Bias in survival estimates from tag-recovery models where catch-and-release is common, with an example from Atlantic striped bass (*Morone saxatilis*)

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Abstract: Survival rate is underestimated when tag-recovery models include tags recovered from harvested and caught-and-released fish. The magnitude of the bias depends on tag-recovery rate, proportion of catch released alive, and reporting rate; changes in these factors over time confound temporal changes in survival. The bias is of potential concern for any tagging study where catch-and-release is mandatory or practiced voluntarily. The bias is of concern particularly for the Atlantic striped bass (*Morone saxatilis*) tagging study where catch-and-release is common and anglers commonly remove the tag upon capture regardless of fish disposition. Biased estimates of striped bass survival did not change with changes in harvest regulation during the mid-1990s. However, bias-adjusted estimates of survival showed a decrease, which corresponds to the regulatory change made in 1995. Year-specific reporting rate is critical to bias adjustment, underscoring the need for reward tags in fish tagging studies. Tag-recovery modeling allows for a diverse set of models, each of which can produce widely different estimates with far-reaching consequences for management. We applied model averaging to base inference on a weighted average of parameter estimates and to account for model selection uncertainty.

Résumé : Le taux de survie est sous-estimé lorsque les modèles de récupération des marques incluent les marques récupérées sur des poissons capturés et sur des poissons remis à l'eau. L'ampleur du biais dépend du taux de récupération des marques, de la proportion des poissons pris qui sont remis à l'eau vivants et du taux de déclaration; des changements dans ces facteurs au fil du temps brouillent les changements temporels dans la survie. Le biais peut causer des problèmes dans une étude de marquage lorsque la remise à l'eau est obligatoire ou pratiquée de façon volontaire. Ce biais est particulièrement préoccupant dans l'étude de marquage du bar rayé (*Morone saxatilis*) de l'Atlantique, car la remise à l'eau est courante, et les pêcheurs enlèvent généralement la marque du poisson dès la capture, qu'ils gardent ou non le poisson. Les estimations biaisées de la survie du bar rayé n'ont pas changé malgré la modification du règlement de capture au milieu des années 90. Toutefois, les estimations de la survie ajustées en fonction du biais ont montré une baisse, ce qui correspond aux changements dans la réglementation adoptés en 1995. Le taux de déclaration d'une année donnée est critique pour l'ajustement en fonction du biais, ce qui fait ressortir la nécessité de donner des primes en échange des marques dans les études de marquage des poissons. La modélisation de la récupération des marques permet d'avoir recours à des modèles divers, dont chacun peut produire des estimations très différentes, ce qui peut avoir des conséquences d'une grande ampleur dans la gestion. Nous avons appliqué un moyennage aux modèles pour fonder nos inférences sur la moyenne pondérée des estimations des paramètres et pour prendre en compte l'incertitude dans le choix du modèle.

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Introduction

Brownie et al. (1985) published an influential handbook that presented methods of tag-recovery modeling and synthesized important early work. Hunted populations of waterfowl provided much of the motivation for Brownie et al. (1985). However, lake trout (*Salvelinus namaycush*) was the focus during early development of tag-recovery models (Youngs and Robson 1975), and the methods of Brownie et al. (1985) have been applied and extended to studies of fish populations (e.g., Schwarz and Arnason 1990; Dorazio 1993; Hoenig et al. 1998*b*). One important difference between waterfowl and fish populations involves the disposition of recaptured animals. Although the tag-recovery process for waterfowl (i.e., hunting) results only in dead recoveries, the recovery process for fish can result in dead recoveries (i.e., harvest) or live recaptures (i.e., catch-and-release). The extent of live recaptures (i.e., live release after tag recovery) in a fish tagging study depends on fishing methods and regulations. Analysis of tag recoveries that include live recaptures violates an underlying assumption of the tag-recovery models: the fate of the tag corresponds to the fate of the fish. If a tag is recovered (i.e., the tag "dies") and the recaptured fish is released (i.e., the fish lives), then the connection between the tag and fish is broken. This limitation of tag-recovery models was recognized early on by Youngs and Robson (1975, p. 2365) who stated that "this model is appropriate only for recaptures that are removed from the population."

We were motivated by analysis of Atlantic striped bass (*Morone saxatilis*) tagging data to assess bias in tag-recovery estimates when live recaptures are treated as dead recoveries. Although there are other tagging programs, we have been involved in the cooperative state and federal tagging effort initially funded through the "Emergency Striped Bass Study" (Richards and Rago 1999). In this program, anglers commonly remove the tag, regardless of the disposition of the recaptured fish, prior to reporting the tag's number to the U.S. Fish and Wildlife Service. Tag removal promotes accurate reporting of the tag's number. Unfortunately, tag removal from live recaptures also causes a lack of correspondence between the fate of the tag and the fate of the striped bass. Tag-recovery models have been applied to these data to estimate survival of striped bass, although some tags were recovered from fish caught and released alive (Dorazio 1993, 1997).

Youngs and Robson (1975) ignored live recaptures in their analysis of angler tag recoveries. Their strategy applied to Atlantic striped bass would lead to ignoring a significant amount of data, especially during years when harvest was severely restricted. Burnham (1991) and Barker (1997) developed models to analyze simultaneously dead recoveries and live recaptures. However, the models do not allow for the removal of the tag prior to release, as is the case for the Atlantic striped bass and, perhaps, other tagging programs. Bias in survival estimates based on tag recoveries pooled from both harvested and released fish has not been assessed previously. This bias is of potential concern for any fish tagging study where anglers practice catch-and-release or where regulations on fish length or fishing season cause a portion of the catch to be released.

The purpose of this paper is to discuss estimation of survival and mortality from tag-recovery data, with emphasis on bias due to tags recovered from fish caught and released. We begin with a brief review of the basic tag-recovery model and follow with discussion of a recently presented model selection technique, called model averaging (Burnham and Anderson 1998), and its application to tag-recovery modeling. (Through model averaging, inference is not conditional on one "best" model, but rather, estimates are weighted across a set of models and model selection uncertainty is incorporated as a variance component.) We then derive formulae for the bias due to recovery of tags from live recaptures, and we present methods to assess the bias. We apply the methods to estimate survival and mortality for Atlantic coast striped bass tagged in the Hudson River, the Maryland portion of the Chesapeake Bay, and the Delaware River during the period 1988–1997.

Materials and methods

Basic tag-recovery models

The building blocks of tag-recovery models are the expected probabilities of tag recoveries, which arise from the potential fates of tagged animals. After release of a tagged fish in year i, a tag is recovered during year $j = i$, $i + 1$, $i + 2$, and so on until the final year of the study or the tag is not recovered at all. The expected probability (π_{ij}) that a tag is released in year i and recovered in year j is modeled as a function of annual survival and recovery rates. This relationship provides the basis for estimating animal survival (or its complement, mortality) from tag releases and recoveries. In the models presented by Brownie et al. (1985), the recovery rate, which is interpreted as a measure of sampling intensity, is a function of tagging-induced mortality, tag retention, catch rate, and tag reporting rate (Hoenig et al. 1998*a*).

