# Age- and Time-specific Estimates of Natural and Fishing Mortality Rates for Striped Bass 

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Prepared by:

Dr. John M. Hoenig
Department of Fisheries Science
School of Marine Science, Virginia Institute of Marine Science

The College of William and Mary, PO Box 1346, Gloucester Point, Virginia 23062 and

Dr. Kenneth H. Pollock
Department of Zoology and Department of Statistics and Biomathematics North Carolina State University

Raleigh, NC 27563-8203

The goal of this project was to develop new methodology for estimating age- and time-specific mortality rates of an exploited fish population using tag-recovery data, and to apply these methods to tagging data for striped bass (Morone saxatilis) from Maryland and from Virginia. In this report, we present models for estimating mortality rates that can accommodate two factors pertinent to the assessment of striped bass: 1) some fishers clip the tag off of recaptured fish and release the fish alive, with some (but not necessarily all) of the tags reported to the fisheries authorities, and 2) both natural mortality rate and fishing mortality rate may vary according to the age of the fish. We apply the methods to tagging data from Maryland and Virginia. This report is in the form of a manuscript for the Journal of Agricultural, Biological and Environmental Statistics and another one for the North American Journal of Fisheries Management. The former manuscript received a favorable review and has been revised and resubmitted to the journal. The latter manuscript has been accepted for publication. The software used to obtain the parameter estimates is being posted on the website of North Carolina State University. We also presented results of the tagging data from Virginia in a technical report to the Atlantic States Marine Fisheries Commission Striped Bass Technical Committee's Tagging Subcommittee and made an oral presentation to that Subcommittee. Those results are presented in the Appendix to this report.

Tag Return Models allowing for Harvest and Catch and Release: Evidence of

## Environmental and Management Impacts on Striped Bass Fishing and Natural Mortality

## Rates

HONGHUA JIANG
Department of Statistics, North Carolina State University, Raleigh, North Carolina 27695, USA
KENNETH H. POLLOCK*
Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695, USA CAVELL BROWNIE

Department of Statistics, North Carolina State University, Raleigh, North Carolina 27695, USA JOHN M. HOENIG and ROBERT J. LATOUR

Virginia Institute of Marine Science, Virginia College of William and Mary, Post Office Box 1346, Gloucester Point, Virginia 23062, USA

BRIAN K. WELLS
NOAA/NMFS, 110 Shaffer Road, Santa Cruz, California 95060, USA JOSEPH E. HIGHTOWER
U. S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695, USA

* Corresponding author: Pollock@unity.ncsu.edu

Abstract.- Catch-and-release fisheries have become very important in 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. We extend the instantaneous rate formulation of tag return models to allow
for catch and release as well as harvest. The key point of our methods is that, given an estimate of the tag reporting rate, the fishing mortality rate $F$ is separated into two components: mortality on harvested fish, and "mortality" on tags (because the tag is removed) of fish released alive. The total fishing mortality rate for untagged fish is the sum of $F$ s due to harvest and hooking mortality suffered by fish released alive. Natural mortality rates can also be estimated. Both ageindependent models and age-dependent models are constructed and the age-dependent models are illustrated by application to data from a study on striped bass Morone saxatilis in Chesapeake Bay from 1991-2003 by the Maryland Department of Natural Resources. By fitting models with limited age and year dependence of the natural mortality rate $M$, we demonstrate an overall decrease in natural mortality rates as fish age and, in addition, provide evidence of an increase in natural mortality beginning in the late 1990s when an outbreak of the disease mycobacteriosis is thought to have begun. Our results indicate that fishing mortality is age-dependent, with selectivity increasing up to age 6 when fish appear to be fully recruited to the fishery. There is also evidence of an increase in fishing mortality since 1995 when regulations were relaxed.

In traditional fisheries tag return studies (e.g., Hoenig et al. 1998a, b), all caught fish are assumed to be harvested. However, many present day fisheries include substantial catch-andrelease fishing, so that only a fraction of the captured fish are harvested while the remainder are released alive. The goal is to provide recreational fishing opportunities, while conserving the stock. Catch-and-release fisheries have become very important to the management of overexploited recreational fish stocks. However, little work has been done on how to estimate
population demographic parameters (such as fishing and natural mortality) for catch-and-release fisheries using tagging studies. Estimation methods that account for catch-and-release fishing are essential in order to assess the effectiveness of conservation efforts.

For released fish the probability of the tag being reported may differ from the probability of the tag from harvested fish being reported. In some fisheries, 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, these fish remain marked and could be recaptured multiple times, providing additional information on survival. This can be viewed as a generalized type of Jolly-Seber model (Seber 1982, Williams et al. 2002).

The method used to estimate the tag reporting rate also may 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. However, 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 a report of the released tag numbers. Here, 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 ad hoc adjustment involved parameters for the short-term mortality after release (i.e., hooking mortality) and the tag reporting rate $\lambda$. Assuming known values for the instantaneous natural mortality $(M=0.15)$ and hooking mortality $(0.09)$, an iterative process was used to obtain estimates of reporting rate, fishing mortality and survival that accounted for catch-and-release fishing. We develop an alternative probability model and likelihood for the tag return data that is simpler and more intuitive. We use the methodology developed to analyze data from a tagging study carried out by the Maryland Department of Natural Resources. We conclude with a discussion of the important issues raised, including important model assumptions and suggestions for future research.

## Age-Independent Models

The key point in modeling tag returns from catch-and-release fishing is to note that removing tags from fish that are caught-and-released leads to an additional source of mortality on the tags that is not necessarily experienced by the fish. Jiang (2005) assumed that tag returns were recorded separately for fish that were harvested, and for fish that were caught-and-released, and developed a generalization of the Hoenig et al. (1998a) instantaneous rates models. Here we present the key elements of this approach. We first consider the situation where tagged fish are assumed to be fully recruited and all rates can be considered age-independent, and later present age-dependent versions of the method.

Glossary of Terms
We define the following quantities:
$N_{i}$ is the number of adult fish tagged and released in year $i(i=1,2, \ldots I)$,
$R_{i j}$ is the number of these $N_{i}$ fish that are subsequently harvested and reported in year $j$,
for $j=i, i+1, i+2, \ldots, J$,
$R_{i j}{ }^{\prime}$ 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 fish in year $j$,
$F_{j}{ }^{\prime}$ 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,
$P_{i j}$ is the probability that a fish tagged and released in year $i$, is harvested and
its tag reported in year $j$,
$P_{i j}{ }^{\prime}$ 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 annual survival rate in year $j$ for tags on fish alive at the beginning of year
$j$,
$\lambda$ is the tag-reporting rate (the probability that the tag is reported), given that a tagged
fish is harvested, and
$\lambda^{\prime}$ is the tag-reporting rate (the probability that the tag is reported), given that a tagged
fish is recaptured, the tag is clipped off, and the fish is released alive.

To reduce problems associated with near-singularity of the models (Jiang 2005), we had to assume that the tag reporting rates $\lambda$ and $\lambda^{\prime}$ are equal and constant over years. (If information on how $\lambda$ and $\lambda$ ' differ, and how they vary over time, is available, the models can be modified in a straightforward manner to accommodate this.) Similarly, in the basic model, the natural mortality rate $M$ is assumed to be constant over years. All parameters are age independent, although extensions to multi-age models (with age- and year-dependent $M$ s) are presented in a later section.

## Model Development

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

$$
E\left[R_{i j}\right]=N_{i} P_{i j},
$$

where

$$
\begin{align*}
& P_{i j}= \begin{cases}\left(\prod_{v=i}^{j-1} S_{v}\right)\left(1-S_{j}\right) \frac{F_{j}}{F_{j}+F_{j}{ }^{\prime}+M} \lambda & (\text { when } j>i) \\
\left(1-S_{j}\right) \frac{F_{j}}{F_{j}+F_{j}{ }^{\prime}+M} \lambda & (\text { when } j=i)\end{cases}  \tag{1}\\
& S_{j}=\exp \left(-F_{j}-F_{j}{ }^{\prime}-M\right)
\end{align*}
$$

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:

$$
E\left[R_{i j}{ }^{\prime}\right]=N_{i} P_{i j}^{\prime},
$$

where

$$
\begin{align*}
& P_{i j}^{\prime}= \begin{cases}\left(\prod_{v=i}^{j-1} S_{v}\right)\left(1-S_{j}\right) \frac{F_{j}^{\prime}}{F_{j}+F_{j}^{\prime}+M} \lambda^{\prime} & (\text { when } j>i) \\
\left(1-S_{j}\right) \frac{F_{j}^{\prime}}{F_{j}+F_{j}{ }^{\prime}+M} \lambda^{\prime} & (\text { when } j=i)\end{cases}  \tag{2}\\
& S_{j}=\exp \left(-F_{j}-F_{j}{ }^{\prime}-M\right) .
\end{align*}
$$

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

$$
\begin{align*}
L= & \prod_{i=1}^{I}\left(\begin{array}{l}
N_{i} \\
R_{i i}, R_{i i+1}, \ldots R_{i J}, R_{i i}{ }^{\prime}, \\
\left.R_{i i+1}{ }^{\prime}, \ldots R_{i J}{ }^{\prime}, N_{i}-\sum_{j=i}^{J}\left(R_{i j}+R_{i j}{ }^{\prime}\right)\right) \times \\
\\
\\
\left(\prod_{j=i}^{J} P_{i j} R_{i j} P_{i j}{ }^{\prime} R_{i j}{ }^{\prime}\right)\left(1-\sum_{v=i}^{J}\left(P_{i v}+P_{i v}{ }^{\prime}\right)\right)^{N_{i}-\sum_{v=i}^{J}\left(R_{i v}+R_{i v}{ }^{\prime}\right)} .
\end{array} .\right.
\end{align*}
$$

Theoretically, maximum likelihood estimators of the instantaneous rates $F_{j}, F_{j}{ }^{\prime}$ $(j=1,2, \ldots, J)$, and $M$, and the tag reporting rates $\lambda$ and $\lambda^{\prime}$ can be obtained from this likelihood using software such as program SURVIV (White 1983). Total annual mortality rates for fish then can be estimated from the instantaneous rates. However, it is often very difficult to obtain good estimates of the tag reporting rates in addition to the other parameters. If reliable values of the tag reporting rates $\lambda$ and $\lambda^{\prime}$ are available from other sources such as a high-reward tagging study,
then these parameters can be treated as known, and estimates are obtained for $F_{j}, F_{j}{ }^{\prime}$ $(j=1,2, \ldots, J)$, and $M$. An even better approach, if data for estimating the reporting rate are available (e.g., from a reward tagging study), is to include an additional component in the likelihood and estimate all parameters, including $\lambda$ and $\lambda^{\prime}$ from the one analysis (see Hoenig et al. (1998a)).

