor that can be calculated by,

$$\hat{c} = x^2/df,$$

where x^2 and df correspond to the goodness-of-fit test of the most general model in the model set.

3.2.2.2 Results

Results of *AIC*, ΔAIC (change in AIC compared to the lowest AIC value), QAIC, and $\Delta QAIC$ (change of QAIC compared to the lowest QAIC value) of models where we assume that tag reporting rates are known and equal to 0.43 are displayed in Table 3.1. Since we do not know exactly when the disease effects first occurred, we tried a series of models, assuming the disease effects began in 1997, or 1998, or 1999, or 2000. Based on AIC and QAIC values (Table 3.1), the models that assume an increase in natural mortality beginning in 1999 or 2000 are the best ones (models 1, 2, 8). Note that the *AIC* value (1793.26) for model $(F_y, F'_y, M_{91-99}, M_{00-03})$ (model 1) is much smaller than for model (F_y, F'_y, M) (model 9) (1867.78) (Table 3.1), and a likelihood ratio test for the two models results in $\chi^2 = 215.8$ with 1 df, providing strong evidence that the natural mortality rate changed over years.

Table 3.1. AIC values for models with M constant over all years or within two periods, where we assume $\lambda = \lambda' = 0.43$.

Model	K	AIC	ΔAIC	QAIC	$\Delta QAIC$
1	28	1793.26	0.00	1601.60	0.74
2	17	1795.16	1.90	1600.87	0.00
3	17	1807.82	14.56	1612.13	11.26
4	16	1834.46	41.20	1635.61	34.74
5	16	1821.66	28.40	1624.22	23.36
6	28	1819.57	26.31	1625.01	24.14
7	28	1840.08	46.39	1643.26	42.39
8	28	1794.18	0.92	1602.42	1.56
9	27	1867.78	74.52	1667.68	66.82

Note: $\hat{c} = 1.124$, based on model $(F_y, F'_y, M_{91-99}, M_{00-03})$, k is the number of parameters in the model.

Model:
1: $(F_y, F'_y, M_{91-99}, M_{00-03})$
2: $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03})$
3: $(F_y, F'_{91-94}, F'_{95-03}, M_{91-99}, M_{00-03})$
4: $(F, F'_y, M_{91-99}, M_{00-03})$
5: $(F_y, F', M_{91-99}, M_{00-03})$
6: $(F_y, F'_y, M_{91-96}, M_{97-03})$
7: $(F_y, F'_y, M_{91-97}, M_{98-03})$
8: $(F_y, F'_y, M_{91-98}, M_{99-03})$
9: (F_y, F'_y, M)

To assess the impact of changes in fishing regulations, we next consider the reduced model $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03})$, where fishing mortality on harvested fish, F, is constant from 1991 to 1994 and constant from 1995 to 2003. Based on the AIC values and on a likelihood ratio test between this reduced model and the more general model $(F_y, F'_y, M_{91-99}, M_{00-03})$ which results in $\chi^2 = 23.9$ with 11 degree of freedom, the

more general model is preferred. This suggests that variation in the fishing mortality on harvested fish is not explained entirely by a change in the regulation.

Table 3.2. Parameter estimates with standard errors in parentheses from fitting two-period M models (a) $(F_y, F'_y, M_{91-99}, M_{00-03})$ and (b) $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03})$ to adult (age 6+ years) striped bass data.

Parameter	(a)		(b)	
F(91)	0.129	(0.019)	0.163	(0.009)
F(92)	0.175	(0.018)	0.163	(0.009)
F(93)	0.175	(0.016)	0.163	(0.009)
F(94)	0.159	(0.014)	0.163	(0.009)
F(95)	0.236	(0.017)	0.241	(0.009)
F(96)	0.206	(0.015)	0.241	(0.009)
F(97)	0.271	(0.021)	0.241	(0.009)
F(98)	0.297	(0.025)	0.241	(0.009)
F(99)	0.275	(0.026)	0.241	(0.009)
F(00)	0.213	(0.019)	0.241	(0.009)
F(01)	0.269	(0.026)	0.241	(0.009)
F(02)	0.204	(0.022)	0.241	(0.009)
F(03)	0.182	(0.037)	0.241	(0.009)
F'(91)	0.124	(0.019)	0.125	(0.019)
F'(92)	0.170	(0.018)	0.170	(0.018)
F'(93)	0.111	(0.012)	0.112	(0.012)
F'(94)	0.123	(0.012)	0.122	(0.012)
F'(95)	0.103	(0.011)	0.106	(0.011)
F'(96)	0.121	(0.012)	0.119	(0.011)
F'(97)	0.082	(0.011)	0.077	(0.010)
F'(98)	0.081	(0.012)	0.078	(0.012)
F'(99)	0.070	(0.012)	0.065	(0.011)
F'(00)	0.122	(0.014)	0.119	(0.013)
F'(01)	0.092	(0.013)	0.095	(0.013)
F'(02)	0.065	(0.010)	0.078	(0.011)
F'(03)	0.040	(0.013)	0.048	(0.015)
M_{91-99}	0.166	(0.009)	0.160	(0.009)
M_{00-03}	0.635	(0.058)	0.713	(0.038)

Parameter estimates and their standard errors from fitting the model $(F_y, F'_y, M_{91-99}, M_{00-03})$ (model 1) and the reduced model $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03})$ (model 2) are presented in Table 3.2. The estimates of standard errors,

produced by program SURVIV, are based on the estimated information matrix. Estimates obtained under model $(F_y, F'_y, M_{91-99}, M_{00-03})$ have good precision. As expected, the natural mortality rate in later years (0.64, SE=0.06) is higher than in early years (0.17, SE=0.01), also, the estimate $\hat{M}_{91-99} = 0.17$ agrees well with the value of 0.15 assumed by Smith et al. (2000) for a comparable period. Estimates under model $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03})$ are precise, with standard errors for fishing mortality rates on harvested fish noticeably smaller than those from model $(F_y, F'_y, M_{91-99}, M_{00-03})$. The estimate of the mortality rate on harvested fish for later years (from 1995 to 2003) is higher than that for earlier years (from 1991 to 1994), suggesting an increase in the fishing mortality rate on harvested fish after the relaxation of fishing regulations (see also Smith et al. 2000)..