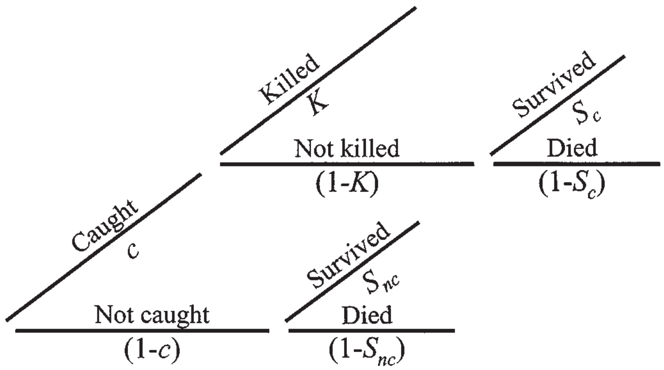
Consider a simple model where survival (S) and recovery rates (f) are equal among years, N_i fish are tagged and released in year i, and all fish caught are killed. For a tag to be recovered during the first year after release, the tagged fish must survive the tagging process with tag intact, be caught, and have its tag reported (i.e., $\pi_{i,i} = f$). For the tag to be recovered during the second year, the tagged fish must survive the first year after release with tag intact and then be recovered (i.e., $\pi_{i,i+1} = S \cdot f$). For the tag to be recovered during the third year, the tagged fish must survive the first and the second year after release with the tag intact and then be recovered (i.e., $\pi_{i,i+2} = S \cdot S \cdot f$). In this way, a tag-recovery model is developed and could be generalized to allow survival and recovery rates to vary, by time for example.

By releasing multiple batches (or cohorts) of tagged fish and making certain assumptions (such as tagged cohorts share the same recovery and survival rates, and fates of tagged fish are independent) the set of releases $\{N_i\}$ and recoveries $\{R_{ij}\}$ can be modeled using a product multinomial distribution with likelihood function

$$(1) \qquad L(\pi_{ij}; R_{ij}, N_i) = \prod_{i=1}^{k} \left[\binom{N_i}{R_{ii}, \ldots, R_{il}, R_{i,l+1}} \prod_{j=i}^{l+1} \pi_{ij}^{R_{ij}} \right]$$

The π_{ij} in the likelihood function are the expected probabilities of recovery and are functions of the recovery and survival rates (f_j and S_j). This model representing a theoretical expectation can be compared with the number of tags released in year i and recovered in year j (R_{ij}). Consequently, the maximum likelihood estimates are those values of S and f that maximize the likelihood function. Brownie et al. (1985) listed the important assumptions underlying these models.

Fig. 1. Potential fates of tagged fish alive at the start of the tagging occasion. Fishing capture probability is denoted by c, and K denotes probability that a caught fish is killed. Survival probabilities of fish caught but rereleased and fish never caught are denoted by S_c and S_{nc}, respectively.



Model averaging

The basic tag-recovery model is generalized by allowing parameters to vary across time, space, and demographic characteristics. The result is a set of candidate models, some of which will be selected for estimation of survival rates. The approach for model selection presented by Brownie et al. (1985) combines goodness-of-fit (GOF) statistics with likelihood ratio tests (LRT) to arrive at a "best-fitting" model. However, there are a couple of shortcomings with this approach. First, LRT can be used only with "nested" models. A thorough analysis will often include models that are not nested. Second, it is common for more than one model to be equal, or essentially equal, in their fit to the data, which frustrates the goal of selecting the "best" model.

Recent work indicates that greater reliance should be placed on other measures of model fit that are useful for nonnested models, e.g., Akaike's information criteria (AIC), over LRTs for model selection (Burnham et al. 1995). Also, Buckland et al. (1997) considered the problem of model selection and presented methods to estimate parameters by a weighted average of the "better-fitting" models, with the weights being a function of the AIC (also see Burnham and Anderson 1998). Thus, by use of model averaging, the need to select one model for estimating parameters is avoided and model selection uncertainty is incorporated into the variance of parameter estimates.

Estimates of model-averaged survival rates are obtained by (Buckland et al. 1997)

$$(2) \qquad \hat{S}_t = \sum_{i=1}^{C} w_i \hat{S}_{t,i}$$

where $\hat{S}_t$ is estimated survival rate for year t, C is total number of candidate models, $\hat{S}_{t,i}$ is estimated survival rate for year t and model i, and w_i is relative weight for model i. Buckland et al. (1997) recommend that the weight be a function of the AIC. The number of estimable parameters and model likelihood are used to compute the AIC for a given model by AIC = $-2 \ln L + 2np$, where $\ln L$ is the natural log of the likelihood and np is the number of estimated model parameters. Then the weight w_i is calculated by

$$(3) \qquad w_i = \frac{e^{-\frac{\Delta \mathrm{AIC}_i}{2}}}{\sum_{j=1}^{C} e^{-\frac{\Delta \mathrm{AIC}_j}{2}}}$$

where $\Delta\mathrm{AIC}_i$ is the difference between the AIC for the ith model and the minimum AIC, $i = 1,..., C$ (Burnham and Anderson 1998). Thus, the better the model fit, the smaller the AIC and the larger the value of w_i. Burnham and Anderson (1998) used the term "Akaike weight" for w_i and recommended AICc, a small-sample version of AIC, which is compatible with model averaging.

An approximate standard error for $\hat{S}_t$ is given by Buckland et al. (1997):

$$(4) \qquad \sigma_t = \sum_{i=1}^{C} w_i (V_{t,i} + [\hat{S}_{t,i} - \hat{S}_t]^2)^{1/2}$$

where $V_{t,i}$ is estimated variance from model i. We computed approximate $(1 - \alpha)$% confidence intervals based on a logit transformation of $\hat{S}_t$, i.e., $y_t = \ln\left(\frac{\hat{S}_t}{1-\hat{S}_t}\right)$ (Burnham et al. 1987, p. 214). The confidence limits for $\hat{S}_t$ were calculated by

$$(5) \qquad \left[\frac{\exp\left(y_t - Z_{1-\frac{\alpha}{2}} \frac{\sigma_t}{\hat{S}_t(1-\hat{S}_t)}\right)}{1+\exp\left(y_t - Z_{1-\frac{\alpha}{2}} \frac{\sigma_t}{\hat{S}_t(1-\hat{S}_t)}\right)}, \frac{\exp\left(y_t - Z_{1-\frac{\alpha}{2}} \frac{\sigma_t}{\hat{S}_t(1-\hat{S}_t)}\right)}{1+\exp\left(y_t - Z_{1-\frac{\alpha}{2}} \frac{\sigma_t}{\hat{S}_t(1-\hat{S}_t)}\right)}\right]$$

where $Z_{1-\frac{\alpha}{2}}$ is the $(1 - \frac{\alpha}{2})$ percentile of the standard normal distribution.

Bias due to release of recaptured fish

White and Burnham (1999) reparameterized recovery rate in tag-recovery models to create a consistent framework for modeling mark–recapture data. The framework provided the basis for the program MARK, which is a comprehensive software program for the analysis of capture–recapture data (White and Burnham 1999). In their formulation, recovery rate was redefined as $f = (1 - S)r$, where r is the rate at which tags are reported from dead fish, regardless of the source of mortality. The parameterization of tag recovery, $(1 - S)r$, makes clear the implicit assumption that the tagged animal dies before the tag is reported. The assumption is violated when tags are recovered from fish caught and released. This can be demonstrated when we consider the extreme case where no fish from a tagged cohort die from any cause (i.e., $S = 1$) and some fish are caught but released (tags are recovered and the fish suffered no ill effect from catch-and-release). If the resulting releases and recoveries are used for the tag-recovery models, then the estimate of S will be <1, even though S is in fact 1. Heuristically, there is a bias due to including recoveries from live recaptures, and the tag-based estimates of survival underestimate true survival.

Let c be fishing capture probability and K be the probability that a caught fish is killed. Let S_c and S_{nc} be the survival probabilities of a fish caught but rereleased and a fish never caught, respectively. Then the fate of each fish alive at the start of a time interval falls into one of five categories (Fig. 1). Tags can be recovered from fish caught and killed (cK) or from fish caught and released alive ($c(1 - K)$), subject to reporting rates for killed fish (λ_K) and fish released alive (λ_L). The λ_K and λ_L are the rates that anglers report tags recovered from captured fish; these rates are distinguished from the

Table 1. Expected probabilities of recovery for tag recoveries arising from fish that were harvested or released alive after recapture but with the tag removed.