From (2), the total instantaneous mortality for tags $\left(Z_{j, \text { tags }}\right)$, and the annual survival rate for tags ( $S_{j, \text { tags }}$ ), in year $j$, are:

$$
\begin{aligned}
& Z_{j, \text { tags }}=F_{j}+F_{j}{ }^{\prime}+M \\
& S_{j, \text { tags }}=\exp \left(-F_{j}-F_{j}{ }^{\prime}-M\right) .
\end{aligned}
$$

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

$$
U_{j, \text { tags }}(k e p t)=\frac{F_{j}}{F_{j}+F_{j}{ }^{\prime}+M}\left[1-\exp \left\{-\left(F_{j}+F_{j}{ }^{\prime}+M\right)\right\}\right],
$$

and

$$
U_{j, \text { tags }}(\text { rels })=\frac{F_{j}{ }^{\prime}}{F_{j}+F_{j}{ }^{\prime}+M}\left[1-\exp \left\{-\left(F_{j}+F_{j}{ }^{\prime}+M\right)\right\}\right]
$$

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

$$
S_{j, f i s h}=\exp \left\{-\left(F_{j}+\delta F_{j}{ }^{\prime}+M\right)\right\}
$$

$$
Z_{j, ~ f i s h}=F_{j}+\delta F_{j}{ }^{\prime}+M
$$

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:

$$
S_{j, ~ f i s h}=\exp \left\{-\left(F_{j}+F_{j}^{\prime}+M\right)\right\}
$$

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

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

$$
S_{j, f i s h}=\exp \left\{-\left(F_{j}+M\right)\right\}
$$

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

Diodati and Richards (1996) conducted an experiment to estimate the hooking mortality on striped bass. They found that many factors influence hooking mortality, including hook penetration, gear type, and angler experiences. The water temperatures in their study did not exceed $25^{\circ} \mathrm{C}$ 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 was $9 \%(\mathrm{SE}=2 \%)$. This estimate of hooking mortality is a finite rate, but it can be used as an approximation to the hooking mortality rate, $\delta$, in our instantaneous rates formulation. The proof for this approximation is given in Jiang (2005). In Jiang (2005), an age-independent example of the analysis is presented for striped bass. It included use of the $9 \%$ hooking mortality
rates to obtain adjusted total mortality rates. However, here, in the interests of brevity, we move
immediately to the age-dependent model development and then illustrate the methodology with the striped bass analysis allowing age dependence of fishing and natural mortality rates.

## Age-Dependent Models

Jiang (2005) presented a likelihood function for data from traditional multiple age tagging studies, where all the recaptured fish were harvested. Merging that approach with work in the previous section, we present a likelihood function for data from multiple age tagging studies on fisheries that include both harvest and catch-and-release.

## Glossary of Terms

We extend the notation in the previous section by including an additional subscript $k$ to denote age at tagging.
$N_{i k}$ is the number of fish tagged at age $k(k=1,2, \ldots, K)$ and released in year $i(i=1,2, \ldots, I)$.
$R_{i j k}$ is the number of these $N_{i k}$ fish that are subsequently harvested and reported in year $j$.
$R_{i j k}$ ' is the number of these $N_{i k}$ fish that are caught, reported and released (without a tag) in year $j$, for $j=i, i+1, i+2, \ldots, J$.

We assume that the components of fishing mortality on tags attached to fish of age $a$ in year $j$ are:

$$
F_{j a}=\operatorname{Sel}_{a} F_{j}, \text { and }
$$

$$
F_{j a}^{\prime}=\operatorname{Sel}_{a} F_{j}^{\prime}
$$

$F_{j}$ is the instantaneous rate of fishing mortality for fully recruited fish that are harvested.
$F_{j}{ }^{\prime}$ is the instantaneous rate of fishing mortality on the tags for fully recruited fish that are released alive. Sel ${ }_{a}$ is the selectivity coefficient for age $a$ fish at the time of recovery.
$\lambda$ is the tag-reporting rate (the probability that the tag is reported), given that a tagged fish is harvested, $\lambda^{\prime}$ is the tag-reporting rate (the probability that the tag is reported), given that a tagged fish is recaptured, the tag is clipped off, and the fish is released alive.

Selectivity is assumed to be constant over years for each age, and is assumed to be 1 for all fish above a certain age $\left(a_{c}\right)\left(\operatorname{Sel}_{a} \equiv 1\right.$ for $\left.a \geq a_{c}\right)$. Relating age at tagging (k) to age at recovery (a) we have $a=k+j-i$ which is used in the expressions which follow. Here the parameters $\lambda$ and $\lambda$ 'are assumed to be age independent because we do not know of practical cases where age-specific reporting rates have been estimated. If such data became available we could easily extend the models to allow age dependence of reporting rates. For $P_{i j k}, P_{i j k}$ 'and $S_{i j k}$ the subscript $k$ indicates the age at tagging. In the basic model, we assume that the natural mortality rate $M$ is constant over ages and years.

## Model Development

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

$$
E\left[R_{i j k}\right]=N_{i k} P_{i j k}
$$

where

$$
\begin{aligned}
& P_{i j k}= \begin{cases}\left(\prod_{v=i}^{j-1} S_{i v k}\right)\left(1-S_{i j k}\right) \frac{F_{j} \operatorname{Sel}_{k+j-i}}{\left(F_{j}{ }^{\prime}+F_{j}\right) \operatorname{Sel}_{k+j-i}+M} \lambda & (\text { when } j>i) \\
\left(1-S_{i j k}\right) \frac{F_{j} \operatorname{Sel}_{k}}{\left(F_{j}{ }^{\prime}+F_{j}\right) \operatorname{Sel}_{k}+M} \lambda & (\text { when } j=i)\end{cases} \\
& S_{i j k}=\exp \left[-\left(F_{j}+F_{j}{ }^{\prime}\right) \operatorname{Sel}_{k+j-i}-M\right] .
\end{aligned}
$$

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

$$
E\left[R_{i j k} '\right]=N_{i k} P_{i j k}^{\prime},
$$

where

$$
\begin{aligned}
& P_{i j k}^{\prime}= \begin{cases}\left(\prod_{v=i}^{j-1} S_{i v k}\right)\left(1-S_{i j k}\right) \frac{F_{j}{ }^{\prime} \operatorname{Sel}_{k+j-i}}{\left(F_{j}{ }^{\prime}+F_{j}\right) \operatorname{Sel}_{k+j-i}+M} \lambda^{\prime} & (\text { when } j>i) \\
\left(1-S_{i j k}\right) \frac{F_{j}{ }^{\prime} \operatorname{Sel}_{k}}{\left(F_{j}{ }^{\prime}+F_{j}\right) \operatorname{Sel}_{k}+M} \lambda^{\prime} & (\text { when } j=i)\end{cases} \\
& S_{i j k}=\exp \left[-\left(F_{j}+F_{j}{ }^{\prime}\right) \operatorname{Sel}_{k+j-i}-M\right] .
\end{aligned}
$$

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

$$
L=\prod_{k=1}^{K} \prod_{i=1}^{I}\binom{N_{i k}}{R_{i k}, R_{i i+1 k}, \ldots, R_{i j k}, R_{i i k}{ }^{\prime}, R_{i i+1 k}{ }^{\prime}, \ldots, R_{i j k}{ }^{\prime}, N_{i k}-\sum_{j=i}^{J}\left(R_{i j k}+R_{i j k}{ }^{\prime}\right)} \times
$$

$$
\left(\prod_{j=i}^{J} P_{i j k}^{R_{i j}} P_{i j k}, R_{i j k^{\prime}}\right)\left(1-\sum_{v=i}^{J}\left(P_{i v k}+P_{i v k}{ }^{\prime}\right)\right)^{N_{i k}-\sum_{v i}^{J}\left(R_{i k k}+R_{i v k}{ }^{\prime}\right)}
$$

We use the method of maximum likelihood to estimate $F_{j}, F_{j}{ }^{\prime}(j=1,2, \ldots, J), M$, selectivities $\operatorname{Sel}_{a}\left(a=1, \ldots, a_{c}-1\right)$ and the tag reporting rates $\lambda$ and $\lambda^{\prime}$. If the tag reporting rates $\lambda$ and $\lambda^{\prime}$ are known, estimates are obtained for $F_{j}, F_{j}{ }^{\prime}(j=1,2, \ldots, J), M$, and selectivities $\operatorname{Sel}_{a}\left(a=1, \ldots, a_{c}\right.$ 1). Due to their important biological interest we also investigate models where $M$ is year and/or age dependent, but only to a limited extent in order to avoid parameter identifiability problems. Following the same approach we took for the age-independent mortality model we could estimate total mortality allowing for hooking mortality.

Example

## Study description

We illustrate the analysis of age-dependent tag return data, from a fishery with harvest and catch-and-release, using 1991-2003 Maryland Department of Natural Resources (MDNR) data for striped bass (Appendix A in Jiang 2005). Over 24,533 striped bass were marked (March through June) with an internal anchor tag (Floy Tag \# FM-84) and released in the upper Chesapeake Bay. A scale-based aging method was used to identify the ages of approximately $30 \%$ of the tagged fish and then the remaining fish were aged based on length bins. This resulted in seven age groups (from age 2 years to age $8+$ years). Scales work reliably for up to age 8
striped bass and there is no need for an otolith-based method (Secor et al. 1995). Tag returns from fish at large for less than a week were excluded to ensure reasonable mixing. We only analyzed the data for striped bass classified as age 3 and greater ( 24,356 total fish), because the sample sizes for those marked at age 2 were too small. A total of 4,593 tags were returned to fishery agencies with $2,960(64 \%)$ harvested (killed) and 1,633 ( $36 \%$ ) released alive after the tag was removed.

Age effects on fishing mortality on harvested fish, $F$, and on tags of fish that were caught and released, $F^{\prime}$, were incorporated through selectivity. Selectivity was estimated separately for striped bass of age 3,4 , and 5 , respectively $\left(\mathrm{Sel}_{3}, \mathrm{Sel}_{4}\right.$, and $\left.\mathrm{Sel}_{5}\right)$. Selectivity was assumed to be 1 for age 6 and older because in preliminary runs of our models where we estimated selectivity we found it to be 1 for age 6 fish. We considered the basic model $\left(F_{y}, F_{y}{ }_{y}, M, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$ with $F$ and $F^{\prime}$ age-dependent through selectivity and allowed to vary by year (subscript $y$ ), $M$ constant over years and ages. Tag shedding and tag induced mortality were assumed to be negligible based on special studies (following Smith et al. 2000) and we assumed reporting rates, $\lambda=\lambda^{\prime}=0.43$. This value is based on a high reward tagging study conducted by the Delaware Division of Fish and Wildlife, and also is the average reporting rate for 1991 and 1997 estimated in Smith et al. (2000; range $0.38-0.48$ ). We also fit the corresponding model $\left(F_{y}, F^{\prime}{ }_{y}, M, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}, \lambda, \lambda^{\prime}\right)$ where $\lambda$ and $\lambda^{\prime}$ are estimated.

To investigate the assumption that natural mortality is constant over ages, we fitted a $\operatorname{model}\left(F_{y}, F_{y}^{\prime}, M_{Y}, M_{A}\right.$, Sel $_{3}$, Sel $_{4}$, Sel $\left._{5}\right)$ where we assumed that young (Y) fish of age 3, 4, and 5 had a common natural mortality rate, different from that of adult (A) fish of 6 and greater. We
also fitted model $\left(F_{y}, F_{y}^{\prime}, M_{3}, M_{4}, M_{5}, M_{A}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$ that allowed fish of age 3,4 , and 5 to each have a different natural mortality rate. The corresponding models, with reporting rates $\lambda$ and $\lambda^{\prime}$ estimated, were also investigated.

It was of special interest to investigate models that allow the natural mortality rate to differ with time because of possible disease effects. A bacterial disease known as mycobacteriosis, caused by bacteria in the genus Mycobacterium, appeared in Chesapeake Bay striped bass in the late 1990s (Cardinal 2001). Symptoms include external lesions (open sores on the skin) and internal lesions that look like lumps in the spleen and kidney. There are about a dozen species of Mycobacteria in 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 Rap. River, Virginia in late summer (Cardinal 2001). Due to concerns about parameter redundancy problems, we assumed that natural mortality was constant in the years before the disease effects occurred (1999) and constant at a different value after any disease effects began. Finally, reduced models that reflect the effects of the relaxation of fishing regulations on fishing mortality in 1995 (Richards and Rago 1999) were also investigated.