Other reduced two-period M models were also fitted to the adult striped bass data, including models $(F, F'_y, M_{91-99}, M_{00-03})$ ($\Delta AIC = 41.20$), and $(F_y, F', M_{91-99}, M_{00-03})$ ($\Delta AIC = 28.40$), which assume, respectively, that fishing mortality on harvested fish is constant, and that fishing mortality on tags of fish released alive is constant. According to AIC and QAIC values, neither of these models is better than model $(F_y, F'_y, M_{91-99}, M_{00-03})$ or model $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03})$, suggesting these mortality rates did vary over years. We also investigated model $(F_y, F'_{91-94}, F'_{95-03}, M_{91-99}, M_{00-03})$ ($\Delta AIC = 14.56$), but saw no reason to consider this model further.

All of the results presented so far are based on the assumption that tag reporting rates are constant and equal to 0.43. Assuming a known value for λ and λ' has the advantage of avoiding serious problems related to parameter redundancy as demonstrated in Chapter 1, but at the cost of introducing possibly substantial biases in estimates. We address this problem in two ways, first by examining results from models where λ and λ' are estimated, and by carrying out sensitivity analyses to see the impact of different values of λ and λ' on estimates.

Estimates, with their standard errors in parentheses, from fitting the model $(F_y, F'_y, M_{91-99}, M_{00-03}, \lambda, \lambda')$ and the reduced model $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03}, \lambda, \lambda')$ to the adult striped bass data are displayed in Table 3.3. We assume that the change in natural mortality begins in the year 2000, and that F is constant from 1991 to 1994 and constant from 1995 to 2003 in the reduced model. Estimates under model $(F_y, F'_y, M_{91-99}, M_{00-03}, \lambda, \lambda')$ have poor precision with relatively high fishing mortality rate estimates and relatively low natural mortality rate estimates. In addition, estimates are sensitive to the initial values supplied to the iterative optimization process in SURVIV. Estimates under model $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03}, \lambda, \lambda')$ have large standard errors, estimates of λ, λ' and M are suspiciously high and estimates of F and F' are suspiciously low. The poor results of the models where λ and λ' are estimated are related to the problems of over-parameterization noted in Chapter 1, and to the small sample sizes for the striped bass data. The poor performance of the models when λ and λ' are estimated also emphasizes the importance of obtaining good estimates of λ and λ' using external sources (Pollock et al. 1991, 2001, and 2002; Hearn et al. 2003).

It is worth noting that estimates of λ and λ' under model $(F_y, F'_y, M_{91-99},$

$M_{00-03}, \lambda, \lambda')$ are reasonably close to the value of 0.43, whereas estimates under model

$(F_{91-94,} F_{95-03}, F'_y, M_{91-99}, M_{00-03}, \lambda, \lambda')$ are unrealistic.

Table 3.3. Parameter estimates, with standard errors in parentheses, for the adult (age 6+

years) striped bass data, for two-period M models (a) $(F_y, F'_y, M_{91-99}, M_{00-03}, \lambda, \lambda')$,

and (b) $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03}, \lambda, \lambda')$, in which reporting rates are estimated.

Parameter	(a)		(b)	
F(91)	0.182	(0.096)	0.083	(0.128)
F(92)	0.234	(0.124)	0.083	(0.128)
F(93)	0.233	(0.127)	0.083	(0.128)
F(94)	0.207	(0.108)	0.083	(0.128)
F(95)	0.318	(0.162)	0.120	(0.186)
F(96)	0.280	(0.144)	0.120	(0.186)
F(97)	0.362	(0.186)	0.120	(0.186)
F(98)	0.405	(0.212)	0.120	(0.186)
F(99)	0.388	(0.208)	0.120	(0.186)
F(00)	0.291	(0.154)	0.120	(0.186)
F(01)	0.363	(0.191)	0.120	(0.186)
F(02)	0.269	(0.131)	0.120	(0.186)
F(03)	0.221	(0.088)	0.120	(0.186)
F'(91)	0.127	(0.181)	0.064	(0.137)
F'(92)	0.176	(0.255)	0.086	(0.186)
F'(93)	0.115	(0.167)	0.056	(0.121)
F'(94)	0.122	(0.176)	0.063	(0.134)
F'(95)	0.108	(0.154)	0.054	(0.115)
F'(96)	0.121	(0.174)	0.059	(0.127)
F'(97)	0.080	(0.116)	0.038	(0.082)
F'(98)	0.084	(0.122)	0.038	(0.081)
F'(99)	0.072	(0.104)	0.031	(0.067)
F'(00)	0.123	(0.178)	0.059	(0.126)
F'(01)	0.092	(0.133)	0.047	(0.101)
F'(02)	0.070	(0.099)	0.039	(0.084)
F'(03)	0.036	(0.047)	0.024	(0.052)
M_{91-99}	0.092	(0.303)	0.318	(0.271)
M_{00-03}	0.534	(0.324)	0.877	(0.275)
λ	0.318	(0.165)	0.859	(1.326)
λ'	0.420	(0.603)	0.863	(1.845)

For several models, we also performed sensitivity analysis of the effects of

different values of tag reporting rates, λ and λ', on the parameter estimates. In general, as

the values of λ and λ' increase the estimates of fishing mortality rates on harvested fish and on tags of fish released alive decrease, and the estimates of natural mortality rate, M, increase. For example, under model (F_y, F'_y, M), we obtain $\hat{F}_{91} = 0.18$ (SE=0.03), $\hat{M} = 0.05$ (SE=0.01) for $\lambda = \lambda' = 0.30$, and $\hat{F}_{91} = 0.11$ (SE=0.02), $\hat{M} = 0.24$ (SE=0.01) for $\lambda = \lambda' = 0.50$. So it is essential to obtain accurate information about λ and λ' to provide unbiased parameter estimates. If we are not certain about the values of λ and λ' we should try different, plausible values of λ and λ', and obtain a range of the estimates of other parameters of interest.