Release year	Fate of catch	Expected probabilities of recovery for year: 1	2	3
1	Released	f_{L1}	$S_1\left\{\frac{\lambda_1-(f_{L1}+f_{K1})}{\lambda_1-\left[(1-\theta_1)f_{L1}+f_{K1}\right]}\right\}f_{L2}$	$S_1\left\{\frac{\lambda_1-(f_{L1}+f_{K1})}{\lambda_1-\left[(1-\theta_1)f_{L1}+f_{K1}\right]}\right\}S_2\left\{\frac{\lambda_2-(f_{L2}+f_{K2})}{\lambda_2-\left[(1-\theta_2)f_{L2}+f_{K2}\right]}\right\}f_{L3}$
	Harvested	f_{K1}	$S_1\left\{\frac{\lambda_1-(f_{L1}+f_{K1})}{\lambda_1-\left[(1-\theta_1)f_{L1}+f_{K1}\right]}\right\}f_{K2}$	$S_1\left\{\frac{\lambda_1-(f_{L1}+f_{K1})}{\lambda_1-\left[(1-\theta_1)f_{L1}+f_{K1}\right]}\right\}S_2\left\{\frac{\lambda_2-(f_{L2}+f_{K2})}{\lambda_2-\left[(1-\theta_2)f_{L2}+f_{K2}\right]}\right\}f_{K3}$
2	Released		f_{L2}	$S_2\left\{\frac{\lambda_2-(f_{L2}+f_{K2})}{\lambda_2-\left[(1-\theta_2)f_{L2}+f_{K2}\right]}\right\}f_{L3}$
	Harvested		f_{K2}	$S_2\left\{\frac{\lambda_2-(f_{L2}+f_{K2})}{\lambda_2-\left[(1-\theta_2)f_{L2}+f_{K2}\right]}\right\}f_{K3}$
3	Released			f_{L3}
	Harvested			f_{K3}

Note: Information on fate of catch is supplied by those who report the tag. To estimate survival and recovery rates, independent estimates of year-specific reporting rate (λ_i) and survival immediately after catch-and-release (θ_i) must be added as constants. A superior approach is to specify likelihoods for λ_i and θ_i and construct a full likelihood, i.e., $L(\pi_{ij};R_{ij},N_i)L(\theta)L(\lambda)$, so that all relevant parameters can be estimated simultaneously.

reporting rate r of the MARK formulation. Survival conditioned on the event that the fish was caught (S_c) applies to the entire time interval, but only for fish caught and rereleased.

Fish survival rate is $S_{fish} = c(1-K)S_c + (1-c)S_{nc}$, but tag survival rate is $S_{tag} = (1-c)S_{nc}$. The rate that fish are caught and killed is finite exploitation rate, $cK = f_K/\lambda_K$. Similarly, the rate that fish are caught and released is $c(1-K) = f_L/\lambda_L$. Thus, the relationship between fish survival and tag survival is

$$(6)\qquad S_{tag} = S_{fish} - c(1-K)S_c = S_{fish} - \left(\frac{f_L}{\lambda_L}\right)S_c$$

Capture is known to affect survival (Diodati and Richards 1996), leading to the possibility that $S_c < S_{nc}$. On the other hand, the conditioning event of capture is relevant because the fish must have survived to capture. Consequently, it is possible that $S_c > S_{nc}$. However, to make the problem tractable, we proceed by assuming $S_c = S_{nc}$ and rearranging $S_{fish} = c(1-K)S_c + (1-c)S_{nc}$, which leads to $S_{fish}/(1-cK) = S_c = S_{nc}$. Thus, we have

$$(7)\qquad S_{tag} = S_{fish}\left(1-\frac{f_L/\lambda_L}{1-f_K/\lambda_K}\right)$$

An alternative form relies on the recovery rate ($f = f_L + f_K$) and the proportion of tags recovered from fish caught and released alive ($P_L = f_L/f$):

$$(8)\qquad S_{tag} = S_{fish}\left[1-\frac{P_L\ f/\lambda_L}{1-(1-P_L)\ f/\lambda_K}\right]$$

Typically, λ_L and λ_K are unknown and there is no information in the recovery data about these reporting rates. We might assume they are the same, $\lambda_L = \lambda_K = \lambda$, and hence:

$$(9)\qquad S_{tag} = S_{fish}\left[1-\frac{P_L\ f/\lambda}{1-(1-P_L)\ f/\lambda}\right]$$

One unknown parameter, λ, remains. If all fish are harvested upon capture, then $P_L = 0$ and $S_{tag} = S_{fish}$.

From the tag-recovery models, $E(\hat{S}_{tag}) \cong S_{tag}$, so we can correct for the bias by

$$(10)\qquad \hat{S}_{fish} = \hat{S}_{tag}\left[\frac{1-(1-\hat{\theta}\hat{P}_L)\ \hat{f}/\hat{\lambda}}{1-\hat{f}/\hat{\lambda}}\right]$$

where $\hat{S}_{fish}$ is the adjusted survival rate (i.e., an estimate of fish survival), $\hat{\theta}$ is estimated survival immediately after the capture–release event (or the complement of mortality due to catch-and-release), and other estimators are of parameters defined previously. We obtained the variance for the adjusted survival by the delta method (Appendix A). An alternative parameterization can be used to specify cell probabilities for recovery models (Table 1). The models presented in Table 1 require independent, year-specific estimates of λ and θ. Ideally, given studies to estimate reporting and acute mortality rates (which are concurrent with the tagging study), likelihoods for λ and θ can be specified, and a full likelihood can be constructed, i.e., $L(\pi_{ij};R_{ij},N_i)L(\theta)L(\lambda)$, so that all relevant parameters can be estimated simultaneously.

We can assess approximate relative bias (i.e., $(S_{tag} - S_{fish})/S_{fish}$) by

$$(11)\qquad -\frac{\theta P_L\ (f/\lambda)}{1-(1-\theta P_L)\ f/\lambda}$$

which approximates the relative error when $\hat{S}_{tag}$ is used to estimate S_{fish}. Diodati and Richards (1996) reported that 9% (SE = 2%) of striped bass die shortly after release because of hooking and handling. Thus, a possible value for θ is 0.91.

To adjust for the bias, reporting rate (λ) must be estimated. Pollock et al. (1991) discussed study designs to estimate reporting rate independently from the tagging study, and Hoenig et al. (1998*a*) discussed ways to incorporate tag reporting rate into tag-recovery modeling. We present an ad hoc method to estimate reporting rate from tag recovery based estimates of survival and recovery rate and assumed rates of natural mortality and survival immediately after catch-and-release. Given finite survival (S) and instantaneous natural mortality (M), instantaneous fishing mortality (F) can be found by $F = -\ln(S) - M$. Alternatively, fishing mortality can be based on rates of finite exploitation (u) and survival (Ricker 1975):

$$(12) \qquad u = \frac{F}{-\ln(S)}(1 - S)$$

Exploitation is a function of recovery rate, proportion released alive, survival immediately after catch-and-release, and reporting rate, i.e.,

$$(13) \qquad u = \frac{f_K}{\lambda} = \frac{(1 - \theta P_L)\,f}{\lambda}$$

Thus, based on eqs. 12 and 13, an alternative formula for fishing mortality is

$$(14) \qquad F = -\ln(S)\,\frac{(1 - \theta P_L)\,f}{\lambda(1 - S)}$$

At this point, neither $F = -\ln(S) - M$ nor eq. 14 will yield an unbiased estimate of fishing mortality because we lack an unbiased estimate of survival and the tagging data alone provide no estimate of natural mortality, reporting rate, or survival immediately after catch-and-release. Bias-adjusted survival ($\hat{S}_{\text{fish}}$) from eq. 10 is a function of reporting rate and survival immediately after catch-and-release. Thus, a strategy to assess bias in fishing mortality is to set θ and M to widely accepted values (say, θ*and M*) and solve iteratively for λ using

$$(15) \qquad -\ln(\hat{S}_{\text{fish}})\,\frac{(1 - \theta^* \hat{P}_L)\,\hat{f}}{\lambda(1 - \hat{S}_{\text{fish}})} = -\ln(\hat{S}_{\text{fish}}) - M^*$$

where is $\hat{f}$ and $\hat{P}_L$ are estimated from tagging data and $\hat{S}_{\text{fish}}$ is found by eq. 10. Although the ad hoc method permits time-specific rates, widely accepted values are likely to be constant values derived from theory or estimates averaged over a range of conditions. Unfortunately, the assumption of constant rates in this ad hoc method is untestable.