We used Akaike's information criterion (AIC) to choose between models because this method is able to compare multiple nested and nonnested models. Akaike's information criteria 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). It can be computed as:

$$
A I C=-2 \log [l(\underline{\hat{\theta}} \mid y)]+2 k
$$

where $\log [l(\underline{\hat{\theta}} \mid y)]$ is the $\log$ likelihood function evaluated at the MLEs $\underline{\hat{\theta}}$ given the data $y$, and $k$ is the number of parameters. The model with the minimum AIC value was 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 (Burnham and Anderson 2002) to deal with the problem and that was the approach we followed in this paper. The corresponding criterion is QAIC, defined as:

$$
Q A I C=-2 \log [l(\underline{\hat{\theta}} \mid y)] / \hat{c}+2 k,
$$

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

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

where $x^{2}$ and $d f$ correspond to the value of the Pearson goodness-of-fit test of the most general model in the model set and its degrees of freedom. The small sample correction on AIC and QAIC (Burnham and Anderson 2002) made no difference for this example and is not reported.

Results
All models with tag reporting rates fixed at $\lambda=\lambda^{\prime}=0.43$ produced parameter estimates with high precision (small standard errors). The AIC and QAIC values for models where we assumed $\lambda$ and $\lambda^{\prime}$ were known are presented in Table 1. According to the AIC and QAIC values, the two best models were the full model $\left(F_{y}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03,}, M_{A_{-} 91-98}\right.$, $M_{A_{99-03}}$, Sel $_{3}, \mathrm{Sel}_{4}, \mathrm{Sel}_{5}$ ) with annual values for $F$ and $F^{\prime}$ and the reduced model
$\left(F_{91-94,} F_{95-03}, F_{y}^{\prime}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$ where $F$ was constant in the years before (1991 to 1994) and after (1995 to 2003) a regulation change. Both of the best models allowed the natural mortality rate, $M$, to vary by age and year. There was little difference between the two criteria AIC and QAIC because the inflation factor $\hat{c}=1.20$ is very close to 1.0 . This suggests little evidence of overdispersion in this example. These models assumed that $M$ was 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 1991 to 1998 and from 1999 to 2003. In combination, we had four different natural mortality rates to estimate.

Based on AIC and QAIC 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. Of all the models in Table 1, the constant $M$ model has the worst fit. Comparing the two best models using a likelihood ratio test results in $\chi^{2}=14$ with $11 d f(p$ value $=0.23)$, suggesting that the reduced $F$ model $\left(F_{91-94}, F_{95-03}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}\right.$, Sel $_{3}$, Sel $_{4}$, Sel $\left._{5}\right) \quad$ is preferred over the more general model $\left(F_{91-94}, F_{95-03}, F_{y}^{\prime}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}\right.$, Sel $_{4}$, Sel $\left._{5}\right)$ (which agrees with the QAIC criterion), 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 $\left(F_{y}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}\right.$, Sel $\left._{5}\right)$ and the reduced $F$ version $\left(F_{91-94}, F_{95-03}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}\right.$, Sel $_{3}$, Sel $_{4}$, Sel $\left._{5}\right)$, for the striped bass data,
are displayed in Table 2. 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 1.0 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 $(\mathrm{SE}=0.02)$, which is larger than that for adults $(0.15, \mathrm{SE}=0.01)$. From 1999 to 2003, the estimated natural mortality for young fish is $0.86(\mathrm{SE}=0.06)$, which is higher than for adults ( $0.65, \mathrm{SE}=0.03$ ). 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.

For the models investigated in Tables 1 and 2, we assume that $\lambda=\lambda^{\prime}=0.43$ based on the best information available on reporting rates. If the true values of $\lambda$ and $\lambda^{\prime}$ are not 0.43 , we will obtain biased parameter estimates. The increase in estimates of $M$ in later years could actually be due to a decrease in $\lambda$ and $\lambda^{\prime}$ in later years and we investigated that alternative. However, the decrease necessary for $\lambda$ and $\lambda^{\prime}$ in order for estimates of $M$ to be about equal is to values less than $20 \%$ and we believe this very unlikely. Thus, the evidence for an increase in $M$ over time is robust but the magnitude of the increase is tied to the values of the tag reporting rate. This emphasizes the importance of obtaining accurate, independent information about the reporting rates.

Models where $\lambda$ and $\lambda^{\prime}$ were estimated, were also considered (Table 3). $\operatorname{Model}\left(F_{y}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}, \lambda, \lambda\right.$ ') produced reasonable point estimates but generally had low precision except for the selectivity estimates. It is very
interesting that estimates of $\lambda$ and $\lambda^{\prime}(0.41$ and 0.43 , respectively) agree well with the common value of 0.43 assumed in the previous models . The model $\left(F_{91-94}, F_{95-03}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}\right.$, Sel $_{3}, \operatorname{Sel}_{4}$, Sel $\left._{5}, \lambda, \lambda '\right)$ produces some unreasonable estimates and again generally estimates have low precision. In particular notice that the adult natural mortality from 1991-1998 is estimated to be 0.001 which is not at all reasonable. Estimates obtained under the models where reporting rates were estimated are sensitive to the initial values of the parameters used in the estimation process. The poor performance of the models with reporting rates estimated suggested that we should use external sources such as special high-reward tagging studies to obtain accurate information on reporting rates.

Recall that estimates of $F_{y}^{\prime}$ in Tables 2 and 3 represent a mortality force on tags removed from fish that are released. To calculate estimates of total mortality for fish, we account for mortality of fish that are released by adjusting the estimate of $F_{y}^{\prime}$ using an estimate of hooking mortality as described for the age-independent case. For example, assuming that $\lambda=\lambda^{\prime}=0.43$, and that hooking mortality $\delta=0.09$, under the reduced $F$ model in Table 2, we calculate total mortality for adult fish in 1991 as

$$
\begin{aligned}
\hat{Z}_{A_{-} 91-94, f i s h} & =\hat{F}_{91-94}+\delta \hat{F}_{91}^{\prime}+\hat{M}_{A_{-} 91-98} \\
& =0.154+(0.09)(0.124)+0.15 \\
& =0.315
\end{aligned}
$$

The annual survival rate for adult fish in 1991 is estimated to be $e^{-0.315}=0.73$.

Different approaches exist for estimating survival and mortality rates from tag return data where tagged fish are subject to harvest as well as catch-and-release. Youngs and Robson (1975) did not include fish that were released alive in their analysis of lake trout (Salvelinus namaycush) data. Burnham (1993) 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; Millard et al. 2003). Thus, the Youngs and Robson (1975), Burnham (1993), 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-andreleased fish, adjusting the bias caused by fish released alive with tag removed before reporting to the fishery agency. In their somewhat ad hoc methods, they assumed that the natural mortality rate is 0.15 , that reporting rates are constant and known, and that all parameters are ageindependent. In contrast, our models assume that the reporting rates are constant and known, and allow age- and year-dependence for $M$. Our models also allow for estimation of the reporting rates and for the incorporation of additional components of the likelihood to account for
supplemental data relating to the tag reporting rate in order to obtain estimates with good precision.

We extend the instantaneous rate formulation of tag return models to analyze the catch-and-release study data. Natural mortality rate is difficult to estimate for all fish species (Vetter 1988; Hoenig et al. 1998a) and for striped bass in particular (Hightower et al. 2001) despite its great importance to stock assessments. 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. Analyses of the Chesapeake Bay striped bass data from Maryland demonstrate that a model with a limited degree of age- and year- dependent natural mortality, $M$, is strongly 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.

One very important result for fisheries managers from our paper is that we provide some of the first empirical evidence that $M$ has increased in recent years for the Maryland Chesapeake Bay population of striped bass. This may be due to the emergence of mycobacteriosis in Chesapeake Bay striped bass in the late 1990s (Cardinal 2001). A large drop in reporting rate (to less than $20 \%$ ) is an alternative explanation, but one we believe is extremely unlikely.

We attempted to address the issue of uncertainty about reporting rates directly by estimating them internal to our analysis. However, due to parameter redundancy problems, we found models where tag reporting rates were estimated produced some unrealistic estimates and even the realistic estimates had low precision. Thus the importance of estimating tag reporting rates using special external information such as high reward tagging studies or possibly angler
surveys (Pollock et al. 2001, 2002; Hearn et al. 2003) is obvious. This is clearly an important area for future research and we recommend in particular that special ongoing high-reward tagging studies be initiated to obtain better estimates of the reporting rates for harvested and released fish. This would also enable scientists to empirically examine the critical assumptions: that these two reporting rates are equal, constant over years, and constant over ages of fish. The current methods used by Smith et al. (2000) also made these same critical assumptions about reporting rates.

The approach developed here assumes that fish are correctly assigned to age categories, either by examining some hard structure such as a scale or through use of an age-length key. Even if age assignments are unbiased, there will be some level of misclassification using either method. These misclassifications could result in some bias in model estimates if parameters varied substantially among ages. For the Chesapeake Bay striped bass example, there were moderate differences in estimated selectivity across ages 3-5 years, but natural mortality was quite different for the young (3-5) and adult (6+) age categories. The potential for bias, when hard parts are used to assign fish to age classes, can be assessed through age validation studies (Beamish and McFarlane 1983). When an age-length key is used, the overlap in length distributions among ages provides some indication of the potential bias.

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 (Seber 1982, 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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511 Table 1. Akaike Information Criteria (AIC) and Akaike Information Criteria adjusted for over
512 dispersion (QAIC) values for 11 models with $F$ and $F^{\prime}$ age-dependent through selectivity, $M$
513 constant or with some age and/or year- specificity, and assuming $\lambda=\lambda^{\prime}=0.43$. K is the number
514 of parameters in the model.

| 515 | Pr |  |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 516 | Model K | AIC | $\Delta$ AIC | QAIC | $\Delta$ QAIC |  |
| 517 | 1 | 30 | $3,637.18$ | 249.66 | $3,040.98$ | 210.72 |
| 518 | 2 | 31 | $3,528.01$ | 140.49 | $2,950.34$ | 120.08 |
| 519 | 3 | 33 | $3,546.80$ | 159.28 | $2,966.67$ | 136.40 |
| 520 | 4 | 31 | $3,502.25$ | 114.73 | $2,928.88$ | 98.61 |
| 521 | 5 | 31 | $3,542.58$ | 155.06 | $2,962.48$ | 132.22 |
| 522 | 6 | 31 | $3,511.79$ | 124.27 | $2,936.83$ | 106.56 |
| 523 | 7 | 31 | $3,551.56$ | 164.04 | 2969.97 | 139.70 |
| 524 | 8 | 33 | $3,395.87$ | 8.35 | $2,840.89$ | 10.63 |
| 525 | 9 | 22 | $3,387.52$ | 0.00 | $2,830.27$ | 0.00 |
| 526 | 10 | 21 | $3,464.59$ | 77.07 | $2,894.16$ | 63.89 |
| 527 | 11 | 21 | $3,432.84$ | 45.32 | $2,867.70$ | 37.43 |

$\left(F_{y}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03,}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$.