Difficulties associated with estimating λ and λ' also raise questions about the conclusion that natural mortality has increased. For example, is a model with constant M and year-dependent λ and λ' equally plausible? This led to fitting a series of models $(F_y, F'_y, M_{91-99}, M_{00-03})$ in which the reporting rates are constant from 1991 to 1999 ($\lambda_{91-99} = \lambda'_{91-99}$) and constant from 2000 to 2003 ($\lambda_{00-03} = \lambda'_{00-03}$). Results (Figure 3.1) show that if we keep $\lambda_{91-99} = \lambda'_{91-99} = 0.43$, and allow λ_{00-03} and λ'_{00-03} to decrease, the estimate of M_{91-99} is stable and the estimate of M_{00-03} decreases, and approaches the value of $\hat{M}_{91-99}$. Eventually, when $\lambda_{00-03} = \lambda'_{00-03} = 0.18$ the estimates of M_{91-99} and M_{00-03} are approximately equal with a value 0.18. So an alternative to the conclusion of an increase of M in later years is that there was a decrease of λ and λ' in later years with no change in M. We can not be certain which interpretation is correct unless we have accurate information about λ and λ'. We suspect that the alternative explanation is not correct because $\lambda_{00-03} = \lambda'_{00-03} = 0.18$ is too low in practice, and because fishery biologists have seen evidence of disease beginning in the late 1990's.

Figure 3.1. Sensitivity analysis of the effects of different values of λ and λ' on the estimates of M for 1991-1999 (early years) and 2000-2003 (late years).
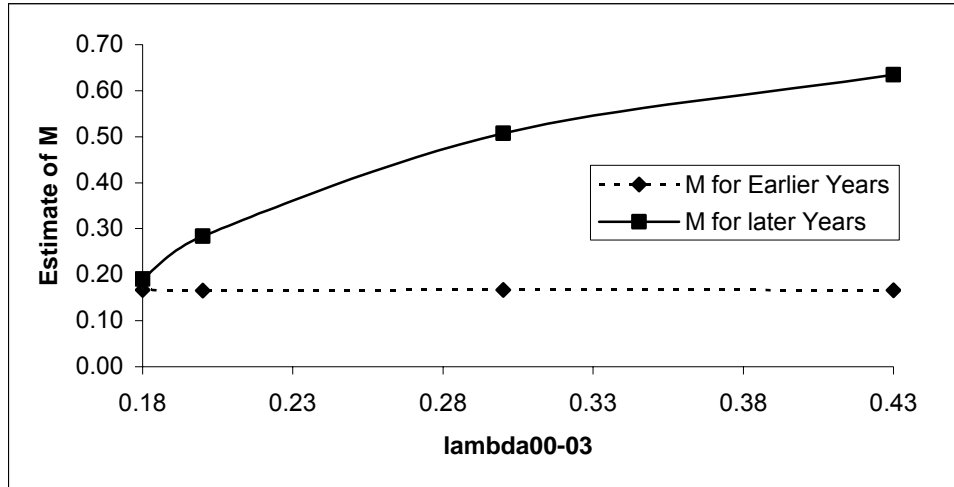
Note: we assume that $\lambda_{00-03} = \lambda'_{00-03}$. We keep $\lambda_{91-99} = \lambda'_{91-99} = 0.43$.

Estimates obtained under model $(F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03})$ were used to calculate total mortality rates ($\hat{Z}_{fish}$) and annual survival rates ($\hat{S}_{fish}$) for fish. Hooking mortality was accounted for as explained in Section 3.2.1 and assuming $\delta = 0.09$. Estimates of total mortality rates and annual survival rates for tags and fish are presented in Table 3.4. $\hat{Z}_{fish}$ increases and $\hat{S}_{fish}$ decreases after 1995, reflecting the effects of relaxation of harvest regulations on the mortality rate and annual survival rate of fish. $\hat{S}_{fish}$ is bigger than $\hat{S}_{tag}$, reflecting additional survival of the fish released alive after experiencing hooking mortality. We note that our estimates $\hat{S}_{fish}$ and $\hat{S}_{tag}$ are similar to those obtained by Smith et al. (2000) for a comparable period.

We can use delta method to compute the variances of these estimators. For example, to compute the variance of $\hat{S}_{fish}$, we can let

$$\hat{S}_{fish} = \exp\left(-(F + \delta F' + M)\right) = f(\theta),$$

where θ is a vector of parameters F, F', M, and δ. We can obtain the estimated covariance matrix for $\hat{F}$, $\hat{F}'$ and $\hat{M}$ from SURVIV. We assume that hooking mortality, δ, is estimated independently of the other three parameters. So we are able to obtain the covariance matrix for θ, $\Sigma(\theta)$. According to delta method, the estimates of variance of $\hat{S}_{fish}$, $V(\hat{S}_{fish})$, can be computed as,

$$V(\hat{S}_{fish}) = \left(\frac{\partial f(\theta)}{\partial \theta}\right)^T \Sigma(\theta) \frac{\partial f(\theta)}{\partial \theta},$$

where $\dfrac{\partial f(\theta)}{\partial \theta}$ is the vector of first derivatives:

$$\frac{\partial f(\theta)}{\partial \theta} = [-e^{-F-\delta F'-M}, -\delta e^{-F-\delta F'-M}, -F' e^{-F-\delta F'-M}, -e^{-F-\delta F'-M}]^T.$$

Table 3.4. Total mortality on tags ($\hat{Z}_{tag}$) and fish ($\hat{Z}_{fish}$), and survival rates for tags ($\hat{S}_{tag}$) and for fish ($\hat{S}_{fish}$) based on the estimates from model ($F_{91-94}, F_{95-03}, F'_y, M_{91-99}, M_{00-03}$) where we assume that $\lambda = \lambda' = 0.43$, and $\delta = 0.09$.