Application: Atlantic striped bass

Between 1987 and 1997, over 175 000 wild Atlantic striped bass were tagged through a cooperative coastwide tagging study involving 15 state and federal agencies. Recreational and commercial anglers and researchers recapture tagged fish and report the tags to the U.S. Fish and Wildlife Service, which manages the tagging database. The initial purpose of the cooperative coastwide tagging study, with its genesis during the stock collapse of the mid-1980s, was to evaluate efforts to restore stocks of Atlantic striped bass (Wooley et al. 1990). Currently, fishery biologists use the tagging data to monitor mortality and migration of striped bass in a restored fishery.

Harvest regulations have been liberalized in a stepwise fashion during the tagging study (Richards and Rago 1999), providing an opportunity to study effects of management on mortality. Harvest regulations can be summarized into three distinct periods: a period of highly restricted fishing from 1985 to 1989, an interim fishery from 1990 to 1994, and a restored fishery, which took effect in 1995. At the beginning of the tagging study, a moratorium on fishing had been in effect in the Maryland portion of Chesapeake Bay and the Delaware River, which remained through 1989. A moratorium on commercial striped bass fishing was in effect throughout the study in the Hudson River because of PCB contamination. From 1990 to 1994, fishing was permitted coastwide under an interim level of fishing mortality (i.e., target $F = 0.25$). Then in 1995, the Atlantic striped bass stock was declared restored and harvest regulation was relaxed again to achieve an increased target fishing mortality (i.e., target $F = 0.31$).

We modeled tag recoveries of striped bass ≥ 711 mm that were tagged in the Maryland portion of Chesapeake Bay, Hudson River, and Delaware River (Appendix B). Striped bass ≥ 711 mm are considered by the Atlantic States Marine Fisheries Commission to be fully recruited to the fishery. Because a major objective of the tagging program has been stock-specific estimates of mortality, tagging has been conducted in areas where spawning occurs. These efforts are best represented by decade-long spring tagging programs in the Maryland portion of the Chesapeake Bay and in the Hudson River that began in 1987 and 1988, respectively, and by a more recent tagging program in the Delaware River that began in 1991. We did not include 1987 releases for the Maryland portion of Chesapeake Bay or 1991 and 1992 for Delaware River because of low numbers of releases of striped bass ≥ 711 mm in those years.

Tags and tagging methods are standardized among tagging programs, but methods and timing of capture differ. Internal anchor tags with external streamers, supplied by the U.S. Fish and Wildlife Service, are inserted into an incision made in the left ventral side of healthy fish slightly behind and below the tip of the smoothed back pectoral fin. In the Hudson River, haul seines are used to catch striped bass for tagging primarily during May. In the Maryland portion of Chesapeake Bay, experimental drift gill nets are used to catch striped bass primarily during April and May. In the Delaware River, electrofishing is used to capture striped bass on the spawning grounds during April and May.

Dunning et al. (1987) studied tag retention and tag-induced mortality in striped bass. They reported that retention of internal anchor tags, over 1 year, was 98% and that tagged and control fish survived equally over 180 days after tagging. Thus, we did not attempt to adjust for bias due to these sources. For a tagged fish to be included in the release cohort, it must have been at large for at least 7 days prior to recapture unless it was recaptured within 7 days and released with the tag intact. To account for lengthy tagging periods (>1 month), we first defined the median week of tagging as the week at which 50% of the tags were released in that year. If the difference between the median weeks of tagging in successive years exceeded 4 weeks, then we used a feature in program MARK to adjust survival estimate by $\hat{S}_i^{52/t}$, where $\hat{S}_i$ is the survival estimate for the ith year and t is the number of weeks between the median week of tagging in successive years.

Following the procedures outlined by Buckland et al. (1997) and Burnham and Anderson (1998), prior to data analysis, we specified a set of candidate models. The model parameters were functions of two factors: stock (i.e., Chesapeake Bay, Hudson River, or Delaware River) and time. We allowed model parameters to be either fully stock specific or equal for all stocks. In addition, because of the small sample size for the Delaware River and its proximity to Chesapeake Bay, we allowed model parameters to be equal for the Delaware River and Chesapeake Bay but different from the Hudson River. We specified models allowing parameters to be year specific or constant across time. Because we hypothesized that harvest regulation affects survival and catch rates, we specified models allowing parameters to differ among the three periods of harvest regulation (i.e., 1988–1989, 1990–1994, and 1995–1997). For models including both stock and time effects, we specified models where (*i*) temporal changes in parameters depended on stock (i.e., there was an interaction between stock and time effects) and (*ii*) temporal changes in parameters were equal among stocks but parameters were stock specific (i.e., there was an additive stock and time effect).

For the purpose of assessing bias due to catch-and-release, we calculated the proportion released alive and recovery rate; we then assumed values for natural mortality and survival immediately after catch-and-release and solved for reporting rate. We calculated proportion released alive as the ratio of striped bass released alive to striped bass caught in a recovery period; this information is supplied by the angler who reports the tag. We estimated f from the fully time-specific tag-recovery models of Brownie et al. (1985). We assumed natural mortality to be 0.15, which is the value used in the Atlantic States Marine Fisheries Commission striped bass

Table 2. Statistics for the set of tag-recovery models that do not account for recoveries coming from live recaptures and harvested fish.

Model label[a]	ΔAICc[b]	*np*	GOF *P* value	Akaike weight
$S(\{CB = DR,HR\} \times p)r(g + p)$	0.00	11	0.237	0.413
$S(\{CB = DR,HR\} \times p)r(g \times p)$	1.63	14	0.306	0.183
$S(\{CB = DR,HR\} \times t)r(g)$	2.01	24	0.581	0.151
$S(g \times p)r(g + p)$	3.88	13	0.179	0.059
$S(\{CB = DR,HR\} \times t)r(g + p)$	3.90	26	0.615	0.059
$S(\{CB = DR,HR\} \times p)r(g)$	4.36	9	0.127	0.047
$S(g \times p)r(g \times p)$	4.94	16	0.266	0.035
$S(\{CB = DR,HR\} + p)r(g + p)$	7.61	9	0.111	0.009
$S(\{CB = DR,HR\} + p)r(g \times p)$	7.83	12	0.118	0.007
$S(g \times p)r(g)$	8.15	11	0.089	0.006
$S(g \times t)r(g + p)$	8.43	32	0.536	0.006
$S(g \times t)r(g)$	8.56	31	0.470	0.006
$S(\{CB = DR,HR\} \times t)r(g \times p)$	8.61	29	0.574	0.005
$S(p)r(g \times p)$	8.77	11	0.110	0.005
$S(g + p)r(g + p)$	9.59	10	0.087	0.003
$S(g + p)r(g \times p)$	9.78	13	0.107	0.003

Note: A total of 84 models were proposed, and only those with ΔAICc < 10 are shown here. See table footnote *a* for a description of the notation to interpret the model label. AICc is a small sample size adjusted version of AIC, ΔAICc is the difference between the model AICc and the minimum AICc, *np* is the number of estimable parameters, GOF *P* value is the probability of a larger Pearson chi-square statistic to test goodness-of-fit, and Akaike weight is the value for w_i used in model averaging from Buckland et al. (1997) and Burnham and Anderson (1998).

