CCSBT-ESC/0509/Info 03

CSIRO
MARINE RESEARCH

Estimation of mortality rates and abundance for southern bluefin tuna (*Thunnus maccoyii*) using tag-return and catch data from 1991 to 1997.

Appendix from Final Report *In Progress* for FRDC Project 2002/015

J. Paige Eveson
Tom Polacheck
Geoff M. Laslett

Prepared for the CCSBT 6th Meeting of the Stock Assessment Group (SAG6) and the 10th Meeting of the Extended Scientific Committee (SC10)
29 August-3 September, and 5-8 September 2005, Taipei, Taiwan

Appendix 15:

Estimation of mortality rates and abundance for southern bluefin tuna (*Thunnus maccoyii*) using tag-return and catch data from 1991 to 1997

J. Paige Eveson, Tom Polacheck and Geoff M. Laslett

FRDC Project 2002/015

Introduction

Data from conventional tagging experiments have become increasingly important in assessing the stock status of southern bluefin tuna (SBT) because they provide one of the few viable alternatives to catch-per-unit-effort data for estimating mortality rates and abundance. Extensive tagging programs have been carried out on juvenile SBT during various periods from the 1960s to present. Although some analyses of the tag-return data from these experiments have been conducted, especially for the 1990s data, a comprehensive analysis of the data taking into account all of the major potential sources of heterogeneity has not been completed because of the lack of a comprehensive modelling framework.

Polacheck et al. (1996, 1997, 1998) analysed the 1990s SBT tag-return data using Brownie models to provide estimates of fishing and natural mortality rates; however, in all of these analyses, tag shedding was assumed to be minimal enough that it could be ignored and reporting rates were assumed to be known without error. Recent analyses of the double-tagging data for SBT suggest that tag shedding can be substantial for some taggers (Appendix 14), so estimates of mortality rates and abundance obtained ignoring shedding are likely to be biased. Also, reporting rates are one of the more uncertain inputs in the tag-return models, so assuming they are known without error gives overly optimistic estimates of the variance of the parameter estimates.

The 1990s tag-return data have also been included in many of the integrated stock assessments for SBT (e.g., Kolody and Polacheck 2001; Polacheck et al. 2001). Like the analyses mentioned above, these stock assessments also assume that tag shedding is negligible and that reporting rates are known without error. Furthermore, the multi-year nature of the tagging data has not been fully exploited in the assessment models, as none of them incorporate a Brownie-type estimator for the tagging data. Instead, they tend to use attrition models that only allow for total mortality to be estimated and not the breakdown into fishing and natural mortality.

In the current appendix, we draw upon the non-spatial methods developed and presented throughout this report to construct a rigorous model for analysing the 1990s SBT tag-return data. We use as a base model the combined Brownie and Petersen model described in Appendix 5, which integrates catch at age data with tag-return data in order to provide joint estimates of mortality rates (both fishing and natural) and abundance. More specifically, we use the modified version of the model described in the 'Application to southern bluefin tuna' section of Appendix 5 that allows for an initial period of non-mixing in the tag-return probabilities. This model assumes reporting rates are known without error, so we add an additional component to the model to take into account uncertainty in the reporting rate estimates. We also modify the tag-return probabilities as outlined in Appendix 14 to allow for instantaneous and continuous tag shedding. In a similar manner to the reporting rate estimates, we add an additional component to the model to take into account uncertainty in the estimates of the tag shedding parameters. The model is applied to SBT data collected from 1991 to 1997 to provide estimates of fishing mortality rates, natural mortality rates, and initial abundance for a number of cohorts.

Materials and Methods

Southern bluefin tuna data

Four sets of data on southern bluefin tuna are used as input to the model: tag-return data from tagging experiments conducted from 1991 to 1997; estimates of tag reporting rates for years 1991 to 1997; estimates of tag shedding rates for six groups of taggers; and catch at age data from the commercial fisheries from 1991 to 1997. Further details about each data set are given below.