Year	$\hat{Z}_{tag}$	$\hat{Z}_{fish}$	$\hat{S}_{tag}$	$\hat{S}_{fish}$
1991	0.45	0.34	0.64	0.71
1992	0.50	0.34	0.61	0.71
1993	0.44	0.34	0.64	0.71
1994	0.45	0.34	0.64	0.71
1995	0.51	0.42	0.60	0.66
1996	0.53	0.42	0.59	0.66
1997	0.48	0.41	0.62	0.66
1998	0.49	0.41	0.62	0.66
1999	0.47	0.41	0.62	0.66
2000	1.00	0.89	0.37	0.41
2001	0.97	0.88	0.38	0.41
2002	0.95	0.88	0.39	0.41
2003	0.92	0.88	0.40	0.41

3.3 Age-Dependent Models

3.3.1 Model Structure

In chapter 1 we presented a likelihood for data from traditional multiple age tagging studies, where all the recaptured fish were harvested. Following the same spirit, here we present a likelihood for data from catch-and-release multiple age tagging studies. Let N_{ik} be the number of fish tagged at age k ($k=1, 2, ..., K$) and released in year i ($i=1, 2, ..., I$). Let R_{ijk} be the number of these N_{ik} fish that are subsequently harvested and reported in year j, and R_{ijk}' be the number of these N_{ik} fish that are caught, released (without a tag), and reported in year j, for $j = i, i+1, i+2, ..., J$. We assume that the components of fishing mortality on tags attached to fish of age k in year j are:

$$F_{jk} = Sel_k F_j, \text{ and}$$

$$F_{jk}' = Sel_k F_j',$$

where F_j is the instantaneous rate of fishing mortality for fully recruited fish that are harvested, F_j' is the instantaneous rate of fishing mortality on the tags for fully recruited fish that are released alive, and Sel_k is the selectivity coefficient for age k fish. Selectivity is assumed to be constant over years for each age, and is assumed to be 1 for fish of age K_c and greater ($Sel_k \equiv 1 \ for \ k \geq k_c$).

Other parameters are defined as:

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

P_{ijk}' is the probability that a fish tagged at age k and released in year i, is recaptured and released, and its tag removed and reported, in year j,

S_{ijk} is the conditional survival rate in year j for fish tagged at age k in year i, and alive, still carrying the tag, at the beginning of year j,

M is the instantaneous natural mortality rate,

λ is the tag-reporting rate (the probability that the tag is reported), given that a tagged fish is harvested,

λ' is the tag-reporting rate (the probability that the tag is reported), given that a tagged fish is recaptured and released alive.

We assume that the tag reporting rates λ and λ' are constant over years and ages. In the basic model, we assume that the natural mortality rate M is constant over ages and

years. We also investigate models where M is year-and/or age-dependent, but only to a limited extent in order to avoid parameter redundancy problems (Chapter 1).

The expected number of tag returns from fish tagged at age k and released in year i, then harvested in year j, is:

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

where

$$P_{ijk} = \begin{cases} \left(\displaystyle\prod_{v=i}^{j-1} S_{ivk}\right)(1-S_{ijk})\dfrac{F_j\, Sel_{k+j-i}}{(F_j{'}+F_j)\, Sel_{k+j-i}+M}\,\lambda & (when\ j>i) \\[4ex] (1-S_{ijk})\dfrac{F_j\, Sel_k}{(F_j{'}+F_j)\, Sel_k+M}\,\lambda & (when\ j=i) \end{cases}$$

$$S_{ijk} = \exp[-(F_j+F_j{'})Sel_{k+j-i}-M].$$

The expected number of tag returns from fish tagged at age *k* and released in year i, then recaptured and released (without a tag) in year j, is:

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

where

$$P_{ijk}{'} = \begin{cases} \left(\displaystyle\prod_{v=i}^{j-1} S_{ivk}\right)(1-S_{ijk})\dfrac{F_j{'}\, Sel_{k+j-i}}{(F_j{'}+F_j)\, Sel_{k+j-i}+M}\,\lambda{'} & (when\ j>i) \\[4ex] (1-S_{ijk})\dfrac{F_j{'}\, Sel_k}{(F_j{'}+F_j)\, Sel_k+M}\,\lambda{'} & (when\ j=i) \end{cases}$$

$$S_{ijk} = \exp[-(F_j+F_j{'})Sel_{k+j-i}-M].$$

For those N_{ik} fish that are tagged at age k and released in year i, the tag returns in subsequent years, R_{ijk} and R_{ijk}', follow a multinomial distribution. The full likelihood function is product multinomial:

$$L = \prod_{k=1}^{K}\prod_{i=1}^{I}\binom{N_{ik}}{R_{iik},R_{ii+1k},...,R_{iJk},R_{iik}',R_{ii+1k}',...,R_{iJk}',N_{ik}-\sum_{j=i}^{J}(R_{ijk}+R_{ijk}')} \times$$

$$\left(\prod_{j=i}^{J}P_{ijk}^{R_{ijk}}P_{ijk}'^{R_{ijk}'}\right)\left(1-\sum_{v=i}^{J}(P_{ivk}+P_{ivk}')\right)^{N_{ik}-\sum_{v=i}^{J}(R_{ivk}+R_{ivk}')}.$$

We use maximum likelihood to estimate F_j, F_j' $(j=1, 2, ..., J)$, M, selectivities Sel_k $(k=1,..., K_c)$, and the tag reporting rates λ and λ'. If the tag reporting rates λ and λ' are known, estimates are obtained for F_j, F_j' $(j=1, 2, ..., J)$, M, and selectivities Sel_k $(k=1, ..., K_c)$. To address questions of biological interest while avoiding non-identifiability problems (Chapter 1), models in which M has a limited degree of age- and/or year-dependence are also examined.

3.3.2 Example

3.3.2.1 Study Description

We use the Maryland striped bass data (Appendix A) to illustrate the analysis of tag-return data from an age-dependent catch-and-release study. Of the total 24533 marked striped bass released in the upper Chesapeake Bay, 24356 were classified as age 3 years and greater, using the age-length method. We only analyze the data for striped

bass marked at age 3 years and greater, because the sample sizes for those marked at age 2 years are too small. From those 24356 striped bass marked at age 3 years and greater, a total of 4593 tags were returned to fishery agencies. Of those 4593 recaptured and reported striped bass, 2960 (64%) were harvested (killed) and 1633 (36%) were released alive after the tag was removed.

Striped bass of age 6 years and older are considered to be fully recruited. Age effects on fishing mortality on harvested fish, F, and on tags of fish, F', that are caught and released, are incorporated through selectivity. Sel3, Sel4, and Sel5 represent the selectivity coefficients for striped bass of age 3, 4 and 5 years respectively. Selectivity is assumed to be 1 for age 6 years and older. To analyze the Maryland striped bass data for all fish tagged at age 3 years and greater, we investigate a series of models with different assumptions about the natural mortality rate, M. We consider the basic model $(F_y, F'_y, M, Sel_3, Sel_4, Sel_5)$ with F and F' age-dependent through selectivity, M constant over years and ages, and λ and λ' assumed equal to 0.43. We also fit the corresponding model $(F_y, F'_y, M, Sel_3, Sel_4, Sel_5, \lambda, \lambda')$ where λ and λ' are estimated.