[a]Model notation: $S(\cdot)$ and $r(\cdot)$ indicate that survival and reporting rate parameters are functions of factors specified in parentheses. The letters *g*, *t*, and *p* denote that parameters are stock specific, year specific, and specific to harvest regulation period, respectively. The notation {CB = DR,HR} indicates a type of stock-specific restriction where Chesapeake Bay (CB) and the Delaware River (DR) have equal survival but that survival differs from survival in the Hudson River (HR). If either stock- or time-specific notation is not included in the parentheses, then parameters are assumed constant in that respect. When parameters are simultaneously a function of stock and time, then stock and time effects can interact fully (e.g., denoted $g \times t$) or the effects can be additive (e.g., denoted $g + t$).

[b]For this best model, AICc ≡ minimum AICc = 16725.736.

stock assessment, and survival immediately after catch-and-release to be 0.91 (Diodati and Richards 1996). We then found the reporting rate that satisfied eq. 15 and applied that reporting rate to calculate a bias-adjusted fishing mortality.

We used program SURVIV (White 1983) to compute survival based on the model structure presented in Table 1, which incorporates the bias-adjustment factor (eq. 10). We assumed that reporting rate (λ) and survival immediately after catch-and-release (θ) were known constants. We took λ from the iterative procedure discussed above and θ from the results of Diodati and Richards (1996). We ran the model using data from the Maryland portion of Chesapeake Bay for 1991–1997 because reporting rate appeared to be relatively constant for that program during that time span. We fit models that incorporated year-specific and regulation-specific parameters.

Results

A total of 84 tag-recovery models, which assume that tags are recovered only from dead fish, were proposed and fit to the data; of these, 16 had ΔAICc < 10 (Table 2). GOF statistics indicated that the 16 models with the lowest AICc were plausible summaries of the data (i.e., GOF *P* values > 0.05). Temporal changes in estimates of survival depended on stock; however, survival of Delaware River striped bass was similar to that of the Chesapeake Bay stock, at least from 1993 to 1997. Models that structured time into harvest regulation periods were among the better-fitting models, thus indicating that estimates of survival changed with regulation changes.

We averaged model parameters across the 16 best-fitting models and found that 76% of the weighting came from the top three best-fitting models (Table 2). Sixty one percent of the weight came from models with time categorized according to periods of harvest regulation and with survival of the Delaware River stock equal to that of the Chesapeake Bay stock.

Model-averaged estimates of survival were highest during the moratorium (1988–1989) and then declined and remained relatively stable during the transitional fishery (1990–1994) and the full fishery (1995–1997) (Table 3). Model-averaged estimates of survival in the Maryland portion of Chesapeake Bay were significantly higher during the moratorium and slightly higher during the transitional fishery than in the Hudson River.

Recovery rates increased slightly during the tagging study, whereas proportion of catch released alive decreased (Fig. 2; Table 4). These trends caused the bias in estimates of survival to decrease over the course of the tagging study. Consequently, the temporal pattern in bias-adjusted *F* differed from the *F* calculated directly from model-averaged estimates of survival (Fig. 3; Table 4). Unadjusted *F* increased in a stepwise fashion after the moratorium and then leveled off; however, bias-adjusted *F* increased throughout the tagging study (Fig. 3). Bias was greatest in 1990 immediately

Fig. 2. Recovery rate (circles) and proportion released alive (triangles) for striped bass >711 mm in three tagging programs: (*a*) Hudson River, 1988–1997, (*b*) Delaware River, 1993–1997, and (*c*) the Maryland portion of Chesapeake Bay, 1988–1997. Recovery rate was estimated from the stock- and time-specific survival and recovery rate model under the model parameterization of Brownie et al. (1985). The proportion of catch released alive was calculated using all recaptures in a given recovery year, regardless of release year.

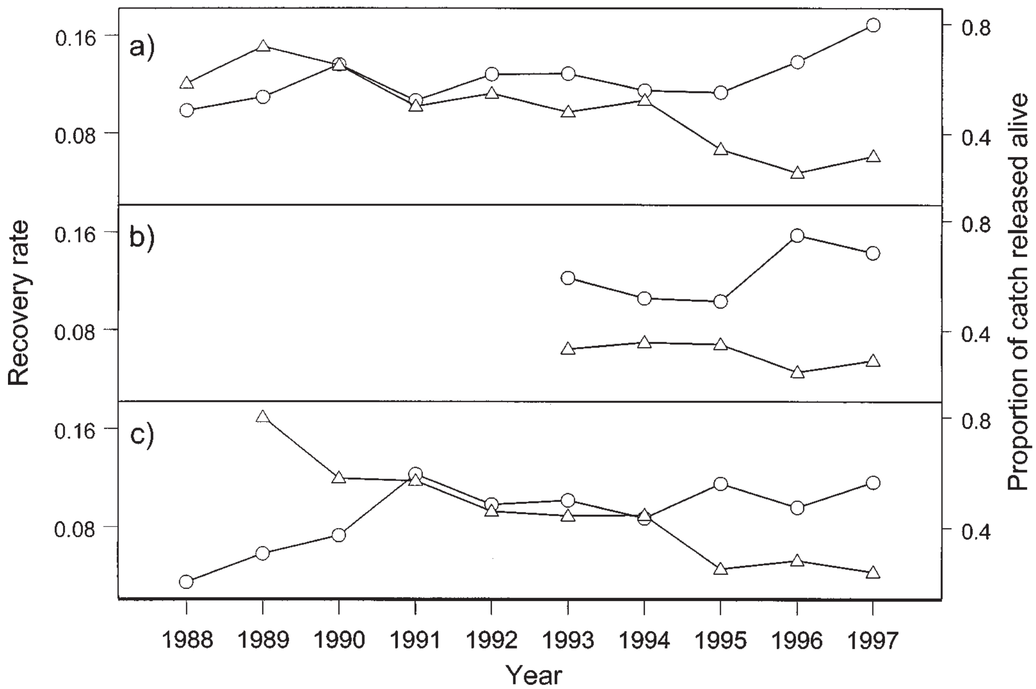


Table 3. Model-averaged estimates of biased survival ($\hat{S}_{tag}$) for spring tagging programs conducted in the Maryland portion of Chesapeake Bay, the Hudson River, and the Delaware River, 1988–1997.

	Maryland portion of Chesapeake Bay			Hudson River			Delaware River		
Year	$\hat{S}_{tag}$	SE	95% CI	$\hat{S}_{tag}$	SE	95% CI	$\hat{S}_{tag}$	SE	95% CI
1988	0.90	0.098	(0.52, 0.99)	0.75	0.087	(0.54, 0.88)			
1989	0.88	0.098	(0.55, 0.98)	0.72	0.093	(0.51, 0.86)			
1990	0.66	0.063	(0.53, 0.77)	0.62	0.053	(0.51, 0.72)			
1991	0.63	0.062	(0.51, 0.74)	0.63	0.060	(0.51, 0.74)			
1992	0.65	0.057	(0.53, 0.75)	0.62	0.052	(0.52, 0.72)			
1993	0.66	0.059	(0.53, 0.76)	0.62	0.052	(0.52, 0.72)	0.66	0.070	(0.52, 0.77)
1994	0.66	0.063	(0.53, 0.77)	0.63	0.059	(0.51, 0.74)	0.66	0.071	(0.51, 0.77)
1995	0.63	0.074	(0.48, 0.76)	0.66	0.073	(0.51, 0.78)	0.64	0.081	(0.47, 0.77)
1996	0.64	0.074	(0.50, 0.77)	0.65	0.076	(0.49, 0.78)	0.64	0.081	(0.47, 0.78)
1997	0.64	0.075	(0.48, 0.77)	0.63	0.089	(0.44, 0.78)	0.64	0.082	(0.47, 0.78)

Note: These estimates underestimate survival because the basic tag-recovery models do not allow for tag recoveries from fish caught and released alive, which occurs frequently with Atlantic striped bass. Confidence intervals are based on a logit transformation of $\hat{S}_{tag}$.

following the moratorium and decreased thereafter. Reporting rate dropped after the moratorium (Table 4). In the Hudson River and Delaware River, reporting rate increased during the two most recent years. In the Maryland portion of Chesapeake Bay, reporting rate remained level at around 40% after 1991.