Tagging operations were carried out by CSIRO Marine Research from 1991 to 1997 in which juvenile SBT were caught, tagged, and released primarily in the coastal waters south of Western Australia and South Australia. Tagged fish were subsequently recaptured in the commercial fisheries and tags returned to CSIRO along with the date and location of recapture. A complete description of the tag-return data, including the tagging protocol, sampling procedures, method of age determination, and data screening processes, can be found in Appendix 4. Table 1a provides a summary of the 1990s tag-return data by cohort, age of release and year of recapture. Note that we have constrained our analysis to releases for ages 1 through 3. While there were a small number of age 4 and 5 releases (<300 in total), these were not included in our analyses (and are not included in Table 1) because the number for any cohort was too small to provide meaningful estimates. The data are presented in terms of cohorts of fish to be consistent with the way that the model is developed and presented.

Estimating reporting rates for SBT is complicated because of limited data and because the complex nature of the SBT fishery, which comprises multiple components with varying reporting rates. Some limited observer data and tag seeding data exist, and these data have been used along with a number of alternative assumptions to provide year- and age-specific estimates of reporting rates for SBT from 1991 to 1997 (see Appendix 19 for details). A large number of alternatives have been provided but the reporting rate estimates used in our primary analysis (given in Table 1b) correspond to the reporting rates presented in Table 5a, option 8, of Appendix 19[1]. This is considered the 'most plausible' option because it is the most highly information-based (Anon. 2005). These reporting rate values differ from those presented in Appendix 5 because they correspond to a different option and because the reporting rate estimates were updated in 2005 after the analysis in Appendix 5 had been completed.

Essentially all SBT tagged in the 1990s were double-tagged. Data on the number of tagged fish that were recaptured with only one tag still attached versus both tags still attached were used to estimate shedding rates for SBT (Appendix 14). Tags were

[1] The reporting rate estimates in Appendix 19 were prepared in 2005 for the CCSBT, for which it was decided that the discarded catch of small SBT recorded by the Japanese longline fishery in 1995 and 1996 should not be included in the catch at age data. For our current analysis, we prefer to include the estimated non-surviving portion of the discarded catches (Preece et al. 2001) in the catch data. As such, the reporting rate estimates presented in Table 1b of the current appendix differ very slightly in these two years from those presented in Table 5a of Appendix 19.

assumed to have an immediate component of shedding and a long-term constant proportional rate of shedding. Specifically, the proportion of tags retained as a function of time since release, τ, was assumed to be $Q(\tau) = \xi e^{-\Omega\tau}$, where ξ is the fraction of tags immediately retained (i.e. proportion 1 - ξ are immediately shed) and Ω is the continuous shedding rate. The shedding parameters were assumed to be independent of age or year; however, they were found to differ significantly between taggers. Six groups of taggers with similar shedding rates were identified. Estimates of the instantaneous and continuous shedding parameters for the six tagger groups are given in Table 1c, along with standard errors and correlations for the estimates (these are all taken from Table 7a of Appendix 14). Note that because shedding rates were found to differ between groups of taggers, the probability of a tag being returned depends in part on the tagger group. As such, the model requires the release and recapture data in Table 1a to be broken down by tagger group as well as by cohort and release age; for brevity, we have not presented the data at this level of detail.

SBT are caught by a number of different fishing fleets and countries and the catch information available for each component differs considerably; thus, compiling total catch numbers by age is a complicated process. The catch at age data used in our analysis are taken from the catch at age data used in the 2004 stock assessments for SBT conducted by CSIRO. The only differences are:

1) Significant numbers of small SBT were caught and released by Japanese longline vessels in 1995 and 1996, and we have chosen to include the estimated non-surviving portion of the discarded catches in our catch data, whereas the data used in the assessments did not (Preece et al. 2001; Preece et al. 2004).
2) The catch at age data for the assessments were compiled by calendar year (starting January 1) whereas for our analysis we compiled the data by ‘fishing’ year, defined as starting November 1, to be more consistent with the major fishing seasons for SBT.

More information about the fishery components and the processing and compiling of the catch data can be found in Appendix 4. Table 1d summarizes the total SBT catch data by cohort and year for 1991 to 1997. These numbers differ slightly from those presented in

Appendix 5 because the catch data were updated for the 2004 stock assessment, after the analysis in Appendix 5 had been completed.