To investigate the assumption that natural mortality is constant over ages we fitted model $(F_y, F'_y, M_Y, M_A, Sel_3, Sel_4, Sel_5)$ where we assume that young (Y) fish of age 3, 4 and 5 years have a common natural mortality rate, different from that of adult (A) fish of 6 years and greater. We also fitted model $(F_y, F'_y, M_3, M_4, M_5, M_A, Sel_3, Sel_4, Sel_5)$ that allows fish of age 3, 4, and 5 years to each have a different natural mortality rate. The corresponding models with λ and λ' estimated were also investigated.

It is of special interest to investigate models that allow the natural mortality rate to differ with time because of disease effects, as mentioned in section 3.2. Due to concerns

about parameter redundancy problems (Chapter 1), we assume that natural mortality was constant in the years before the disease effects occurred and constant after the disease effects began. Finally, reduced models that reflect the effects of the relaxation of fishing regulations on fishing mortality are also investigated. AIC criteria, which deal with the tradeoff between reduced bias and smaller estimator variance, are used for model selection.

3.3.2.2 Results

All models with tag reporting rates fixed at $\lambda = \lambda'=0.43$ produce parameter estimates with high precision. AIC and QAIC values for models where we assume λ and λ' are known are presented in Table 3.5. According to the AIC and QAIC values, the model $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ where we assume natural mortality rate, M, is both age- and year-specific, and the reduced model $(F_{91-94,} F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ where we assume that F is constant from 1991 to 1994 and constant from 1995 to 2003 are the best. These models assume that M is different for two age groups, young (from age 3 years to age 5 years) and adult (from age 6 years and greater), and for two time periods, from year 1991 to 1998 and from year 1999 to 2003. In combination, we have four different natural mortality rates to estimate. Note that the subscript Y_91-98 indicates a rate for young fish during year 1991 to 1998, subscript A_91-98 refers to adult fish during year 1991 to 1998, and so on.

Table 3.5. AIC values for models with F and F' age-dependent through selectivity, M constant or with some age- and/or year- specificity, and assuming $\lambda = \lambda' = 0.43$.

Model	K	AIC	ΔAIC	QAIC	ΔQAIC
1	30	3637.18	249.66	3040.98	210.72
2	31	3528.01	140.49	2950.34	120.08
3	33	3546.80	159.28	2966.67	136.40
4	31	3502.25	114.73	2928.88	98.61
5	31	3542.58	155.06	2962.48	132.22
6	31	3511.79	124.27	2936.83	106.56
7	31	3551.56	164.04	2969.97	139.70
8	33	3395.87	8.35	2840.89	10.63
9	22	3387.52	0.00	2830.27	0.00
10	21	3464.59	77.07	2894.16	63.89
11	21	3432.84	45.32	2867.70	37.43

Note: $\hat{c} = 1.197$, based on the model $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$. k is the number of parameters in the model.

Model
1: $(F_y, F'_y, M, Sel_3, Sel_4, Sel_5)$
2: $(F_y, F'_y, M_Y, M_A, Sel_3, Sel_4, Sel_5)$
3: $(F_y, F'_y, M_3, M_4, M_5, M_{6+}, Sel_3, Sel_4, Sel_5)$
4: $(F_y, F'_y, M_{91-98}, M_{99-03}, Sel_3, Sel_4, Sel_5)$
5: $(F_y, F'_y, M_{91-99}, M_{00-03}, Sel_3, Sel_4, Sel_5)$
6: $(F_y, F'_y, M_{91-97}, M_{98-03}, Sel_3, Sel_4, Sel_5)$
7: $(F_y, F'_y, M_{91-96}, M_{97-03}, Sel_3, Sel_4, Sel_5)$
8: $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$
9: $(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$
10: $(F_y, F', M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$
11: $(F, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$

Based on AIC values for models 2 to 7, we focused on models with natural mortality M assumed different for young (3 − 5 years) and old (6+ years) fish, and/or different for the periods 1991 to 1998 and 1999 to 2003. We found the best models to be model $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ and model

$(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$, both of which have substantially smaller AIC values than either the age-specific-M model $(F_y, F'_y, M_Y, M_A, Sel_3, Sel_4, Sel_5)$ or the year-specific-M model $(F_y, F'_y, M_{91-98},$ $M_{99-03}, Sel_3, Sel_4, Sel_5)$ (Table 3.5). Of all the models in Table 3.5, the constant M model has the worst fit. Comparing the two best models using a likelihood ratio test results in $\chi^2 = 14$ with 11 df (p value = 0.23), suggesting that the reduced F model $(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ is preferred over the more general model (agrees with AIC criteria), and that variation in fishing mortality is mainly associated with an increase after the relaxation of fishing regulations.

Estimates with standard errors in parentheses under both model $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$ and the reduced F version $(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$, for the striped bass data, are displayed in Table 3.6. Both models result in estimates with good precision; relative standard errors for most parameter estimates are less than 10%. As might be expected, estimated precision for fishing mortality rates F is better under the reduced F model. Selectivity estimates have the expected trend under both models, with an estimate of about 1 for fish of age 5 years. Under the reduced F model, from 1991 to 1998, the estimated natural mortality for young fish is 0.40 (SE=0.02), which is larger than that for adults (0.15, SE=0.01). From 1999 to 2003, the estimated natural mortality for young fish is 0.86 (SE=0.06), which is higher than for adults (0.65, SE=0.03). Estimates also indicate that, for both young and adult striped bass, the natural mortality

rate in earlier years is lower than in later years and that fishing mortality increased after

fishing regulations were relaxed in 1995.

Table 3.6. Parameter estimates with standard errors in parentheses from fitting the age- and year-specific M models (a) $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03,} M_{A\_91-98}, M_{A\_99-03},$ $Sel_3, Sel_4, Sel_5)$ and (b) $(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03},$ $Sel_3, Sel_4, Sel_5)$ to the striped bass data.