Hypothetically, relative bias was most severe (–0.51) when reporting rate was low (0.25), recovery rate was high (0.15), and the proportion of catch released alive was high (0.75). Relative bias ranged from –0.02 to –0.51 for reporting rates from 0.25 to 0.75, recovery rates from 0.05 to 0.15, and proportions released alive from 0.25 to 0.75 (Table 5). Relative bias was –0.02 to –0.15 in all cases when reporting rate was high (0.75), which suggests that efforts to increase reporting rate would help minimize the bias. In 1997, proportions of catch released alive were 0.32, 0.21, and 0.29 for the Hudson River, Chesapeake Bay, and Delaware River tagging programs, respectively. Recovery rates in those same programs were 0.17, 0.12, and 0.14 during 1997. If we assume a reporting rate approaching 0.50 and recent values for recovery rates and proportion released alive, then we expect that the relative bias in recent estimates of striped bass survival is between –0.13 and –0.07. For example, for true survival of 0.70, relative bias of –0.13 to –0.07 would lead to estimates of survival between 0.61 and 0.65 from traditional tag-recovery models.

Nine tag-recovery models, based on recovery probabilities in Table 1, were fit to data from the Maryland tagging study

Table 4. Bias-adjusted estimates of survival and fishing morality and related parameters.

Stock and year	$\hat{f}$	$\hat{P}_L$	Biased $\hat{S}_{tag}$	Biased $\hat{F}_{tag}$	Bias adjusted $\hat{S}_{fish}$	Bias adjusted $\hat{F}_{fish}$	$\hat{\lambda}$
Hudson River							
1988	0.10	0.56	0.75	0.14	0.81	0.07	0.76
1989	0.11	0.72	0.72	0.18	0.81	0.06	0.68
1990	0.14	0.63	0.62	0.33	0.76	0.13	0.50
1991	0.11	0.51	0.63	0.31	0.73	0.16	0.42
1992	0.13	0.56	0.62	0.32	0.74	0.15	0.48
1993	0.13	0.49	0.62	0.32	0.72	0.18	0.48
1994	0.11	0.50	0.63	0.31	0.74	0.16	0.45
1995	0.11	0.34	0.66	0.27	0.72	0.18	0.50
1996	0.14	0.26	0.65	0.29	0.69	0.22	0.58
1997	0.17	0.32	0.63	0.32	0.69	0.22	0.65
Maryland portion of Chesapeake Bay							
1988	0.03	0.60	0.90	0.00	0.91	0.00	1.00
1989	0.06	0.79	0.88	0.00	0.91	0.00	1.00
1990	0.07	0.59	0.66	0.27	0.76	0.12	0.32
1991	0.12	0.60	0.63	0.31	0.75	0.13	0.48
1992	0.10	0.47	0.65	0.28	0.74	0.16	0.41
1993	0.10	0.45	0.66	0.27	0.74	0.16	0.44
1994	0.09	0.44	0.66	0.27	0.74	0.16	0.38
1995	0.11	0.25	0.63	0.31	0.68	0.23	0.46
1996	0.10	0.29	0.64	0.29	0.70	0.21	0.40
1997	0.12	0.21	0.64	0.30	0.68	0.24	0.47
Delaware River							
1993	0.12	0.40	0.66	0.27	0.73	0.16	0.55
1994	0.11	0.38	0.66	0.26	0.73	0.17	0.48
1995	0.10	0.35	0.64	0.30	0.70	0.20	0.41
1996	0.16	0.25	0.64	0.29	0.69	0.22	0.65
1997	0.14	0.29	0.64	0.30	0.69	0.22	0.58

Note: Recovery rate ($\hat{f}$) is estimated from the stock- and time-specific model using Brownie et al. (1985) parameterization. The estimate of proportion of catch released alive is denoted by $\hat{P}_L$. Biased survival ($\hat{S}_{tag}$) is the standard tag-recovery estimates of survival rate that are biased due to tag recoveries from caught-and-released striped bass. Biased fishing mortality rate is computed from $\hat{S}_{tag}$ and by assuming a natural mortality of 0.15, i.e., biased $\hat{F}_{tag} = -\ln(\hat{S}_{tag}) - 0.15$. Bias-adjusted survival ($\hat{S}_{fish}$) and fishing mortality are computed iteratively by assuming that natural mortality is 0.15 and survival immediately after catch-and-release is 0.91 and by finding a reporting rate ($\hat{\lambda}$) that satisfies eq. 15.

during 1991–1997. Reporting rate and survival immediately after catch-and-release were assumed known and constant, 0.43 and 0.91, respectively. Models that structured survival or recovery rates by regulatory period accounted for 97.6% of the Akaike weights (Table 6). Survival dropped in conjunction with regulatory change made in 1995 (Table 7). In addition, regulatory change had an effect on recovery rates. Harvest recovery rates diverged dramatically from live-recapture recovery rates after 1994.

Discussion

Survival rate was underestimated when tag-recovery models included tags from harvested and caught-and-released striped bass. And the magnitude of the bias changed over time. Thus, temporal changes in survival estimates were confounded by temporal changes in recovery rate, proportion released alive, and possibly reporting rate (although we do not have independent, time-specific estimates of reporting rate). Unadjusted estimates of survival decreased immediately after the moratorium but then leveled off and remained relatively constant through 1997. This pattern, however, was misleading because changes in recovery rate and proportion released alive caused bias to decrease during the tagging study. After adjusting for the bias, we found that survival decreased with regulatory changes that occurred after the moratorium was lifted. An important additional consideration is that the bias can differ among subpopulations if proportion released alive, recovery rate, or reporting rate depends on subpopulation. For example, striped bass < 711 mm are not fully recruited to the fishery. Proportion released alive is likely to be higher for these smaller striped bass. As a result, the magnitude of bias, in absolute terms, will be higher for the prerecruited segment of the population.

Bias in survival estimates from tag-recovery models due to recoveries from live recaptures is an important finding that affects interpretation of previous tag-based estimates of striped bass survival. Implications are less clear for other tagging studies. When all catch is harvested, this bias is not an issue. However, catch-and-release, which is increasingly popular, can result in live recapture of large numbers of tagged fish. For example, high proportions of striped bass

Fig. 3. Fishing mortality for striped bass > 711 mm tagged during spring in (*a*) the Hudson River, 1988–1997, (*b*) the Delaware River, 1993–1997, and (*c*) the Maryland portion of Chesapeake Bay, 1988–1997. Unadjusted fishing mortality (squares) is calculated as $F = -\ln(\hat{S}_{tag}) - M$, where $\hat{S}_{tag}$ is the tag-based estimate of biased survival and M is assumed to be 0.15. Bias-adjusted fishing mortality (diamonds) accounts for bias due to catch-and-release and is calculated using an iterative method (explained in the text).