1: $\left(F_{y}, F^{\prime}{ }_{y}, M, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$

533 2: $\left(F_{y}, F_{y}^{\prime}, M_{Y}, M_{A}\right.$, Sel $_{3}$, Sel $_{4}$, Sel $\left._{5}\right)$

```
534 3: \(\left(F_{y}, F^{\prime}{ }_{y}, M_{3}, M_{4}, M_{5}, M_{6+}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)\)
535 4: \(\left(F_{y}, F^{\prime}{ }_{y}, M_{91-98}, M_{99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)\)
```

5: $\left(F_{y}, F^{\prime}{ }_{y}, M_{91-99}, M_{00-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$

6: $\quad\left(F_{y}, F^{\prime}{ }_{y}, M_{91-97}, M_{98-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$

7: $\left(F_{y}, F^{\prime}, M_{91-96}, M_{97-03}, \operatorname{Sel}_{3}\right.$, Sel $_{4}$, Sel $\left._{5}\right)$

8: $\quad\left(F_{y}, F^{\prime}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}\right.$, Sel $\left._{4}, \operatorname{Sel}_{5}\right)$

9: $\quad\left(F_{91-94}, F_{95-03}, F_{y}^{\prime}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$

10: $\left(F_{y}, F^{\prime}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$
$11\left(F, F^{\prime}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}\right.$, Sel $\left._{4}, \operatorname{Sel}_{5}\right)$.

Table 2. Parameter estimates with standard errors in parentheses from fitting the catch- and-
release tag return models allowing age- and year-specific natural mortality and a selectivity model for fishing mortality to the Maryland striped bass data. Model (a) allows fishing mortality to vary by year $\left(F_{y}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}\right.$, Sel $\left._{4}, \operatorname{Sel}_{5}\right)$ and $\operatorname{Model}(b)$ allows fishing mortality to be constant before and after 1995, when fishing regulations were liberalized $\left(F_{91-94}, F_{95-03}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}\right.$, Sel $_{4}$, Sel $\left._{5}\right)$. Reporting rates for both harvested and released fish were fixed at 0.43 .

| 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) |
| $\mathrm{F}^{\prime}(91)$ | 0.125 | (0.016) | 0.124 | (0.016) |
| $\mathrm{F}^{\prime}$ (92) | 0.156 | (0.013) | 0.160 | (0.014) |


| 568 | $F^{\prime}(93)$ | 0.105 | (0.009) | 0.109 | (0.009) |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 569 | $F^{\prime}(94)$ | 0.132 | (0.010) | 0.131 | (0.010) |
| 570 | $\mathrm{F}^{\prime}(95)$ | 0.106 | (0.009) | 0.117 | (0.009) |
| 571 | $F^{\prime}(96)$ | 0.116 | (0.009) | 0.125 | (0.010) |
| 572 | $\mathrm{F}^{\prime}$ (97) | 0.092 | (0.009) | 0.099 | (0.009) |
| 573 | $\mathrm{F}^{\prime}$ (98) | 0.094 | (0.010) | 0.095 | (0.010) |
| 574 | $F^{\prime}$ (99) | 0.074 | (0.010) | 0.082 | (0.010) |
| 575 | $\mathrm{F}^{\prime}(00)$ | 0.169 | (0.014) | 0.168 | (0.014) |
| 576 | $F^{\prime}(01)$ | 0.126 | (0.013) | 0.123 | (0.012) |
| 577 | $\mathrm{F}^{\prime}$ (02) | 0.081 | (0.009) | 0.092 | (0.009) |
| 578 | $F^{\prime}$ (03) | 0.056 | (0.012) | 0.050 | (0.011) |
| 579 | Sel3 | 0.663 | (0.061) | 0.627 | (0.058) |
| 580 | Sel4 | 0.730 | (0.044) | 0.739 | (0.044) |
| 581 | Sel5 | 0.967 | (0.047) | 1.000 | (0.048) |
| 582 | MY_91-98 | 0.378 | (0.021) | 0.399 | (0.021) |
| 583 | MY_99-03 | 0.836 | (0.063) | 0.858 | (0.056) |
| 584 | MA_91-98 | 0.145 | (0.009) | 0.150 | (0.009) |
| 585 | MA_99-03 | 0.673 | (0.038) | 0.645 | (0.028) |

588 Table 3. Parameter estimates with standard errors in parentheses from fitting the
589 catch and release tag return models allowing age- and year-specific natural mortality
590 and a selectivity model for fishing mortality to the Maryland striped bass data. In
591 this case unlike in Table 2 the reporting rates are also estimated. Model (a) allows fishing
mortality to vary by year ( $F_{y}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}$, Sel $\left._{4}, \operatorname{Sel}_{5}, \lambda, \lambda{ }^{\prime}\right)$,
and Model (b) allows fishing mortality to be constant before and after 1995
$\left(F_{91-94}, F_{95-03}, F^{\prime}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}\right.$, Sel $_{3}$, Sel $\left._{4}, \operatorname{Sel}_{5}, \lambda, \lambda^{\prime}\right)$

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 | $(0.080)$ |
| $F^{\prime}(91)$ | 0.157 | $(0.150)$ | 0.204 | $(0.091)$ |
| $F^{\prime}(92)$ | 0.158 | $(0.153)$ | 0.268 | $(0.118)$ |


| 613 | $F^{\prime}(93)$ | 0.117 | $(0.112)$ | 0.184 | $(0.082)$ |
| :--- | :--- | :--- | :--- | :--- | :--- |
| 614 | $F^{\prime}(94)$ | 0.122 | $(0.116)$ | 0.216 | $(0.094)$ |
| 615 | $F^{\prime}(95)$ | 0.121 | $(0.115)$ | 0.193 | $(0.085)$ |
| 616 | $F^{\prime}(96)$ | 0.116 | $(0.110)$ | 0.206 | $(0.092)$ |
| 617 | $F^{\prime}(97)$ | 0.114 | $(0.109)$ | 0.161 | $(0.073)$ |
| 618 | $F^{\prime}(98)$ | 0.104 | $(0.099)$ | 0.156 | $(0.070)$ |
| 619 | $F^{\prime}(99)$ | 0.081 | $(0.077)$ | 0.130 | $(0.058)$ |
| 620 | $F^{\prime}(00)$ | 0.125 | $(0.120)$ | 0.275 | $(0.121)$ |
| 621 | $F^{\prime}(01)$ | 0.089 | $(0.085)$ | 0.203 | $(0.092)$ |
| 622 | $F^{\prime}(02)$ | 0.068 | $(0.063)$ | 0.156 | $(0.070)$ |
| 623 | $F^{\prime}(03)$ | 0.035 | $(0.030)$ | 0.083 | $(0.039)$ |
| 624 | $\lambda$ | 0.407 | $(0.170)$ | 0.321 | $(0.081)$ |
| 625 | $\lambda^{\prime}$ | 0.430 | $(0.407)$ | 0.261 | $(0.113)$ |
| 626 | Sel3 | 0.755 | $(0.066)$ | 0.621 | $(0.059)$ |
| 627 | Sel4 | 0.810 | $(0.049)$ | 0.726 | $(0.045)$ |
| 628 | Sel5 | 0.978 | $(0.048)$ | 1.000 | $(0.047)$ |
| 629 | MY_91-98 | 0.405 | $(0.159)$ | 0.283 | $(0.110)$ |
| 630 | MY | $09-03$ | 0.678 | $(0.170)$ | 0.726 |$(0.132)$

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

Honghua JIANG, Kenneth H. POLLOCK, Cavell BROWNIE, Joseph E. HIGHTOWER, John M. HOENIG and William S. HEARN.

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

Key Words: Instantaneous mortality rates, Near-singularity, Striped bass, Tag reporting rate.

## 1. INTRODUCTION

Tag return studies play an important role in providing estimates of mortality rates needed for management of many fisheries. Tagged fish are released annually and the tags from harvested fish are returned to the agency in charge by fishers. Typically, the tagged fish vary over a large range of ages and sizes. For example, the Maryland Department of Natural Resources (MDNR) carried out a study on the Chesapeake Bay striped bass (Morone saxatilis) stock in order to estimate fishing mortality rates. Reliable information is essential for management because this stock supports one of the most important recreational fisheries on the Atlantic coast. A total of 24533 fish, ranging in age from 2 to 8+ years, were tagged between 1991 and 2002. The releases and tag returns for this study are presented in the Appendix.

Brownie et al. (1985) presented models for tag return data based on annual survival and 'reported exploitation' rates. They noted (Brownie et al.,1985, p14) that without additional information on the reporting rate, the exploitation rate cannot be estimated. In fisheries, it is important to obtain separate estimates of the two components of mortality, fishing and natural mortality, and Pollock et al. (1991) showed how to estimate both the instantaneous fishing and natural mortality rates if an estimate of the tag reporting rate is available. Hoenig et al. (1998a) formulated a general theory for the instantaneous rates version of the tag return models. By analysing multiple subsets of a data set on lake trout (Salvelinus namaycush), they showed that it is possible to estimate the tag reporting rate in addition to the fishing and natural mortality rates, but that estimates were not stable. Hoenig et al. (1998b) presented models that allowed for
incomplete mixing of newly tagged fish. Tag reporting rates were assumed to be known or well estimated from another study.

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

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

## 2. MODEL STRUCTURE

### 2.1 BASIC MODEL: CONTINUOUS FISHERY

We consider multiple age tagging studies, where tagging and release occur at the beginning of the year and harvest occurs continuously during the entire year. Let $N_{i k}$ be the number of fish tagged at age $k$ and released in year $i(k=1,2, \ldots, K, i=1,2, \ldots, I)$, and let $R_{i j k}$ be the number of these $N_{i k}$ fish that are subsequently harvested and reported in year $j(j=i, i+1, \ldots, J)$. Age dependence of the instantaneous fishing mortality rate is modeled by allowing recruitment into the fishery to be related to age. Thus for fish of age
$a$ in year $j$, the instantaneous fishing mortality rate is $F_{j a}=F_{j} S e l_{a}$, where $F_{j}$ is the instantaneous fishing mortality rate in year $j$ for fully recruited fish, and $S e l_{a}$ is the selectivity coefficient for age $a$ fish. We assume that the age at which fish are fully recruited, $a_{c}$, is known, and that $a_{c}$ does not exceed the number of age classes tagged. That is, $\operatorname{Sel}_{a} \equiv 1$ for $a>a_{c}$, where $a_{c} \leq K$. Assuming selectivity to be constant over years for each age results in a parsimonious representation of age and year dependence for fishing mortality.