The model

The model consists of four independent likelihood components, one for each of the tag-return data, the reporting rate estimates, the tag shedding estimates, and the catch data. Each of these likelihood components is described in detail below; however, before proceeding we introduce the notation that is used throughout the components.

Data to be inputted into the model:

K = number of tagged cohorts

A_k = minimum age of tagging (and also minimum age of returns) for cohort k

B_k = maximum age of tagging for cohort k

I_k = maximum age of returns for cohort k

T = number of tagger groups

$N_{k,t,a}$ = number of age a fish from cohort k tagged and released by tagger group t

$R_{k,t,a,i}$ = number of tags returned from age i fish from cohort k that were tagged at age a by tagger group t

$C_{k,i}$ = number of age i fish caught from cohort k

υ_C = coefficient of variation of the catch data (common across ages and cohorts)

$\hat{\lambda}_{k,i}$ = estimated reporting rate for tagged fish caught at age i from cohort k

σ_λ = standard error of the estimated reporting rates (common across ages and cohorts)

$\hat{\xi}_t$ = estimated immediate tag shedding rate for tagger group t

σ_{ξ_t} = standard error of $\hat{\xi}_t$

$\hat{\Omega}_t$ = estimated continuous tag shedding rate for tagger group t

σ_{Ω_t} = standard error of $\hat{\Omega}_t$

ρ_t = correlation between $\hat{\xi}_t$ and $\hat{\Omega}_t$

Parameters to be estimated in the model:

M_i = instantaneous natural mortality rate for age i fish

$F_{k,i}$ = instantaneous fishing mortality rate for age i fish from cohort k (excluding fish tagged at age i)

$F^*_{k,t,i}$ = instantaneous fishing mortality rate for age i fish from cohort k tagged by tagger group t at age i (i.e. for newly tagged fish in their first year of tagging)

P_{k,A_k} = population size of cohort k at age A_k (the minimum age of tagging for cohort k)

$\lambda_{k,i}$ = reporting rate for tagged fish captured at age i from cohort k

ξ_t = immediate tag shedding rate for tagger group t

Ω_t = continuous tag shedding rate for tagger group t

Note that we allow fishing mortality (F) to differ between both ages and cohorts, whereas we only allow natural mortality (M) to differ between ages.

Underlying the tag-return and catch likelihoods are the general population dynamics equations commonly used in fisheries, expressed in terms of exponential and competing natural and fishing mortality rates. In particular, for a cohort of animals of a given age, the expected number of animals that survive to the next age and the expected number caught are expressed by

$$P_{k,i+1} = P_{k,i} \exp\left(-F_{k,i} - M_i\right) \tag{1}$$

and

$$C_{k,i} = \frac{F_{k,i}}{F_{k,i} + M_i} P_{k,i} \left(1 - \exp\left(-F_{k,i} - M_i\right)\right) \tag{2}$$

$P_{k,i}$ is the population size of cohort k at age i, and all other notation is as defined above.

First consider the tag-return component of the model. Analogous to the application to SBT in Appendix 5, we modify the likelihood for a standard Brownie model to allow for fishing mortality to differ between tagged fish in the year of tagging and untagged fish in that same year (following the model presented in Hoenig et al. 1998). This is to allow for the fact that newly tagged fish will not be fully mixed with the untagged population immediately after tagging, and for the fact that tagging generally occurs during the fishing season so tagged fish are only vulnerable for part of the season. We assume that tagged and untagged fish are fully mixed by the year following release (all tagging of SBT occurred between November and April so this allows several months for mixing to occur). In addition, we modify the tag-return likelihood to allow for group-specific estimates of tag shedding parameters. In particular, we revise the return probabilities in the same manner as outlined in Appendix 14 (equation 9).