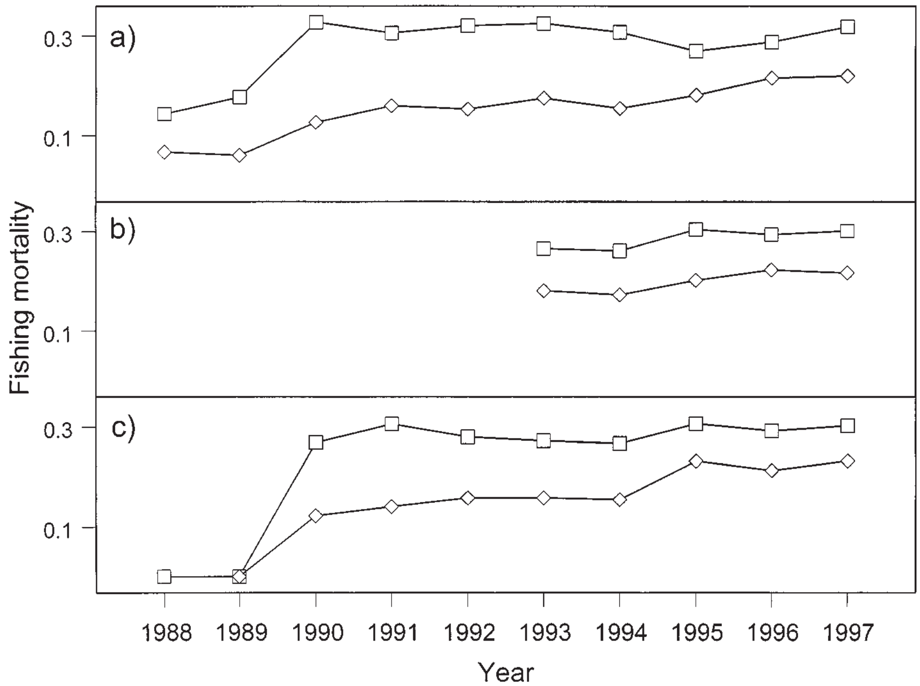


Table 5. Approximate relative bias (i.e., $(S_{tag} - S_{fish})/S_{fish}$) calculated for a range of reporting rates, recovery rates, and proportion of catch released alive and with survival immediately after catch-and-release fixed at 0.91.

	Proportion of catch released alive		
Recovery rate	0.25	0.50	0.75
Reporting rate = 0.25			
0.05	–0.05	–0.10	–0.15
0.10	–0.13	–0.23	–0.31
0.15	–0.25	–0.41	–0.51
Reporting rate = 0.50			
0.05	–0.02	–0.05	–0.07
0.10	–0.05	–0.10	–0.15
0.15	–0.09	–0.16	–0.23
Reporting rate = 0.75			
0.05	–0.02	–0.03	–0.05
0.10	–0.03	–0.07	–0.10
0.15	–0.05	–0.10	–0.15

Table 6. Statistics for tag-recovery models that incorporate a correction for tags recovered from live recaptures.

Model label[a]	ΔAICc[b]	np	GOF P value	Akaike weight
$S(p)f_L(p)f_K(p)$	0.00	6	0.257	0.607
$S(\cdot)f_L(p)f_K(p)$	1.25	5	0.197	0.325
$S(t)f_L(p)f_K(p)$	5.25	10	0.213	0.044
$S(\cdot)f_L(t)f_K(t)$	7.72	15	0.279	0.013
$S(p)f_L(t)f_K(t)$	8.05	16	0.301	0.011

Note: Model structure is presented in Table 1. Nine models were fit to data from the Maryland portion of Chesapeake Bay from 1991 to 1997, and only those with ΔAICc < 10 are shown here. Reporting rate (λ) and survival immediately after catch-and-release (θ) were fixed at 0.43 and 0.91, respectively. See table footnote *a* for a description of the notation to interpret the model label. AICc is a small sample size adjusted version of AIC, ΔAICc is the difference between the model AICc and the minimum AICc, np is the number of estimable parameters, GOF P value is the probability of a larger Pearson chi-square statistic to test goodness-of-fit, and Akaike weight is the value for w_i used in model averaging from Buckland et al. (1997).

[a]There are three types of parameters: fish survival (S), live-recapture recovery rate (f_L), and harvest recovery rate (f_K). Each type of parameter can be constant (·), year specific (t), or regulatory period specific (p). For example model "$S(t)f_L(p)f_K(p)$" denotes a model with year-specific survival and regulatory period specific recovery rates.

[b]For this best model, AICc ≡ minimum AICc = 291.861.

tags were reported from fish caught and released (Table 4; Appendix B). These live recaptures, which are of fish not intended for harvest, can be released with or without the tag intact. Typically, published tagging studies do not report the proportion of catch released alive or the frequency that anglers remove tags prior to release. Thus, it is difficult to assess the generality of this bias, which clearly affected the striped bass tagging study.

In the event that tagged fish are subject to harvest and catch-and-release, we considered three basic approaches to survival estimation. Live recaptures can be excluded from the analysis, as was done by Youngs and Robson (1975). Alternatively, recoveries and multiple live recaptures can be analyzed jointly (Burnham 1991; Barker 1997). Finally, recoveries and first live recapture can be analyzed using tag-recovery models with a bias adjustment. We discuss these approaches in order with emphasis on the striped bass tagging study.

Youngs and Robson (1975) did not include live recaptures

Table 7. Model-averaged estimates of bias-adjusted survival, live-recapture recovery rate, and harvest recovery rate for the spring tagging program conducted in the Maryland portion of Chesapeake Bay, 1991–1997.

	Bias-adjusted survival			Live-recapture recovery rate			Harvest recovery rate		
Year	$\hat{S}_{\text{fish}}$	SE	95% CI	f_{L}	SE	95% CI	f_{K}	SE	95% CI
1991	0.75	0.033	(0.68, 0.81)	0.045	0.005	(0.04, 0.06)	0.051	0.004	(0.04, 0.06)
1992	0.75	0.032	(0.69, 0.81)	0.044	0.004	(0.04, 0.05)	0.051	0.004	(0.04, 0.06)
1993	0.76	0.030	(0.69, 0.81)	0.045	0.004	(0.04, 0.05)	0.051	0.004	(0.04, 0.06)
1994	0.76	0.037	(0.68, 0.82)	0.045	0.004	(0.04, 0.05)	0.051	0.004	(0.04, 0.06)
1995	0.69	0.052	(0.58, 0.78)	0.027	0.003	(0.02, 0.03)	0.080	0.005	(0.07, 0.09)
1996	0.69	0.051	(0.59, 0.78)	0.027	0.003	(0.02, 0.03)	0.080	0.005	(0.07, 0.09)
1997				0.027	0.003	(0.02, 0.03)	0.080	0.005	(0.07, 0.09)

Note: Estimates are based on the model structure presented in Table 1. Several models were fit to the data and used to estimate parameters. Model statistics are presented in Table 6. Reporting rate (λ) and survival immediately after catch-and-release (θ) were fixed at 0.43 and 0.91, respectively. Confidence intervals are based on a logit transformation.

in their analyses; they only used tags recovered from harvested lake trout. The strategy of excluding live recaptures from tag-recovery analysis works only if (*i*) tags are not removed prior to release and (*ii*) catch-and-release does not affect survival. In the Atlantic striped bass fishery, anglers commonly remove tags prior to release, and catch-and-release affects survival (Diodati and Richards 1996). Thus, this approach is not valid for tagging studies of Atlantic striped bass.

Burnham (1991) developed a theory for joint analysis of combined recovery and recapture data; however, it did not account for live recaptures between release periods (i.e., “tag resightings” that occur when anglers catch-and-release fish). Barker (1997) extended Burnham’s (1991) work and developed a modeling framework allowing for recaptures, resightings, and recoveries. However, in the striped bass case, the removal of the tag permanently affects the probability of subsequent capture (the tag can be removed entirely or, more commonly, the tag’s external streamer can be removed while the internal anchor is left in place). Also, catch-and-release affects survival (Diodati and Richards 1996), further complicating the probability structure for the model. Permanent changes in probability of subsequent capture are not part of the Barker (1997) model. Thus, the Barker (1997) model would need to be generalized to accommodate the striped bass tagging study, and large numbers of multiple recaptures would be required to support the extensive parameterization. We did not feel that the number of multiple recaptures of striped bass was sufficient to warrant generalizing the Barker (1997) model.