Parameter	(a)	(b)
F(91)	0.106 (0.014)	0.154 (0.007)
F(92)	0.163 (0.014)	0.154 (0.007)
F(93)	0.152 (0.011)	0.154 (0.007)
F(94)	0.162 (0.011)	0.154 (0.007)
F(95)	0.226 (0.013)	0.235 (0.007)
F(96)	0.190 (0.012)	0.235 (0.007)
F(97)	0.233 (0.015)	0.235 (0.007)
F(98)	0.244 (0.017)	0.235 (0.007)
F(99)	0.254 (0.019)	0.235 (0.007)
F(00)	0.260 (0.018)	0.235 (0.007)
F(01)	0.293 (0.022)	0.235 (0.007)
F(02)	0.230 (0.018)	0.235 (0.007)
F(03)	0.140 (0.022)	0.235 (0.007)
F'(91)	0.125 (0.016)	0.124 (0.016)
F'(92)	0.156 (0.013)	0.160 (0.014)
F'(93)	0.105 (0.009)	0.109 (0.009)
F'(94)	0.132 (0.010)	0.131 (0.010)
F'(95)	0.106 (0.009)	0.117 (0.009)
F'(96)	0.116 (0.009)	0.125 (0.010)
F'(97)	0.092 (0.009)	0.099 (0.009)
F'(98)	0.094 (0.010)	0.095 (0.010)
F'(99)	0.074 (0.010)	0.082 (0.010)
F'(00)	0.169 (0.014)	0.168 (0.014)
F'(01)	0.126 (0.013)	0.123 (0.012)
F'(02)	0.081 (0.009)	0.092 (0.009)
F'(03)	0.056 (0.012)	0.050 (0.011)
Sel3	0.663 (0.061)	0.627 (0.058)
Sel4	0.730 (0.044)	0.739 (0.044)
Sel5	0.967 (0.047)	1.000 (0.048)
MY_91-98	0.378 (0.021)	0.399 (0.021)
MY_99-03	0.836 (0.063)	0.858 (0.056)
MA_91-98	0.145 (0.009)	0.150 (0.009)
MA_99-03	0.673 (0.038)	0.645 (0.028)

For all the models we investigated above, we assume that $\lambda = \lambda' = 0.43$. If the true values of λ and λ' are not 0.43, we will obtain biased parameter estimates. We tried to fit the models with different values of λ and λ'. Larger values of λ and λ' are usually associated with larger estimates of M, and smaller estimates of F and F'. We should keep in mind that the increase in estimates of M in later years could actually be due to a decrease in λ and λ' in later years, rather than to presence of disease, as mentioned in Section 3.2. Again we emphasize the importance of obtaining accurate, independent information about λ and λ'.

Models where λ and λ' are estimated are also considered. Results of estimates with their standard errors in parentheses from fitting models $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda, \lambda')$ and $(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda, \lambda')$ to the striped bass data are displayed in Table 3.7. Model $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda, \lambda')$ produces reasonable estimates but with low precision. Interestingly, estimates of λ and λ' (0.41 and 0.43, respectively) agree well with the value of 0.43 used in the "known λ" models. The model $(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda, \lambda')$ produces poor precision with relatively high estimates of fishing mortality on harvested fish and on tags of fish released alive and relatively low estimates of natural mortality compared with estimates obtained from the model $(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5)$. We notice that estimates obtained under models where λ and λ' are estimated are sensitive to the initial values of the parameters used in the

estimation process. The poor performance of the models with λ and λ' estimated suggests that we should use external sources to obtain accurate information for λ and λ'.

Table 3.7. Parameter estimates with standard errors in parentheses from fitting four M models (a) $(F_y, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda, \lambda')$, (b) $(F_{91-94}, F_{95-03}, F'_y, M_{Y\_91-98}, M_{Y\_99-03}, M_{A\_91-98}, M_{A\_99-03}, Sel_3, Sel_4, Sel_5, \lambda, \lambda')$ to the striped bass data.

Parameter	(a)		(b)	
F(91)	0.173	(0.075)	0.208	(0.053)
F(92)	0.185	(0.080)	0.208	(0.053)
F(93)	0.164	(0.071)	0.208	(0.053)
F(94)	0.144	(0.059)	0.208	(0.053)
F(95)	0.269	(0.110)	0.315	(0.080)
F(96)	0.207	(0.086)	0.315	(0.080)
F(97)	0.238	(0.100)	0.315	(0.080)
F(98)	0.288	(0.125)	0.315	(0.080)
F(99)	0.264	(0.116)	0.315	(0.080)
F(00)	0.236	(0.102)	0.315	(0.080)
F(01)	0.228	(0.096)	0.315	(0.080)
F(02)	0.173	(0.069)	0.315	(0.080)
F(03)	0.108	(0.036)	0.315	(0.080)
F'(91)	0.157	(0.150)	0.204	(0.091)
F'(92)	0.158	(0.153)	0.268	(0.118)
F'(93)	0.117	(0.112)	0.184	(0.082)
F'(94)	0.122	(0.116)	0.216	(0.094)
F'(95)	0.121	(0.115)	0.193	(0.085)
F'(96)	0.116	(0.110)	0.206	(0.092)
F'(97)	0.114	(0.109)	0.161	(0.073)
F'(98)	0.104	(0.099)	0.156	(0.070)
F'(99)	0.081	(0.077)	0.130	(0.058)
F'(00)	0.125	(0.120)	0.275	(0.121)
F'(01)	0.089	(0.085)	0.203	(0.092)
F'(02)	0.068	(0.063)	0.156	(0.070)
F'(03)	0.035	(0.030)	0.083	(0.039)
λ	0.407	(0.170)	0.321	(0.081)
λ'	0.430	(0.407)	0.261	(0.113)
Sel3	0.755	(0.066)	0.621	(0.059)
Sel4	0.810	(0.049)	0.726	(0.045)
Sel5	0.978	(0.048)	1.000	(0.047)
MY_91-98	0.405	(0.159)	0.283	(0.110)
MY_99-03	0.678	(0.170)	0.726	(0.132)
MA_91-98	0.148	(0.183)	0.001	(0.134)
MA_99-03	0.480	(0.185)	0.491	(0.146)

3.4 Discussion

Different approaches exist for estimating the survival and mortality rates from tag return data where tagged fish are subject to harvest and catch-and-release. Youngs and Robson (1975) did not include fish that were released alive in their analysis of lake trout data. Burnham (1991) and Barker (1997) developed methods for the joint analysis of data from fish harvested and caught-and-released. These two methods assume that tags are not removed prior to release and that the catch-and-release procedure does not affect survival. However, for the Maryland striped bass study, tags were removed regardless of the disposition of the recaptured fish prior to reporting the tag numbers to the U.S. Fish and Wildlife Service. High proportions (36% for all fish, 32% for adult fish) of striped bass tags were reported from caught-and-released fish. Also, the catch-and-release procedure affects survival (Diodati and Richards 1996). Thus, the Youngs and Robson (1975), Burnham (1991) and Barker (1997) approaches are not valid for the Maryland striped bass study.