Taking into consideration tag shedding, tag reporting rates, and different return rates for newly tagged fish, the probability of a tag being returned from an age i fish from cohort k that was tagged at age a by tagger group t and has retained at least one tag is

$$p_{k,t,a,i} = \begin{cases} \left(2\xi_t u'^{*}_{k,t,i} - \xi_t^2 u''^{*}_{k,t,i}\right)\lambda_{k,i} & i = a \\ \left(2\xi_t u'_{k,t,i} S'^{*}_{k,t,a} - \xi_t^2 u''_{k,t,i} S'^{*}_{k,t,a}\right)\lambda_{k,i} & i = a+1 \\ \left(2\xi_t u'_{k,t,i} S'^{*}_{k,t,a} \prod_{m=a+1}^{i-1} S'_{k,t,m} - \xi_t^2 u''_{k,\tau,i} S''^{*}_{k,t,a} \prod_{m=a+1}^{i-1} S''_{k,t,m}\right)\lambda_{k,i} & i > a+1 \end{cases}$$

where

$$S'_{k,t,i} = \exp\left(-F_{k,i} - M_i - \Omega_t\right)$$

$$S''_{k,t,i} = \exp\left(-F_{k,i} - M_i - 2\Omega_t\right)$$

$$u'_{k,t,i} = \frac{F_{k,i}}{F_{k,i} + M_i + \Omega_t}\left(1 - S'_{k,t,i}\right)$$

$$u''_{k,t,i} = \frac{F_{k,i}}{F_{k,i} + M_i + 2\Omega_t}\left(1 - S''_{k,t,i}\right)$$

$$S'^{*}_{k,t,i} = \exp\left(-F^{*}_{k,t,i} - M_i - \Omega_t\right)$$

$$S''^{*}_{k,t,i} = \exp\left(-F^{*}_{k,t,i} - M_i - 2\Omega_t\right)$$

$$u'^{*}_{k,t,i} = \frac{F^{*}_{k,t,i}}{F^{*}_{k,t,i} + M_i + \Omega_t}\left(1 - S'^{*}_{k,t,i}\right)$$

$$u''^{*}_{k,t,i} = \frac{F^{*}_{k,t,i}}{F^{*}_{k,t,i} + M_i + 2\Omega_t}\left(1 - S''^{*}_{k,t,i}\right).$$

Note that we allow fishing mortality for newly tagged fish (F^*) to differ not only between ages and cohorts, but also between tagging groups. This is necessary because different tagging groups will tag fish at different locations and different times during the season (and some tagging groups may not tag any fish in a particular year); thus, the probability of fish tagged by a particular tagging group being caught in the same year it was tagged will depend in part on the tagging group. Note that these F^* parameters are nuisance parameters and are of little interest relative to the overall dynamics of the stock.

If tag returns are assumed to be independent, then the number of returns at age (including those not returned) corresponding to releases from a particular cohort at a particular age by a particular tagger group will be multinomial with probabilities as given above. Thus, the likelihood for all the returns at age data, over all cohorts, tagger groups and ages of release, is

$$L_R = \prod_{k=1}^{K}\prod_{t=1}^{T}\prod_{a=A_k}^{B_k}\left\{\mathrm{K}_{k,t,a}\left(\prod_{i=a}^{I_k}\left(p_{k,t,a,i}\right)^{R_{k,t,a,i}}\right)\left(1-\sum_{i=a}^{I_k} p_{k,t,a,i}\right)^{N_{k,t,a}-\sum_{i=a}^{I_k} R_{k,t,a,i}}\right\} \qquad (3)$$

where

$$\mathrm{K}_{k,t,a} = \frac{N_{k,t,a}!}{\prod_{i=a}^{I_k} R_{k,t,a,i}!\left(N_{k,t,a} - \sum_{i=1}^{I_k} R_{k,t,a,i}\right)!}.$$

Note that $\mathrm{K}_{k,t,a}$ is a constant that can be left out when maximizing the likelihood.