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

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

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

$$
E\left[R_{i j k}\right]=N_{i k} P_{i j k} \text {, where }
$$

$P_{i j k}=$ the probability that a fish tagged at age $k$ and released in year $i$, is harvested and returned in year $j$,
$S_{i j k}=$ the conditional probability of surviving year $j$, given it is alive at the start of the year, for a fish tagged at age $k$ in year $i$,
and, for a fishery continuous over the whole year,

$$
\begin{aligned}
& P_{i j k}= \begin{cases}\left(\prod_{v=i}^{j-1} S_{i v k}\right)\left(1-S_{i j k}\right) \frac{F_{j} \operatorname{Sel}_{k+j-i}}{F_{j} \operatorname{Sel}_{k+j-i}+M} \lambda & (\text { when } j>i) \\
\left(1-S_{i j k}\right) \frac{F_{j} \operatorname{Sel}_{k}}{F_{j} \operatorname{Sel}_{k}+M} \lambda & (\text { when } j=i),\end{cases} \\
& S_{i j k}=\exp \left(-F_{j} \operatorname{Sel}_{k+j-i}-M\right) .
\end{aligned}
$$

The full likelihood function is product multinomial:

$$
\begin{equation*}
L_{1}=\prod_{k=1}^{K} \prod_{i=1}^{I}\binom{N_{i k}}{R_{i i k}, R_{i i+1 k}, \ldots R_{i J k}}\left(\prod_{j=i}^{J} P_{i j k}^{R_{i j k}}\right)\left(1-\sum_{v=i}^{J} P_{i v k}\right)^{N_{i k}-\sum_{v i=}^{J} R_{i v k}} \tag{1}
\end{equation*}
$$

Maximum likelihood estimates (MLEs) based on $L_{1}$ are obtained numerically using software such as SURVIV (White 1983). We consider models where $\lambda$ is a known constant, and also models where $\lambda$ must be estimated in addition to the parameters $F_{j}, j$ $=1, \ldots, J, \operatorname{Sel}_{a}, a=1, \ldots, a_{c}$, and $M$. A third case, with important practical implications,
occurs when independent, auxiliary data are available to estimate $\lambda$. For instance, if tag returns are available from high reward tagging (Pollock et al. 2001), in addition to the regular returns, the joint likelihood for the two types of tag returns would be $L_{1} \times L_{2}$, where $L_{2}$, the likelihood for the high reward tags, has the same form as $L_{1}$ but with $\lambda=1$. Or, if a planted tag study has been performed with $m$ tags planted in the catch from which $v$ tags are reported, then the likelihood function for the planted tag data is binomial,

$$
L_{3}=\binom{m}{v} \lambda^{v}(1-\lambda)^{m-v},
$$

and the joint likelihood for the planted and regular tag returns is the product $L_{1} \times L_{3}$

### 2.2 Limited Fishery

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

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

$$
\begin{aligned}
& P_{i j k}= \begin{cases}\left(\prod_{v=i}^{j-1} S_{i v k}\right)\left[1-\exp \left(-F_{j} \operatorname{Sel}_{k+j-i}-T M\right)\right] \frac{F_{j} \operatorname{Sel}_{k+j-i}}{F_{j} \operatorname{Sel}_{k+j-i}+T M} \lambda & (\text { when } j>i) \\
{\left[1-\exp \left(-F_{j} \operatorname{Sel}_{k+j-i}-T M\right)\right] \frac{F_{j} \operatorname{Sel}_{k}}{F_{j} \operatorname{Sel}_{k}+T M} \lambda} & (\text { when } j=i),\end{cases} \\
& S_{i j k}=\exp \left(-F_{j} \operatorname{Sel}_{k+j-i}-M\right) .
\end{aligned}
$$

For a pulse fishery (Ricker 1975), we let $T F_{j}{ }^{\Delta} \rightarrow F_{j}$ as $T \rightarrow 0$, with $P_{i j k}$ modified accordingly.

The likelihood function for the limited and pulse fishery models is obtained from $L_{1}$ in equation (1) by substituting the appropriate expressions for $P_{i j k}$ and $S_{i j k}$.

### 2.3 Incomplete Mixing of Newly Tagged Fish

We also extend the incomplete mixing model of Hoenig et al. (1998b) to allow age dependence, assuming a year-long fishery. For fully recruited fish in year $j$, we let $F_{j}{ }^{*}$ represent the instantaneous fishing mortality rate for newly tagged fish, and let $F_{j}$ be the rate for previously released fish. The definitions of other parameters are unchanged, and the likelihood is given by $L_{1}$ with

$$
\begin{aligned}
& P_{i j k}= \begin{cases}\left(\prod_{v=i}^{j-1} S_{i v k}\right)\left(1-S_{i j k}\right) \frac{F_{j} \operatorname{Sel}_{k+j-i}}{F_{j} \operatorname{Sel}_{k+j-i}+M} \lambda & (\text { when } j>i) \\
\left(1-S_{i j k}\right) \frac{F_{j} * \operatorname{Sel}_{k}}{F_{j} * \operatorname{Sel}_{k}+M} \lambda & (\text { when } j=i),\end{cases} \\
& S_{i j k}= \begin{cases}\exp \left(-F_{j} \operatorname{Sel}_{k+j-i}-M\right) & (\text { when } j>i) \\
\exp \left(-F_{j} * \operatorname{Sel}_{k}-M\right) & (\text { when } j=i) .\end{cases}
\end{aligned}
$$

## 3. PARAMETER REDUNDANCY

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

Catchpole and Morgan (1997) showed that parameter redundancy is equivalent to singularity of the information matrix $\mathbf{I}(\boldsymbol{\theta})$ for a class of models that includes the product multinomial likelihood $L_{1}$. They also showed how to obtain $\mathbf{I}(\boldsymbol{\theta})$, for a multinomial distribution, in terms of the derivative matrix, $\mathbf{D}(\boldsymbol{\theta})$, which has $i j^{\text {th }}$ element $d_{i j}=\frac{\partial \mu_{j}}{\partial \theta_{i}}$, where the cell expectations $\mu_{j}$ are functions of the unknown parameters $\theta_{i}$. Parameter redundancy is demonstrated by showing that $\mathbf{I}(\boldsymbol{\theta})$ is singular, or, equivalently, that $\mathbf{D}(\boldsymbol{\theta})$ is rank deficient.

In order to use the computer algebra approach described by Catchpole, Morgan, and Viallefont (2002), we considered a small study with 3 age classes tagged in each of 3 years and 3 years of recovery. We assumed that the number of age-specific Sel, $M$ and $\lambda$ parameters was at most 3 (the number of age classes identified at tagging) and did not attempt to generalize to situations with extended age dependence or additional years of recovery. The models studied here, and in subsequent Sections, are represented by a list
of parameters in parentheses. A subscript $y$ indicates that the parameter is year specific, a subscript $a$ indicates that the parameter is age specific, and no subscript means that the parameter is constant over ages and years. If the parameter list includes $\lambda$, or $\lambda_{y}$ etc., then the $\lambda$ 's are unknown and must be estimated. Otherwise, the $\lambda$ 's are assumed known. For example, the most general model studied is denoted $\left(F_{\mathrm{y}}, M_{\mathrm{y}} \cdot \mathrm{a}, \operatorname{Sel}_{\mathrm{a}}, \lambda_{\mathrm{y}} \cdot \mathrm{a}\right)$, where the notation $M_{\mathrm{y} \cdot \mathrm{a}}$ indicates that a separable model is used to account for year and age effects on natural mortality $M$. The age-specific rates for year $1\left(M_{1 a}, a=1,2,3+\right)$ are adjusted using year-specific constants for years 2 and $3\left(M_{2 \mathrm{a}}=b M_{1 a}\right.$ and $\left.M_{3 a}=c M_{1 a}, a=1,2,3+\right)$.

The symbolic algebra package MAPLE (Maple 9, Waterloo Maple Inc. 2003) was used to obtain the matrix $\mathbf{D}(\boldsymbol{\theta})$, and where possible its rank was obtained using computer algebra. For the more complex models it was necessary to determine the rank of $\mathbf{D}(\boldsymbol{\theta})$ numerically by specifying the parameter values. Assuming the $\lambda$ 's are known, the general $\operatorname{model}\left(F_{\mathrm{y}}, M_{\mathrm{y}} \cdot{ }_{\mathrm{a}}, S e l_{\mathrm{a}}\right)$, and all reduced models, are full rank. In contrast, if the $\lambda$ 's are unknown, both the general model $\left(F_{\mathrm{y}}, M_{\mathrm{y}} \cdot \mathrm{a}, S e l_{\mathrm{a}}, \lambda_{\mathrm{y}} \cdot \mathrm{a}\right)$, and the simplest possible model $(F, M, \lambda)$, which assumes $\operatorname{Sel}_{a}=1,1 \leq a \leq 5$, are parameter redundant. Various intermediate models are full rank, however, and so we show results in Figure 1 for a number of models where the $\lambda$ 's are unknown. In one set of reduced models (left side of Figure 1), $M$ and/or $\lambda$ are year specific but not age specific and in the other set (right side of Figure 1), $M$ and/or $\lambda$ are age specific but not year specific. All models with $M$ and/or $\lambda$ year specific but not age specific are full rank. The models $\left(F, M_{a}, \operatorname{Sel}_{a}, \lambda\right)$ and $(F, M$, $S e l_{a}, \lambda_{a}$ ), which include two sets of age specific parameters, but no year specificity, are parameter redundant.

To better understand the source of parameter redundancy, we note that the cell probabilities, $P_{i j k}$, are functions of $\theta=F \operatorname{Sel} \lambda$ and $Z=F \operatorname{Sel}+M$, with appropriate subscripts to indicate year and age dependence. If for a particular model, the number of $F, M, S e l, \lambda$ parameters is greater than the number of distinct $\theta, Z$ parameters, the model is parameter redundant. It is easily seen that the simplest model $(F, M, \lambda)$ is overparameterized, because the $P_{i j k}$ can be written in terms of just two parameters, $\theta=F \lambda$ and $Z=F+M$. For models with $F$ constant, and both Sel, $M$, or both Sel, $\lambda$, age dependent, the number of $F, M, \operatorname{Sel}, \lambda$ parameters exceeds the number of estimable $\theta, Z$ parameters. For example, under model $\left(F, M_{a}, \operatorname{Sel}_{a}, \lambda\right)$, the basic parameters are $\theta_{a}=$ $F S e l_{a} \lambda$, and $Z_{a}=F S e l_{a}+M_{a}$, fewer than the number of $F, M_{a}, S e l_{a}, \lambda$ parameters. In contrast, when $F$ is year specific, there is a greater number of $\theta_{a y}$ and $Z_{a y}$ parameters, and more information for identification of the $F, M, \operatorname{Sel}, \lambda$ parameters.

Parameter redundancy of the simplest model $(F, M, \lambda)$ suggests that full rank models in Figure 1 will exhibit problems associated with near-singularity (Catchpole et al., 2001, Nasution et al., 2004). Following Catchpole et al. (2001), we therefore evaluated $\mathbf{I}(\boldsymbol{\theta})$ and its eigenvalues, and examined the eigenvector corresponding to the smallest eigenvalue ( $\mathrm{EV}_{\text {min }}$ ), for various models and parameter values similar to those used in the simulations below. All calculations assumed $N=1000$ fish tagged and released annually in each age class. As expected, $E V_{\min }$ was smaller for models with $\lambda$ estimated compared to the $\lambda$ known cases, for example, $\mathrm{EV}_{\min }=4.2$ compared to 23.8 for models $\left(F_{y}, M, \operatorname{Sel}_{a}, \lambda\right)$ and $\left(F_{y}, M, \operatorname{Sel}_{a}\right)$, respectively. Near singularity was slightly worse when the number of $M$ parameters increased from 1 to 3 [values of $E V_{\text {min }}$ were 4.2 and 3.4 for models $\left(F_{y}, M, \operatorname{Sel}_{a}, \lambda\right)$ and $\left(F_{y}, M_{a}, \operatorname{Sel}_{a}, \lambda\right)$, respectively]. In the $\lambda$ known case,
reducing the number of Sel parameters by fixing $\mathrm{Sel}_{3}=1$ had a large impact, $E V_{\text {min }}$ increased from 23.8 to 119 for the basic model $\left(F_{y}, M, \operatorname{Sel}_{a}\right)$ and from 8.2 to 61.5 for model $\left(F_{y}, M_{a}, S e l_{a}\right)$. As predicted from the structure of the $\theta, Z$ parameters, values of $\mathrm{EV}_{\text {min }}$ increased with increasing variation in the values of $F_{y}$.