Smith et al. (2000) developed models to estimate the finite rates of survival and recovery from the catch-and-release data where high proportions of tags were reported from caught-and-released fish, adjusting the bias caused by fish released alive with tag removed before reporting to the fishery agency. In their methods, they assumed that the natural mortality rate was known to be 0.15, and that all parameters were age-independent. In contrast, our models assume reporting rates are constant and known, and allow age- and year-dependence for M.

We extend the instantaneous rate formulation of tag return models to analyze the catch-and-release study data. In our methods, we separate the fishing mortality into two

parts: mortality on fish that are harvested, and mortality on tags of fish that are released alive. We show how to use experimentally determined estimates of hooking mortality (Diodati and Richards, 1996) to adjust mortality rates for tags to estimate the total fishing mortality and annual survival rates for fish. Traditionally, the natural mortality rate is difficult to estimate (Hightower et al. 2001). One very important feature of our models is that a limited degree of age- and/or year-dependence can be allowed in the estimation of natural mortality, assuming reporting rates are known. Analyses of the striped bass data demonstrate that a model with a limited degree of age- and year- dependent natural mortality, M, is preferred over models with more restrictive assumptions about M. For both young and adult fish, results show that total mortality increases and annual survival decreases after 1995, likely reflecting the effects of the change of harvest regulations as well as disease. Because of parameter redundancy problems (Chapter 1), models where tag reporting rates are estimated produce unreliable estimates, indicating the importance of estimating tag reporting rates using external information (Pollock et al. 1991, 2001, and 2002; Hearn et al. 2003).

For the Maryland striped bass study, tags were removed from the fish before they were released alive. In studies where tags are not cut off from fish before release, the marked fish can be recaptured multiple times, and additional information on survival can be obtained. For future research, the generalized Jolly-Seber model (Williams et al. 2002) can be applied to the case where the tags of fish released alive are not cut off.

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Table A.1. Release and tag return data from the study on striped bass carried out from 1991-2003 by Maryland Department of Natural Resources (fish released alive are treated as dead for purposes of illustration).

Age 3

Year of release	Number Tagged	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
1991	288	20	8	11	6	3	3	2	1	0	0	0	0	0
1992	380		21	5	12	6	6	1	2	0	0	0	0	0
1993	159			5	6	7	1	2	0	0	0	0	0	0
1994	92				3	6	3	0	0	0	0	0	0	0
1995	221					11	11	7	7	1	1	0	0	0
1996	393						23	23	14	5	1	2	0	0
1997	31							2	0	0	1	0	0	0
1998	131								6	1	0	0	1	0
1999	178									21	5	1	2	0
2000	116										10	2	2	0
2001	116											11	3	1
2002	73												4	4

Age 4

Year of release	Number Tagged	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
1991	202	11	15	2	5	2	1	2	0	0	0	0	0	0
1992	325		24	19	13	6	4	2	1	0	0	0	0	0
1993	721			32	41	27	14	9	4	3	0	0	0	0
1994	333				18	22	11	3	4	0	0	1	0	0
1995	112					7	5	5	4	0	2	0	0	0
1996	352						36	18	8	1	2	0	0	0
1997	372							18	22	0	7	2	1	0
1998	72								4	0	0	0	0	0
1999	221									15	7	4	3	0
2000	596										57	14	6	2
2001	412											39	13	4
2002	442												39	3

Age 5

		1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
1991	217	9	16	10	5	6	0	1	0	0	0	0	0	1
1992	209		13	10	7	5	2	2	0	3	0	0	0	0
1993	452			33	27	16	7	6	2	2	1	1	0	0
1994	593				56	46	14	15	8	4	3	0	0	0
1995	190					27	14	6	2	1	0	1	0	0
1996	95						7	5	9	0	1	0	0	0
1997	210							34	13	2	4	0	1	1
1998	516								62	17	11	4	2	0
1999	376									45	9	4	1	0
2000	543										59	3	2	0
2001	586											59	20	2
2002	1130												80	16

Age 6

		1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
1991	344	30	34	15	6	7	3	3	3	1	0	0	0	1
1992	334		46	22	17	6	2	0	0	2	0	1	0	0
1993	285			32	21	13	9	1	2	3	0	0	1	0
1994	430				46	33	18	10	6	3	1	0	0	0
1995	434					50	28	17	6	5	0	1	0	1
1996	171						23	9	5	4	0	1	1	0
1997	63							10	3	6	0	0	0	0
1998	101								15	5	1	0	0	0
1999	245									28	10	2	0	0
2000	898										85	24	10	2
2001	438											61	8	2
2002	709												60	21

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

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

Table A.2: Release and tag return data from the study on striped bass carried out from 1991-2003 by Maryland Department of Natural Resources.