Next consider the reporting rate estimates. The procedure used to produce these estimates did not provide associated standard error estimates, so we assume that the reporting rate estimates have a common and known standard error and explore the effect of varying this value. The reporting rate estimates ($\hat{\lambda}_{k,i}$'s) and their assumed standard error (σ_λ) are brought into the model as data through an independent likelihood term. We assume that $x_{k,i} = n_{k,i}\hat{\lambda}_{k,i}$ is the number of tags reported at age *i* from cohort *k*, and that $x_{k,i}$ is binomial with probability $\lambda_{k,i}$ and sample size $n_{k,i}$. Note $n_{k,i}$ can be thought of as the sample size required to achieve the level of precision in the reporting rate estimate $\hat{\lambda}_{k,i}$ specified by σ_λ. Using the variance formula for a binomial distribution, we know that

$$Var\left(\hat{\lambda}_{k,i}\right) = \frac{\lambda_{k,i}\left(1-\lambda_{k,i}\right)}{n_{k,i}}.$$

We also know that

$$Var\left(\hat{\lambda}_{k,i}\right) = \sigma_\lambda^{\ 2},$$

so setting these equal we can solve for the sample size as

$$n_{k,i} = \frac{\lambda_{k,i}\left(1-\lambda_{k,i}\right)}{\sigma_\lambda^{\ 2}} \approx \frac{\hat{\lambda}_{k,i}\left(1-\hat{\lambda}_{k,i}\right)}{\sigma_\lambda^{\ 2}}.$$

Thus, the likelihood for the reporting rates can be specified as

$$L_\lambda = \prod_{k=1}^{K}\prod_{i=A_k}^{I_k} \frac{n_{k,i}\,!}{x_{k,i}\,!\left(n_{k,i}-x_{k,i}\right)!}\lambda_{k,i}^{\ x_{k,i}}\left(1-\lambda_{k,i}\right)^{n_{k,i}-x_{k,i}} \tag{4}$$

where $n_{k,i} = \dfrac{\hat{\lambda}_{k,i}\left(1-\hat{\lambda}_{k,i}\right)}{\sigma_{\lambda}^{2}}$ and $x_{k,i} = n_{k,i}\hat{\lambda}_{k,i}$.

For the tag shedding data, we take a similar approach as for the reporting rates and bring the group-specific tag shedding parameter estimates and their estimated standard errors and correlations into the model as data through an independent likelihood term. We assume that the two estimates for a given tagger group, $\hat{\xi}_t$ and $\hat{\Omega}_t$, have a bivariate normal distribution. Thus, the likelihood for the tag shedding data over all tagger groups is

$$L_{\xi,\Omega} = \prod_{t=1}^{T} \frac{1}{2\pi\sigma_{\xi_t}\sigma_{\Omega_t}\sqrt{1-\rho_t^2}} \exp\left(-\frac{1}{2\left(1-\rho_t^2\right)}\left\{\left(\xi_t'\right)^2 - 2\rho_t\,\xi_t'\,\Omega_t' + \left(\Omega_t'\right)^2\right\}\right) \qquad (5)$$

where $\xi_t' = \dfrac{\hat{\xi}_t - \xi_t}{\sigma_{\xi_t}}$ and $\Omega_t' = \dfrac{\hat{\Omega}_t - \Omega_t}{\sigma_{\Omega_t}}$.

Following the arguments presented in Appendix 5, we have chosen to model the error in the catch data as Gaussian with a constant coefficient of variation across ages and years/cohort. The coefficient of variation, denoted by υ_C, is intended to encompass both process error, which results from fishing being a random process, and sampling error, which results from the age distribution of the catch being determined by taking a sample, estimating the ages of fish in the sample (either from lengths or from direct aging of hard parts), and using the estimated age frequencies of the sample to represent the total catch. We assume that υ_C is known because, as discussed in Appendix 5, it cannot be estimated reliably. Assuming the catch data are independent between cohorts and ages, the likelihood for the catch data is

$$L_C = \prod_{k=1}^{K} \prod_{i=A_k}^{I_k} \frac{1}{\sqrt{2\pi}\,\upsilon_C E\left(C_{k,i}\right)} \exp\left(-\frac{1}{2}\left(\frac{C_{k,i} - E\left(C_{k,i}\right)}{\upsilon_C E\left(C_{k,i}\right)} \right)^2 \right) \tag{6}$$