Coefficients in the eigenvector corresponding to $\mathrm{EV}_{\text {min }}$ were of similar absolute magnitude for many of the models with small $\mathrm{EV}_{\text {min }}$ indicating that all parameters are poorly estimated. An exception to this occurred in models with $\mathrm{Sel}_{3}=1$, where the coefficients corresponding to $\mathrm{Sel}_{1}, \mathrm{Sel}_{2}$ indicated better performance for estimators of these parameters. Examining the cell probabilities for direct recoveries, the
approximation $x \approx 1-e^{-x}$, when $x$ is small, gives $P_{i i k}=\left(1-e^{-\left(F S l_{k}+M\right)}\right) \frac{F S e l_{k}}{F S e l_{k}+M} \lambda$ $\approx F \operatorname{Sel}_{k} \lambda$, so that ratios of direct recoveries provide information about ratios of $\operatorname{Sel}_{k}$. Thus if $\operatorname{Sel}_{a}=1$ for one or more of the age classes tagged (i.e., $K>a_{c}$ ), the result is that estimators of $S e l_{a}$ have good precision even when $\lambda$ is estimated (see also Myers and Hoenig, 1997).

## 4. SIMULATION STUDY

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

We used the new version of program SURVIV (White 1983), modified by James Hines of Patuxent Wildlife Research Center, to generate data and to obtain MLEs. We assumed 5 years of tagging and either 5 or 7 years of recovery, with either 500 or 1000 fish tagged annually in each of 5 age classes. Fish were assumed to be fully recruited at age $4\left(\operatorname{Sel}_{a}=1\right.$ for $\left.a>3\right)$. We generated 500 replicate data sets for each case, with parameter values $F_{1}=0.2, F_{2}=0.5, F_{3}=0.3, F_{4}=0.4, F_{5}=0.6, F_{6}=0.3, F_{7}=0.4$, Sel $_{a}=$ $0.6,0.7,0.9$, for $a=1,2,3$, respectively, $M=0.2$, and $\lambda=0.3$. We generated data assuming complete mixing for both a continuous fishery and a pulse fishery. For incomplete mixing models, additional parameter values were $F_{1} *=0.2, F_{2} *=0.6, F_{3} *=$ $0.4, F_{4}{ }^{*}=0.5, F_{5}{ }^{*}=0.7$.

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

Average estimates and standard errors are reported in Table 1 for the case of a continuous fishery with complete mixing, 7 years of recovery, and $F_{y}$ ranging from 0.2 to 0.6. Results for 5 years of recovery showed the same patterns and are not shown.. Similarly, results for the case of a pulse fishery show similar patterns and are not presented here (see Jiang, 2005). When 500 fish are tagged in each age class, estimators under model $\left(F_{y}, M, S e l_{a}\right)$ have good properties with relative bias less than $2 \%$ and
relative standard error (RSE) less than $11 \%$. Under model $\left(F_{y}, M, \operatorname{Sel}_{a}, \lambda\right)$, with the exception of $\hat{\lambda}$, estimators again have little bias, but precision is poor. For example, the RSE of $\hat{\lambda}$ is $42 \%$ for 5 years of recoveries, and $30 \%$ for 7 years of recoveries. RSE for $\hat{M}$ is of similar magnitude. There is a noticeable increase in the precision of estimators when $N=1000$ fish of each age class are tagged annually, compared to tagging 500 fish. For example, RSEs of $\hat{\lambda}$ and $\hat{M}$ are $17 \%$ and $26 \%$, respectively, with $N=1000$, compared to $30 \%$ and $38 \%$, respectively, for $N=500$.

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

Table 1 also shows the effect of augmenting a hypothetical tag return study with a planted tag study with 50 tags planted in the catch to provide an independent estimate of $\lambda$. All estimators are essentially unbiased; relative bias of $\hat{\lambda}$ is less than $2 \%$. With the additional information from the planted tags, the precision of some estimators is still poor, but is substantially improved compared to the case where no external information
about $\lambda$ is available. For instance, the RSEs of $\hat{\lambda}$ and $\hat{M}$ are $15 \%$ and $26 \%$ (compared to $30 \%$ and $38 \%$, respectively, if there are no planted tags) when 500 fish are tagged in each age class each year, and are $13 \%$ and $21 \%$ (compared to $17 \%$ and $26 \%$, respectively, if there are no planted tags) when 1000 fish are tagged in each cohort.

Simulation results for the incomplete mixing situation (Table 2) demonstrate that estimators under model $\left(F_{y}, F^{*}, M, S e l_{a}\right)$ are essentially unbiased and reasonably precise; relative biases for all estimators are less than $2 \%$, and RSEs for most estimators are less than $10 \%$. However, comparing results for the complete and incomplete mixing cases (Tables 1 and 2) we see that standard errors for $\hat{F}_{j}, j=2, \ldots, 5$, are considerably larger in the latter case because of the larger number of parameters that are estimated. Model $\left(F_{y}\right.$, $F^{*}{ }_{y}, M, \operatorname{Sel}_{a}, \lambda$ ) produces estimators with little bias (relative bias less than $5 \%$ for most estimators), but with poor precision, again demonstrating problems associated with nearsingularity when $\lambda$ is estimated.

## 5. STRIPED BASS TAG RETURN STUDY

In the MDNR study, striped bass were tagged with internal anchor tags, the length of each fish was determined, and an age class assigned based on the age length key method (Secor et al. 1995). We grouped data for fish tagged at 8 years or older because of small sample sizes in each year class, and omitted the data for fish tagged at age 2 for the same reason (see the Appendix). Some reported tags were from fish that were caught and released but we assume here that all reported tags represent harvested fish, which results in overestimation of fishing mortality. Methods to account for live releases are discussed in Jiang (2005).

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

Several modifications of the basic models were fit to the data to investigate specific questions of interest. The incomplete mixing models $\left(F_{y}, F_{y}^{*}, M, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \mathrm{Sel}_{5}\right)$ and $\left(F_{y}, F^{*}{ }_{y}, M, \operatorname{Sel}_{3}, \mathrm{Sel}_{4}, \mathrm{Sel}_{5}, \lambda\right)$, were fit to assess whether newly released fish have different fishing mortality rates from previously released fish. To investigate the assumption that $M$ is independent of age, we fit models ( $F_{y}, M_{\mathrm{Y}}, M_{\mathrm{A}}, \operatorname{Sel}_{3}, \mathrm{Sel}_{4}, \mathrm{Sel}_{5}$ ) and $\left(F_{y}, M_{\mathrm{Y}}, M_{\mathrm{A}}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}, \lambda\right)$ which assume complete mixing, and $\left(F_{y}, F^{*}{ }_{y}, M_{\mathrm{Y}}, M_{\mathrm{A}}\right.$, $\left.\operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$ and $\left(F_{y}, F^{*}, M_{\mathrm{Y}}, M_{\mathrm{A}}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}, \lambda\right)$ for the case of incomplete mixing. In these models, $M_{\mathrm{Y}}$ and $M_{\mathrm{A}}$ represent the natural mortality rates for young ( 3 to 5 years) and adult ( $\geq 6$ years) fish, respectively.

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

We used Akaike's information criterion (AIC) to compare multiple nested and nonnested models (Burnham and Anderson 2002). A correction to AIC for small sample sizes made little difference and is not reported. To account for possible overdispersion in the data, due to a lack of independence among fish of capture and survival events, we also implemented the quasilikehood approach recommended by Lebreton et al. (1992) and Burnham and Anderson (2002). The corresponding criterion is QAIC, defined as,

$$
Q A I C=-2 \log [l(\hat{\boldsymbol{\theta}} \mid y)] / \hat{c}+2 p
$$

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

Table 3 displays the values of $A I C, \triangle A I C$ (the change in $A I C$ compared to the smallest $A I C$ value), QAIC and $\triangle Q A I C$ (the change in QAIC compared to the smallest

QAIC value) for models that assume $\lambda=0.43$. The QAIC values were obtained using $\hat{c}=$ 1.18 based on the value of the goodness of fit statistic for Model 1 from SURVIV. With regard to the year when a change in natural mortality may have occurred, AIC and QAIC values (not shown) suggested a change in $M$ beginning in 1999. Of the models investigated, the smallest $A I C$ and $Q A I C$ values were obtained with the most general $\operatorname{model}\left(F_{y}, F^{*}{ }_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$, which assumes year specific $F$ and $F^{*}, M$ both age and period specific, and incomplete mixing of the newly released fish. The next best model differed in that $F$ and $F^{*}$ were constant within the two periods 1991-1994 and 1995-2003 (Model 2 in Table 3). The three models with the best AIC and QAIC values each involved age and period specific $M$, where the subscript A_91-98 indicates a rate for adult fish during 1991 to 1998, Y_91-98 refers to young fish during 1991 to 1998, and so on. Models with age dependent $M$ have better AIC values than those with age independent $M$ (compare Model 5 with 6 , and 7 with 8 ). Comparing each model that includes $F^{*}$ with the corresponding complete mixing model (Models 2 and 4, 5 and 7, 6 and 8, 10 and 12) provides evidence of incomplete mixing because in each case the $A I C$ and $Q A I C$ values are better for the version that includes $F^{*}$.

Evidence that fishing mortality is age dependent is based on noting that the AIC and $Q A I C$ values for the age dependent models $\left(F_{y}, F^{*}, M, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$ and $\left(F_{y}, M, \operatorname{Sel}_{3}, \mathrm{Sel}_{4}, \mathrm{Sel}_{5}\right)$ are substantially smaller than for the corresponding age independent models $\left(F_{y}, F^{*}, M\right)$ and $\left(F_{y}, M\right)$ (compare Model 8 with 12, and 6 with 10 , in Table 3). Likelihood ratio tests also convincingly reject age independence.

Estimates and their standard errors for the striped bass data under model $\left(F_{y}, F^{*}{ }_{y}\right.$, $\left.M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$ with $\lambda=0.43$, and for the
corresponding model with $\lambda$ estimated, are presented in Table 4. Standard error properties agree well with patterns seen in the simulations. When we assume $\lambda=0.43$, the precision of estimates is reasonable (most estimated RSEs $<10 \%$ ), but, except for estimates of selectivity, standard errors are substantially larger when $\lambda$ is estimated.

Point estimates are remarkably similar between the two models, no doubt because $\hat{\lambda}=0.41$ is close to the assumed value of 0.43 . Estimates of selectivity show an increase with age as expected, with an estimate equal to 1 for fish of age 5 years. There is evidence that natural mortality is higher for young fish compared to older fish (0.39 compared to 0.14 from 1991 to 1998 , and 0.63 compared to 0.48 from 1999 to 2003, with $\lambda=0.43$ ). These estimates also reflect an increase in natural mortality for the years 1999 to 2003, compared to the earlier years, coinciding with the observation of mycobacteriosis in striped bass. Estimates of fishing mortality, $F$, do not reflect an increase after relaxation of fishing regulations in 1995.

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

## 6. DISCUSSION

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

Estimators have good properties under models that include year and age dependence of $F$, and limited year and age dependence of $M$, provided that $\lambda$ is known. When $\lambda$ must be estimated, even the basic model with $M$ constant and $F$ year and age dependent shows indications of near-singularity, and estimators have poor precision when as many as 1000 fish are tagged annually in each class. Design options that will lead to better precision include increasing the tag reporting rate (e.g., by using reward tags) or tagging substantially larger numbers of fish. Another option is to include tagging of fish one year younger than that of the first harvest with selectivity assumed to be 0 for this age class (Latour et al. 2003). Our simulation results show that precision can also be improved by obtaining supplemental information about $\lambda$. Thus we support the recommendations of Pollock, Hoenig and Jones (1991), Pollock et al. $(2001,2002)$ and Hearn et al. (2003), that such information should be obtained (e.g., from high reward tagging, observed catches, planted tags) and incorporated into the analysis on a routine basis. Time variation in the tag reporting rate is an additional complication that we have largely ignored, but ideally supplemental information on $\lambda$ should be obtained on a yearly basis.