Estimation of reporting rate is the weak link in adjusting for bias in tag recovery based survival estimates using live recaptures. We used an ad hoc procedure to estimate reporting rate and adjust for bias in survival estimates. However, this procedure depends on knowing natural mortality rate, another parameter that is difficult to estimate and one that is often assumed to be constant, which may not be justified.

We computed maximum likelihood estimates of “bias-adjusted” survival with the program SURVIV (White 1983) assuming recovery probabilities presented in Table 1. However, the method requires independent year-specific estimates of reporting rate that account for nonreporting from commercial, charter boat, and recreational anglers. Such estimates are currently not available, and we assumed that reporting rate was known and constant. Thus, we overestimated precision (underestimated variance) of the survival estimates that appear in Table 7.

Studies to estimate time-specific reporting rate for striped bass should receive high priority. Pollock et al. (1991) reviewed ways to estimate reporting rate. If estimation of time-specific reporting rate (e.g., annual reward tag studies) were a routine component of the striped bass tagging study, then a full likelihood could be specified and uncertainty regarding reporting rate estimates could be included in bias-adjusted estimates of survival rate.

Finally, we note our application of the method of model averaging (Buckland et al. 1997; Burnham and Anderson 1998) to base inference on a weighted average of parameter estimates and to account for model selection uncertainty. The flexibility of tag-recovery modeling, and capture–recapture modeling in general, allows for a diverse set of models, each model representing a unique proposition for the biological and sampling processes that result in the observed tag recoveries. Different tag-recovery models can produce widely different estimates of vital parameters. Thus, model selection can have far-reaching consequences on management decisions. However, model selection is less certain when several models seem to fit the data equally well (i.e., have similar AIC or likelihood values). Furthermore, selection of the “true” model is not a realistic goal, and model selection uncertainty is a component of estimator variance, which is not accounted for when a single model is selected for inference. By model averaging, models contribute to the estimate according to how well the model serves as a parsimonious descriptor of the data. Inference is affected in two ways as a result. The model-averaged estimates reflect, in a balanced way, the patterns that emerge from the set of models, and variance of the model-averaged estimate includes a component for model selection uncertainty.

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Appendix A. Variance for estimate of survival adjusted for release of recaptured fish using eq. 10.

Bias-adjusted survival, $\hat{S}_{\mathrm{fish}}$ (eq. 10), can be written

$$\hat{S}_{\mathrm{fish}} = \hat{S}_{\mathrm{tag}}\left[\frac{\hat{\lambda} - (1-\hat{\theta})\hat{f}_{\mathrm{L}} - \hat{f}_{\mathrm{K}}}{\hat{\lambda} - \hat{f}_{\mathrm{L}} - \hat{f}_{\mathrm{K}}}\right]$$

where $\hat{S}_{\mathrm{tag}}$ is the estimate of survival from standard tag-recovery modeling, f_{L} and f_{K} are tag-recovery rates for live recaptures and harvested fish, respectively, θ is survival immediately after catch-an-release, and λ is the reporting rate. The variance, as derived using the delta method and assuming that λ and θ are estimated independently from other parameters, is

$$\mathrm{var}(\hat{S}_{\mathrm{fish}}) = \left[\frac{S_{\mathrm{fish}}}{S_{\mathrm{tag}}}\right]^2 \mathrm{var}(\hat{S}_{\mathrm{tag}}) + [S_{\mathrm{fish}} - S_{\mathrm{tag}}]^2 Q$$

where Q is

$$Q = \left[\frac{\lambda - f_{\mathrm{K}}}{f_{\mathrm{L}}(\lambda - f_{\mathrm{L}} - f_{\mathrm{K}})}\right]^2 \mathrm{var}(\hat{f}_{\mathrm{L}}) + \left[\frac{1}{\lambda - f_{\mathrm{L}} - f_{\mathrm{K}}}\right]^2 \mathrm{var}(\hat{f}_{\mathrm{K}}) + \left[\frac{1}{\theta}\right]^2 \mathrm{var}(\hat{\theta})$$
$$+ \left[\frac{-1}{\lambda - f_{\mathrm{L}} - f_{\mathrm{K}}}\right]^2 \mathrm{var}(\hat{\lambda}) + 2\left[\frac{S_{\mathrm{fish}}}{S_{\mathrm{tag}}}\right]\left[\frac{\lambda - f_{\mathrm{K}}}{f_{\mathrm{L}}(\lambda - f_{\mathrm{L}} - f_{\mathrm{K}})}\right]^2 \mathrm{cov}(\hat{S}_{\mathrm{tag}}, \hat{f}_{\mathrm{L}})$$
$$+ 2\left[\frac{S_{\mathrm{fish}}}{S_{\mathrm{tag}}}\right]\left[\frac{-1}{\lambda - f_{\mathrm{L}} - f_{\mathrm{K}}}\right] \mathrm{cov}(\hat{S}_{\mathrm{tag}}, \hat{f}_{\mathrm{K}}) + 2\left[\frac{\lambda - f_{\mathrm{K}}}{f_{\mathrm{L}}(\lambda - f_{\mathrm{L}} - f_{\mathrm{K}})^2}\right] \mathrm{cov}(\hat{f}_{\mathrm{L}}, \hat{f}_{\mathrm{K}})$$

Appendix B. Release and recovery matrices of striped bass for tagging programs in the Maryland portion of Chesapeake Bay (1988–1997), the Hudson River (1988–1997), and the Delaware River (1993–1997).

Year of release	Number released	Disposition of catch	Number recaptured									
			1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
Maryland portion of Chesapeake Bay												
1988	128	Released	3	8	5	9	0	1	1	0	0	0
		Harvested	2	2	3	5	4	1	1	0	0	0
1989	219	Released		7	10	13	2	2	2	0	0	0
		Harvested		2	7	3	4	2	1	5	2	0
1990	304	Released			14	7	5	2	1	1	0	0
		Harvested			10	8	5	3	1	3	0	3
1991	392	Released				26	10	6	1	2	0	1
		Harvested				21	11	13	5	6	3	4
1992	404	Released					21	12	5	3	3	1
		Harvested					19	12	8	11	5	7
1993	626	Released						28	19	9	2	1
		Harvested						32	27	30	11	15
1994	538	Released							24	12	4	0
		Harvested							24	29	19	16
1995	523	Released								16	6	5
		Harvested								44	23	19
1996	854	Released									34	16
		Harvested									57	34
1997	336	Released										9
		Harvested										30
Hudson River												
1988	277	Released	15	20	11	2	4	2	2	0	0	1
		Harvested	12	10	8	10	6	3	3	0	3	1
1989	382	Released		32	13	7	4	1	1	0	0	0
		Harvested		10	17	8	3	6	5	5	0	0
1990	442	Released			47	15	16	6	2	0	0	0
		Harvested			16	15	11	9	3	5	1	3
1991	362	Released				24	16	5	4	0	0	3
		Harvested				14	13	10	7	9	7	0
1992	692	Released					49	32	14	10	3	3
		Harvested					37	26	16	11	11	12
1993	534	Released						37	21	13	4	5
		Harvested						34	16	7	15	11
1994	377	Released							24	7	6	2
		Harvested							17	25	20	19
1995	460	Released								20	11	10
		Harvested								34	20	11
1996	676	Released									27	24
		Harvested									72	37
1997	184	Released										7
		Harvested										24
Delaware River												
1993	52	Released						2	2	0	0	0
		Harvested						3	5	2	4	2
1994	79	Released							3	3	2	0
		Harvested							3	6	4	1
1995	88	Released								4	3	4
		Harvested								5	5	0
1996	72	Released									2	3
		Harvested									8	3
1997	77	Released										0
		Harvested										11

Note: Total lengths of all fish were ≥ 711 mm. Fish were tagged during the spawning run in each tagging program.