where

$$E\left(C_{k,i}\right) = \begin{cases} P_{k,A_k} u_{k,A_k} & i = A_k \\ P_{k,A_k} u_{k,A_k} \prod_{m=A_k}^{i-1} S_{k,m} & i > A_k \end{cases}$$

$$S_{k,i} = \exp\left(-F_{k,i} - M_i\right)$$

$$u_{k,i} = \frac{F_{k,i}}{F_{k,i} + M_i}\left(1 - S_{k,i}\right).$$

The overall likelihood is given by the product of the four likelihood terms, namely

$$L_{Total} = L_R \times L_\lambda \times L_{\xi,\Omega} \times L_C \tag{7}$$

Multiplying the likelihood terms together is only a valid procedure if the likelihoods are independent of each other. The assumption of independence between the tag-return and the catch likelihoods may not be met if during the process of sampling the catch data, tags are found and returned; however, we assume that tags are removed at the time of catch, prior to catch sampling. Moreover, if the catch sample is relatively small, then the expected number of tags in the sample will be so small that the independence assumption will not be seriously violated. Independence between the tag shedding and tag-return likelihoods should be a valid assumption – even though the tag shedding estimates were obtained using the tagging data, the shedding estimates only use information on the number of recaptures with one tag versus two, and this information should have no bearing on the mortality rate estimates obtained from the tag-return likelihood. Independence between the reporting rate likelihood and the tag-return likelihood would be true if the reporting rate estimates were based on independent tag seeding data. Alternatively, if reporting rates were estimated using observer data, then their estimation would be incorporated directly into the tag-return and catch likelihoods (see Appendix 7). Unfortunately insufficient data from any one source meant that we had to use a complex method for constructing reporting rate estimates for SBT, combining estimates from tag seeding data and from observer data and using some rather ad hoc assumptions. As such, it is unlikely that the reporting rate likelihood is independent of the other likelihoods (since dependence between the observer data and other data sets has not been accounted for). Nevertheless, we do not expect the violation to be serious, nor do we expect the results, namely the mortality rate and abundance estimates, to be appreciably affected.

The overall likelihood L_{Total} can be maximized (or, more commonly done in practice, the negative log of the likelihood can be minimized) to give estimates of the unknown model parameters (listed at the start of the section). However, it must be noted that not all of the natural mortality parameters can be estimated. Information for estimating M_i comes from tagging a single cohort at consecutive ages; in particular, from the differential between the expected returns at age $i+1$ of fish from the cohort released at age i and those released the next year at age $i+1$. Thus, in an experiment in which n consecutive ages of fish from a particular cohort are tagged, estimates can only be obtained for $n-1$ natural mortality rate parameters (regardless of the number of recapture years). For the SBT data being considered, we have a maximum of three consecutive release ages, so we can only estimate two age-specific natural morality rates. In the application to SBT presented in Appendix 5, we addressed this issue by assuming that $M_i = M_2$ for $i \geq 2$, but this is probably not the most realistic assumption for SBT. Natural mortality is generally assumed to decrease with age for SBT, at least over the young ages we are considering, so in the current analysis we chose to model natural mortality as a linear function of age, and we parameterized the function in terms of natural mortality at the youngest age and the oldest age of returns. For example, if the youngest and oldest returns being included in the model are ages 1 and 5 respectively, then we let

$$M_i = M_1 + \frac{M_5 - M_1}{5-1}(i-1)$$

where M_1 and M_5 are the two parameters to be estimated.

The model fitting was performed using the commercially available software AD Model Builder (Otter Research Ltd., P.O. Box 2040, Sidney BC, V8L 3S3, Canada). The software provides point estimates of the parameters as well as variance estimates calculated using the inverse negative Hessian matrix.