Age 3

Year of release	Number Tagged	1991 H	1991 R	1992 H	1992 R	1993 H	1993 R	1994 H	1994 R	1995 H	1995 R	1996 H	1996 R	1997 H	1997 R	1998 H	1998 R	1999 H	1999 R	2000 H	2000 R	2001 H	2001 R	2002 H	2002 R	2003 H	2003 R
1991	288	8	12	3	5	6	5	2	4	3	0	3	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
1992	380			9	12	3	2	9	3	4	2	4	2	1	0	2	0	0	0	0	0	0	0	0	0	0	0
1993	159					0	5	3	3	7	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
1994	92							2	1	4	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1995	221									7	4	6	5	5	2	4	3	1	0	1	0	0	0	0	0	0	0
1996	393											7	16	13	10	11	3	4	1	1	0	2	0	0	0	0	0
1997	31													1	1	0	0	0	0	1	0	0	0	0	0	0	0
1998	131															1	5	0	1	0	0	0	0	0	1	0	0
1999	178																	10	11	2	3	1	0	2	0	0	0
2000	116																			5	5	0	2	2	0	0	0
2001	116																					3	9	3	0	0	1
2002	73																							2	2	3	1

Age 4

Year of release	Number Tagged	1991 H	1991 R	1992 H	1992 R	1993 H	1993 R	1994 H	1994 R	1995 H	1995 R	1996 H	1996 R	1997 H	1997 R	1998 H	1998 R	1999 H	1999 R	2000 H	2000 R	2001 H	2001 R	2002 H	2002 R	2003 H	2003 R
1991	202	5	6	7	8	2	0	2	3	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
1992	325			14	10	13	6	9	4	3	3	3	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0
1993	721					15	17	17	24	15	12	8	6	7	2	4	0	3	0	0	0	0	0	0	0	0	0
1994	333							5	13	12	10	4	7	2	1	3	1	0	0	0	0	0	1	0	0	0	0
1995	112									4	3	1	4	3	2	3	1	0	0	2	0	0	0	0	0	0	0
1996	352											20	16	13	5	7	1	1	0	2	1	0	0	0	0	0	0
1997	372													6	12	14	8	0	0	6	1	1	1	1	0	0	0
1998	72															3	1	0	0	0	0	0	0	0	0	0	0
1999	221																	9	6	2	5	4	0	1	2	0	0
2000	596																			19	38	10	4	3	3	2	0
2001	412																					14	25	10	3	3	1
2002	442																							23	16	2	1

Age 5

		1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002		2003	
		H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R
1991	217	5	4	10	6	5	5	3	2	5	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
1992	209			6	7	5	5	3	4	2	3	1	1	2	0	0	0	3	0	0	0	0	0	0	0	0	0
1993	452					19	14	19	8	12	4	6	1	4	2	2	0	2	0	1	0	1	0	0	0	0	0
1994	593							32	24	35	11	13	1	11	4	6	2	4	0	3	0	0	0	0	0	0	0
1995	190									14	13	10	4	4	2	2	0	1	0	0	0	0	1	0	0	0	0
1996	95											4	3	3	2	6	3	0	0	1	0	0	0	0	0	0	0
1997	210													19	15	6	7	2	0	4	0	0	0	1	0	0	1
1998	516															39	23	10	7	3	8	4	0	2	0	0	0
1999	376																	35	10	8	1	2	2	0	1	0	0
2000	543																			34	25	3	0	2	0	0	0
2001	586																					42	17	17	3	2	0
2002	1130																							54	26	10	6

Age 6

		1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002		2003	
		H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R
1991	344	16	14	21	13	12	3	2	4	6	1	2	1	3	0	3	0	1	0	0	0	0	0	0	0	0	0
1992	334			24	22	12	10	10	7	4	2	1	1	0	0	0	0	2	0	0	0	1	0	0	0	0	0
1993	285					20	12	13	8	8	5	4	5	1	0	1	1	3	0	0	0	0	0	1	0	0	0
1994	430							22	24	21	12	7	11	10	0	5	1	1	2	1	0	0	0	0	0	0	0
1995	434									25	25	20	8	14	3	3	3	4	1	0	0	1	0	0	0	1	0
1996	171											11	12	4	5	4	1	4	0	0	0	1	0	1	0	0	0
1997	63													4	6	3	0	5	1	0	0	0	0	0	0	0	0
1998	101															9	6	4	1	1	0	0	0	0	0	0	0
1999	245																	18	10	6	4	2	0	0	0	0	0
2000	898																			42	43	16	8	6	4	2	0
2001	438																					41	20	7	1	2	0
2002	709																							42	18	16	5

Age 7

		1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002		2003	
		H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R
1991	310	10	18	9	12	8	6	5	2	5	3	3	0	3	0	3	1	1	0	0	0	0	1	0	0	0	0
1992	328			16	23	14	6	6	4	5	3	2	0	2	1	1	0	0	1	0	0	0	0	0	0	0	0
1993	331					15	16	13	11	15	2	5	3	5	0	3	0	2	0	0	0	0	0	0	0	0	0
1994	189							8	11	6	5	2	3	6	1	1	2	5	1	1	0	0	1	0	0	0	0
1995	273									31	10	11	4	6	2	3	2	1	1	3	0	0	0	2	0	1	0
1996	397											28	24	20	9	10	3	4	1	3	1	2	0	0	0	0	0
1997	75													8	2	3	0	2	0	0	0	0	0	0	0	0	0
1998	67															5	4	1	0	4	0	0	0	1	0	0	0
1999	94																	11	1	4	3	0	0	0	0	0	0
2000	413																			37	18	8	2	3	1	1	0
2001	316																					29	5	4	1	1	1
2002	507																							39	11	5	2

Age 8+

		1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002		2003	
		H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R	H	R
1991	365	22	13	12	12	13	4	4	2	4	2	3	0	2	0	1	0	0	0	3	0	0	0	0	0	0	0
1992	384			21	18	13	10	9	6	12	2	5	3	7	2	6	0	3	1	2	0	0	0	0	0	0	0
1993	568					29	20	22	11	21	8	14	1	14	1	6	1	3	1	1	0	2	0	1	0	0	0
1994	371							19	13	18	6	18	1	9	0	12	1	7	1	2	0	2	0	0	0	0	1
1995	374									31	8	12	6	14	5	11	3	4	2	4	0	2	0	0	0	4	0
1996	719											52	33	32	11	32	3	11	2	5	1	5	0	1	0	1	0
1997	350													37	11	19	8	13	0	0	1	2	0	1	0	0	0
1998	280															27	7	11	3	2	1	3	2	2	0	1	0
1999	221																	21	6	6	2	8	2	1	1	0	0
2000	368																			27	12	11	4	2	4	1	1
2001	551																					32	12	11	6	7	0
2002	598																							29	7	13	2

Note: H is harvested, R is released alive.