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

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## APPENDIX

Release and tag return data, by age at tagging, from the MDNR study on striped bass, 1991-2003.


Age 4
$1991 \quad 199219931994199519961997199819992000 \quad 2001 \quad 2002 \quad 2003$

| 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
$1991 \quad 199219931994199519961997199819992000 \quad 2001 \quad 2002 \quad 2003$

| 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
$\begin{array}{lllllllllllllllllllll}1991 & 1992 & 1993 & 1994 & 1995 & 1996 & 1997 & 1998 & 1999 & 2000 & 2001 & 2002 & 2003\end{array}$

| 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
$199119921993199419951996199719981999200020012002 \quad 2003$

| 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+
$1991 \quad 19921993199419951996199719981999 \quad 2000 \quad 2001 \quad 2002 \quad 2003$

| 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 1. Average estimates (with standard errors in parentheses), obtained (a) under model $\left(F_{y}, M, \operatorname{Sel}_{a}\right)$, or $(\mathrm{b}, \mathrm{c})$ under model $\left(F_{y}, M, \operatorname{Sel}_{a}, \lambda\right)$, from simulated data for a continuous complete mixing fishery, assuming a study with 5 years of tagging and 7 years of recoveries. For each of 5 age classes, either $N=500$ fish, or $N=1000$, fish are tagged annually. For (c), the study is supplemented with returns from 50 planted tags.

Results are based on 500 replications.
(a) $\lambda$ known
(b) $\lambda$ estimated no planted tags
(c) $\lambda$ estimated 50 planted tags

| Parameter Value |  |  |  | Continuous complete mixing fishery with $N=500$ |  |
| :--- | :---: | :---: | :---: | ---: | :---: |
|  |  |  |  |  |  |
| $F_{1}$ | 0.2 | $0.20(0.02)$ | $0.20(0.04)$ | $0.20(0.04)$ |  |
| $F_{2}$ | 0.5 | $0.50(0.03)$ | $0.50(0.11)$ | $0.50(0.08)$ |  |
| $F_{3}$ | 0.3 | $0.30(0.02)$ | $0.30(0.07)$ | $0.30(0.05)$ |  |
| $F_{4}$ | 0.4 | $0.40(0.02)$ | $0.40(0.09)$ | $0.40(0.06)$ |  |
| $F_{5}$ | 0.6 | $0.60(0.04)$ | $0.60(0.15)$ | $0.60(0.11)$ |  |
| $F_{6}$ | 0.3 | $0.30(0.03)$ | $0.31(0.09)$ | $0.30(0.07)$ |  |
| $F_{7}$ | 0.4 | $0.40(0.06)$ | $0.42(0.15)$ | $0.41(0.12)$ |  |
| $M$ | 0.2 | $0.20(0.01)$ | $0.20(0.08)$ | $0.20(0.05)$ |  |
| $\lambda$ | 0.3 | - | $0.32(0.09)$ | $0.31(0.05)$ |  |
| $\mathrm{Sel}_{1}$ | 0.6 | $0.61(0.06)$ | $0.61(0.06)$ | $0.61(0.06)$ |  |
| $\mathrm{Sel}_{2}$ | 0.7 | $0.70(0.05)$ | $0.70(0.05)$ | $0.71(0.05)$ |  |
| $\mathrm{Sel}_{3}$ | 0.9 | $0.90(0.06)$ | $0.90(0.06)$ | $0.91(0.06)$ |  |
|  |  |  |  |  |  |

Continuous complete mixing fishery with $N=1000$

| $F_{1}$ | 0.2 | $0.20(0.02)$ | $0.20(0.03)$ | $0.20(0.03)$ |
| :---: | :---: | :---: | :---: | :---: |
| $F_{2}$ | 0.5 | $0.50(0.02)$ | $0.49(0.08)$ | $0.50(0.06)$ |
| $F_{3}$ | 0.3 | $0.30(0.01)$ | $0.30(0.05)$ | $0.30(0.04)$ |
| $F_{4}$ | 0.4 | $0.40(0.02)$ | $0.39(0.06)$ | $0.40(0.05)$ |
| $F_{5}$ | 0.6 | $0.60(0.03)$ | $0.59(0.10)$ | $0.60(0.09)$ |
| $F_{6}$ | 0.3 | $0.30(0.03)$ | $0.30(0.06)$ | $0.30(0.05)$ |
| $F_{7}$ | 0.4 | $0.40(0.05)$ | $0.40(0.10)$ | $0.41(0.09)$ |
| $M$ | 0.2 | $0.20(0.01)$ | $0.20(0.05)$ | $0.20(0.04)$ |
| $\lambda$ | 0.3 | - | $0.31(0.05)$ | $0.30(0.04)$ |
| $\mathrm{Sel}_{1}$ | 0.6 | $0.61(0.04)$ | $0.61(0.04)$ | $0.61(0.04)$ |
| $\mathrm{Sel}_{2}$ | 0.7 | $0.70(0.04)$ | $0.71(0.04)$ | $0.70(0.04)$ |
| $\mathrm{Sel}_{3}$ | 0.9 | $0.90(0.04)$ | $0.90(0.04)$ | $0.91(0.04)$ |

Table 2. Average estimates with standard errors in parentheses from fitting incomplete mixing models (a) $\left(F_{y}, F^{*}, M, \operatorname{Sel}_{a}\right)$ and (b) $\left(F_{y}, F^{*}, M, S_{l}, \lambda\right)$. 500 fish are tagged for each of 5 age classes in each of 5 consecutive years, with either 5 or 7 years of recoveries. Results are based on 500 replications.

|  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
|  |  | 5 Years of recoveries |  |  |  |
| Parameter | Value | (a) $\lambda$ known | (b) $\lambda$ estimated | (a) $\lambda$ known | (b) $\lambda$ estimated |
| $F_{1}^{*}$ | 0.2 | $0.20(0.02)$ | $0.19(0.05)$ | $0.20(0.02)$ | $0.20(0.04)$ |
| $F_{2}^{*}$ | 0.6 | $0.60(0.05)$ | $0.59(0.15)$ | $0.60(0.04)$ | $0.60(0.12)$ |
| $F_{3}^{*}$ | 0.4 | $0.40(0.04)$ | $0.39(0.10)$ | $0.40(0.03)$ | $0.40(0.08)$ |
| $F_{4}^{*}$ | 0.5 | $0.50(0.04)$ | $0.49(0.13)$ | $0.50(0.04)$ | $0.50(0.10)$ |
| $F_{5}^{*}$ | 0.7 | $0.70(0.05)$ | $0.70(0.19)$ | $0.70(0.05)$ | $0.70(0.15)$ |
| $F_{2}$ | 0.5 | $0.50(0.05)$ | $0.49(0.12)$ | $0.50(0.05)$ | $0.50(0.10)$ |
| $F_{3}$ | 0.3 | $0.30(0.03)$ | $0.29(0.08)$ | $0.30(0.03)$ | $0.30(0.06)$ |
| $F_{4}$ | 0.4 | $0.40(0.04)$ | $0.39(0.10)$ | $0.40(0.03)$ | $0.40(0.08)$ |
| $F_{5}$ | 0.6 | $0.60(0.08)$ | $0.61(0.19)$ | $0.60(0.06)$ | $0.60(0.14)$ |
| $F_{6}$ | 0.3 |  |  | $0.30(0.04)$ | $0.31(0.09)$ |
| $F_{7}$ | 0.4 |  |  | $0.40(0.07)$ | $0.42(0.14)$ |
| $M$ | 0.2 | $0.20(0.02)$ | $0.20(0.07)$ | $0.20(0.02)$ | $0.20(0.06)$ |
| $\lambda$ | 0.3 | - | $0.33(0.11)$ | - | $0.31(0.07)$ |
| $\mathrm{Sel}_{1}$ | 0.6 | $0.61(0.06)$ | $0.61(0.06)$ | $0.61(0.06)$ | $0.61(0.06)$ |
| $\mathrm{Sel}_{2}$ | 0.7 | $0.70(0.06)$ | $0.71(0.06)$ | $0.71(0.05)$ | $0.71(0.05)$ |
| $\mathrm{Sel}_{3}$ | 0.9 | $0.90(0.06)$ | $0.90(0.06)$ | $0.90(0.06)$ | $0.90(0.06)$ |
|  |  |  |  |  |  |

Table 3. Values of model selection criteria for a series of models applied to the MDNR striped bass data set. All models assume $\lambda=0.43$.

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

Models
1: $\left(F_{y}, F^{*}{ }_{y}, \quad M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \mathrm{Sel}_{3}, \mathrm{Sel}_{4}, \mathrm{Sel}_{5}\right)$
2: $\left(F_{91-94}, F_{95-03}, F^{91-94}{ }^{*}, F^{*}{ }_{95-03}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}\right.$, Sel $\left._{5}\right)$
3: $\left(F_{y}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}\right.$, Sel $_{4}$, Sel $\left._{5}\right)$
4: ( $F_{91-94}, F_{95-03}, M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}$, Sel $\left._{5}\right)$
5: $\left(F_{y}, M_{Y}, M_{A}, \operatorname{Sel}_{3}, \operatorname{Sel}_{4}, \operatorname{Sel}_{5}\right)$
6. $\left(F_{y}, M, \operatorname{Sel}_{3}\right.$, Sel $_{4}$, Sel $\left._{5}\right)$
7. $\left(F_{y}, F^{*}, M_{Y}, M_{A}, \mathrm{Sel}_{3}, \mathrm{Sel}_{4}, \mathrm{Sel}_{5}\right)$
8. $\left(F_{y}, F^{*}, M, \mathrm{Sel}_{3}, \mathrm{Sel}_{4}, \mathrm{Sel}_{5}\right)$
9. $\left(F_{y}, M_{91-98}, M_{99-03}\right.$, Sel $_{3}$, Sel $_{4}$, Sel $\left._{5}\right)$
10. $\left(F_{y}, M\right)$
11. $\left(F_{y}, F^{*}, M_{91-98}, M_{99-03}\right.$, Sel $_{3}$, Sel $_{4}$, Sel $\left._{5}\right)$
12. $\left(F_{y}, F^{*}, M\right)$

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

Table 4. Estimates, with standard errors in parentheses, for the MDNR striped bass data, (a) with $\lambda=0.43$, and (b) for the case when $\lambda$ is estimated, under the model $\left(F_{y}, F^{*}{ }_{y}\right.$, $\left.M_{Y_{-} 91-98}, M_{Y_{-} 99-03}, M_{A_{-} 91-98}, M_{A_{-} 99-03}, \mathrm{Sel}_{3}, \mathrm{Sel}_{4}, \mathrm{Sel}_{5}\right)$, i.e., Model 1 in Table 3.

| Parameter | (a) $\lambda=0.43$ | (b) $\lambda$ estimated | Parameter | (a) $\lambda=0.43$ | (b) $\lambda$ estimated |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  |  |  |  |  | $F_{91}^{*}$ | 0.25 | $(0.02)$ | 0.26 |$(0.12)$



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

## Appendix: Fishing and Natural Mortality Rates of Striped Bass in Virginia Waters as Determined by Tag Returns.

The tagging data from Virginia were not suitable for estimating age- and timespecific mortality rates due to small sample sizes. Consequently, time-specific estimates of fishing and natural mortality were obtained under the assumption that age-specific factors were relatively unimportant. These analyses were completed by Mr. Honghua Jiang under the supervision of Dr. Kenneth Pollock.

A variety of models were fitted to the data reflecting whether fish aged 2 and above or fish aged 4 and above were used, whether the tag reporting rate was fixed at an assumed value or estimated from the data, and whether natural mortality was assumed constant over time or allowed to vary from one time period to the next. The results are consistent with what was found for Maryland striped bass. Fishing mortality rates have been low, and natural mortality rate appears to have gone up in recent years.

Table 1. Parameter estimates (Param) and standard errors (SE) from fitting models with the following parameters estimated (a) (Fk, Fr, M) and (b) (Fk, Fr, M, $\lambda k, \lambda r$ ) to the Virginia striped bass data (for age 4 and greater). $F k(x x)$ refers to the fishing mortality (fish are killed) in year $x x ; \operatorname{Fr}(x x)$ refers to the force of mortality on tags (fish released) in year $x x ; M$ is the instantaneous rate of natural mortality, $\lambda k$ is the tag reporting rate for killed fish, and $\lambda r$ is the reporting rate for released fish. In model (a), the values of $\lambda k$ and $\lambda r$ were fixed at 0.43.

|  | ( a |  | (b) |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Param | SE | Param | SE |
| Fk(90) | 0.127 | 0.018 | 0.242 | 0.066 |
| Fk(91) | 0.152 | 0.013 | 0.313 | 0.073 |
| Fk(92) | 0.187 | 0.021 | 0.359 | 0.084 |
| Fk(93) | 0.178 | 0.023 | 0.365 | 0.085 |
| Fk(94) | 0.195 | 0.031 | 0.461 | 0.114 |
| Fk(95) | 0.208 | 0.029 | 0.418 | 0.104 |
| Fk(96) | 0.181 | 0.032 | 0.396 | 0.102 |
| Fk(97) | 0.198 | 0.028 | 0.566 | 0.129 |
| Fk(98) | 0.164 | 0.022 | 0.524 | 0.124 |
| Fk(99) | 0.168 | 0.025 | 0.557 | 0.145 |
| Fk(00) | 0.167 | 0.017 | 0.423 | 0.108 |
| Fk(01) | 0.110 | 0.014 | 0.223 | 0.060 |
| Fk(02) | 0.114 | 0.020 | 0.201 | 0.054 |
| Fr(90) | 0.175 | 0.021 | 0.225 | 0.114 |
| Fr(91) | 0.154 | 0.013 | 0.189 | 0.095 |
| Fr(92) | 0.121 | 0.017 | 0.154 | 0.079 |
| Fr(93) | 0.163 | 0.021 | 0.213 | 0.109 |
| Fr(94) | 0.152 | 0.027 | 0.188 | 0.103 |
| Fr(95) | 0.100 | 0.020 | 0.132 | 0.072 |
| $\operatorname{Fr}(96)$ | 0.076 | 0.020 | 0.096 | 0.054 |
| Fr(97) | 0.112 | 0.020 | 0.174 | 0.091 |
| Fr(98) | 0.088 | 0.016 | 0.141 | 0.075 |
| Fr(99) | 0.060 | 0.014 | 0.098 | 0.055 |
| Fr(00) | 0.102 | 0.013 | 0.147 | 0.076 |
| $\operatorname{Fr}(01)$ | 0.066 | 0.011 | 0.080 | 0.041 |
| Fr(02) | 0.076 | 0.016 | 0.091 | 0.043 |
| Fk(03) | 0.181 | 0.032 | 0.265 | 0.073 |
| Fr(03) | 0.083 | 0.020 | 0.084 | 0.035 |
| Fk(04) | 0.239 | 0.036 | 0.396 | 0.109 |
| $\operatorname{Fr}(04)$ | 0.102 | 0.020 | 0.104 | 0.039 |
| M | 0.423 | 0.015 | 0.180 | 0.128 |
| $\lambda \mathrm{k}$ | 0.430 | 0.000 | 0.189 | 0.041 |
| $\lambda r$ | 0.430 | 0.000 | 0.316 | 0.156 |

Table 2. Parameter estimates (Param) and standard errors (SE) from fitting models with the following parameters estimated (a) (Fk, Fr, M90-96,97-04) and (b) (Fk, Fr, M90-96,97-04, $\lambda k, \lambda r$ ) to the Virginia striped bass data (for age 4 and greater). $F k(x x)$ refers to the fishing mortality (fish are killed) in year xx; $\operatorname{Fr}(x x)$ refers to the force of mortality on tags (fish released) in year xx; $M_{90-96,97-04}$ indicates one instantaneous rate of natural mortality is estimated for the period 1990-1996 and a second one is estimated for 1997-2004, $\lambda k$ is the tag reporting rate for killed fish, and $\lambda r$ is the reporting rate for released fish. In model (a), the values of $\lambda k$ and $\lambda r$ were fixed at 0.43.

|  | ( a ) |  | (b) |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Param | SE | Param | SE |
| Fk(90) | 0.130 | 0.019 | 0.267 | 0.058 |
| Fk(91) | 0.164 | 0.015 | 0.348 | 0.059 |
| Fk(92) | 0.231 | 0.028 | 0.410 | 0.076 |
| Fk(93) | 0.219 | 0.029 | 0.471 | 0.087 |
| Fk(94) | 0.242 | 0.040 | 0.467 | 0.101 |
| Fk(95) | 0.239 | 0.034 | 0.485 | 0.096 |
| Fk(96) | 0.217 | 0.039 | 0.493 | 0.104 |
| Fk(97) | 0.214 | 0.029 | 0.750 | 0.118 |
| Fk(98) | 0.160 | 0.021 | 0.760 | 0.120 |
| Fk(99) | 0.149 | 0.022 | 0.713 | 0.134 |
| Fk(00) | 0.150 | 0.015 | 0.543 | 0.098 |
| Fk(01) | 0.095 | 0.012 | 0.217 | 0.046 |
| Fk(02) | 0.080 | 0.014 | 0.225 | 0.049 |
| Fr(90) | 0.184 | 0.022 | 0.151 | 0.086 |
| $\operatorname{Fr}(91)$ | 0.160 | 0.015 | 0.150 | 0.085 |
| Fr(92) | 0.152 | 0.022 | 0.134 | 0.077 |
| $\operatorname{Fr}(93)$ | 0.199 | 0.027 | 0.170 | 0.099 |
| Fr(94) | 0.188 | 0.035 | 0.124 | 0.077 |
| Fr(95) | 0.116 | 0.023 | 0.087 | 0.053 |
| $\operatorname{Fr}(96)$ | 0.091 | 0.024 | 0.059 | 0.037 |
| Fr(97) | 0.126 | 0.022 | 0.112 | 0.066 |
| Fr(98) | 0.086 | 0.015 | 0.094 | 0.056 |
| Fr(99) | 0.055 | 0.013 | 0.058 | 0.036 |
| $\operatorname{Fr}(00)$ | 0.090 | 0.011 | 0.101 | 0.058 |
| $\operatorname{Fr}(01)$ | 0.056 | 0.009 | 0.045 | 0.026 |
| $\operatorname{Fr}(02)$ | 0.058 | 0.012 | 0.057 | 0.030 |
| Fk(03) | 0.119 | 0.020 | 0.260 | 0.063 |
| $\operatorname{Fr}(03)$ | 0.056 | 0.013 | 0.052 | 0.025 |
| Fk(04) | 0.140 | 0.020 | 0.293 | 0.072 |
| $\mathrm{Fr}(04)$ | 0.065 | 0.012 | 0.033 | 0.015 |
| M90-96 | 0.893 | 0.048 | 0.609 | 0.112 |
| M97-04 | 0.297 | 0.017 | 0.083 | 0.099 |
| $\lambda \mathrm{k}$ | 0.430 | 0.000 | 0.168 | 0.023 |
| $\lambda r$ | 0.430 | 0.000 | 0.488 | 0.272 |

Table 3. Parameter estimates (Param) and standard errors (SE) from fitting models with the following parameters estimated (a) (Fk, Fr, M90-96,97-04) and (b) (Fk, Fr, M90-96,97-04, $\lambda k, \lambda r$ ) to the Virginia striped bass data (for age 2 and greater). $F k(x x)$ refers to the fishing mortality (fish are killed) in year xx; $\operatorname{Fr}(x x)$ refers to the force of mortality on tags (fish released) in year xx; $M_{90-96,97-04}$ indicates one instantaneous rate of natural mortality is estimated for the period 1990-1996 and a second one is estimated for 1997-2004, $\lambda k$ is the tag reporting rate for killed fish, and $\lambda r$ is the reporting rate for released fish. In model (a), the values of $\lambda k$ and $\lambda r$ were fixed at 0.43.

|  | ( a |  | (b) |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Param | SE | Param | SE |
| Fk(90) | 0.122 | 0.023 | 0.182 | 0.057 |
| Fk(91) | 0.165 | 0.021 | 0.259 | 0.067 |
| Fk(92) | 0.236 | 0.032 | 0.360 | 0.091 |
| Fk(93) | 0.227 | 0.032 | 0.347 | 0.086 |
| Fk(94) | 0.263 | 0.043 | 0.428 | 0.107 |
| Fk(95) | 0.274 | 0.042 | 0.469 | 0.116 |
| Fk(96) | 0.195 | 0.035 | 0.416 | 0.111 |
| Fk(97) | 0.199 | 0.039 | 0.370 | 0.105 |
| Fk(98) | 0.306 | 0.058 | 0.645 | 0.179 |
| Fk(99) | 0.240 | 0.034 | 0.578 | 0.163 |
| Fk(00) | 0.114 | 0.023 | 0.196 | 0.065 |
| Fk(01) | 0.111 | 0.024 | 0.145 | 0.047 |
| Fk(02) | 0.252 | 0.057 | 0.286 | 0.084 |
| Fr(90) | 0.135 | 0.025 | 0.159 | 0.145 |
| Fr(91) | 0.153 | 0.020 | 0.184 | 0.164 |
| Fr(92) | 0.166 | 0.027 | 0.193 | 0.172 |
| Fr(93) | 0.209 | 0.031 | 0.241 | 0.218 |
| Fr(94) | 0.199 | 0.037 | 0.246 | 0.237 |
| Fr(95) | 0.073 | 0.020 | 0.097 | 0.095 |
| Fr(96) | 0.083 | 0.022 | 0.127 | 0.117 |
| Fr(97) | 0.101 | 0.027 | 0.137 | 0.125 |
| Fr(98) | 0.076 | 0.027 | 0.113 | 0.106 |
| Fr(99) | 0.103 | 0.022 | 0.165 | 0.153 |
| Fr(00) | 0.055 | 0.016 | 0.076 | 0.073 |
| Fr(01) | 0.064 | 0.018 | 0.069 | 0.065 |
| Fr(02) | 0.114 | 0.035 | 0.107 | 0.098 |
| Fk(03) | 0.427 | 0.140 | 0.362 | 0.129 |
| Fr(03) | 0.242 | 0.088 | 0.168 | 0.164 |
| Fk(04) | 0.924 | 0.556 | 0.684 | 0.329 |
| Fr(04) | 0.449 | 0.276 | 0.245 | 0.280 |
| M90-96 | 0.231 | 0.019 | 0.083 | 0.177 |
| M97-04 | 0.407 | 0.037 | 0.168 | 0.125 |
| $\lambda \mathrm{k}$ | 0.430 | 0.000 | 0.250 | 0.057 |
| $\lambda r$ | 0.430 | 0.000 | 0.347 | 0.312 |