To evaluate model fits, we computed 'standardized' residuals for the return data and catch data. Ordinary residuals are difficult to interpret because the variance differs so much between observations within each data set. For the Gaussian catch data, we defined a standardized residual as

$$\frac{C_{k,i} - \hat{C}_{k,i}}{\upsilon_C \hat{C}_{k,i}}$$

where $\hat{C}_{k,i}$ is the fitted catch value. If the assumption that the catch data are independent Gaussian with coefficient of variation as specified is reasonable, then we expect the standardized residuals have a standard normal distribution (so approximately 95% should fall within the range -2 to 2). With regard to the tag return data, there does not appear to be a conventional way to compute standardized residuals for multinomial data; therefore, we defined a standardized residual as

$$\frac{R_{k,t,a,i} - N_{k,t,a}\,\hat{p}_{k,t,a,i}}{\sqrt{N_{k,t,a}\,\hat{p}_{k,t,a,i}\left(1-\hat{p}_{k,t,a,i}\right)}}$$

where $\hat{p}_{k,t,a,i}$ is the fitted tag return probability. Interpretation of these residuals is not straightforward because they are not independent and their distribution is not evident. If the expected return counts were adequately large, then it would seem reasonable to assume the standardized residuals should follow a standard normal distribution; however, for the SBT data, many of the expected return counts are close to zero so this is not likely a good approximation. Nevertheless, the standardized residuals provide a rough diagnostic to check for extreme outliers and patterns that indicate a violation of the model. Also, the sign of the standardized residuals is the same as that of the ordinary residuals, so they can be used without reservation in identifying tendencies for under- or over-estimation.

Results

We present results from analyses that included data from cohorts 1989 through 1994. These are the only cohorts with sufficient release and recapture data to warrant inclusion. Additionally, we only included recaptures up to a maximum of age 5 because the numbers of recaptures beyond age 5 are relatively small and because the assumption that natural mortality is a linear function of age is less likely to hold true at older ages. Thus, in the notation presented in the model section, the number of cohorts being modelled is $K = 6$, which we will index by $k = 1989, 1990, \ldots, 1994$ for ease of reference; the minimum age of release/return is $A_{1989} = 2$ and $A_k = 1$ for all other *k*; the maximum age of release is $B_k = 3$ for all *k*; and the maximum age of return is $I_k = 5$ for $k = 1989, \ldots, 1992$, $I_{1993} = 4$ and $I_{1994} = 3$ (because fish from cohorts 1993 and 1994 are ages 4 and 3 respectively in 1997, which is the last year being considered).

Before applying the model, we needed to specify a coefficient of variation for the catch at age data (υ_C) and a standard error for the reporting rate estimates (σ_λ). In our initial analyses, we set υ_C to be 0.3 based on results from the SBT analysis presented in Appendix 5, and we set σ_λ to be 0.1 since the uncertainty in the reporting rate estimates is expected to be quite high; however, later we will look at the effect of varying these values.

First, we fit the model with all parameters free except for the constraints already discussed (i.e., natural mortality linear with age). We will refer to this as model 1. Second, we fit the model with the constraint that fishing mortality can be separated into a multiplicative age and year effect[2]; i.e., we assumed that $F_{k,j} = F_Y(k+j)F_A(j)$, where $F_Y(k+j)$ is the year-specific component of fishing mortality in year $k+j$ and $F_A(j)$ is the age-specific component of fishing mortality at age *j* (commonly referred to as

[2] This constraint was only applied to the general fishing mortality parameters, not to the fishing mortality parameters for newly tagged fish in their first year of tagging (i.e. the F^* parameters).

selectivity). We refer to this as model 2. Note that F_Y and F_A are only unique up to a multiplicative constant because $F_Y F_A = (gF_Y)(F_A/g)$ for any constant g. Therefore, to get a unique solution, we fixed F_A at age 5 to be 1.0.

The parameter estimates from the two models are compared in Figures 1 to 3 (for completeness, the estimates and their standard deviations for the two models are also tabulated in Annex A). The fishing mortality rate estimates by age and cohort shown in Figure 2 for model 2 can be calculated by multiplying the estimated age effects and year effects obtained from the model together; the standard deviations were outputted from the estimation software (but in theory could be calculated explicitly using statistical methods for calculating the variance of the product of two random variables). Both models provide an estimate of the population size at the minimum age of tagging for each cohort. For the 1989 cohort the minimum age of tagging was age 2, whereas for all other cohorts in the model it was age 1. In order to make the abundance estimates comparable between cohorts, we back-calculated an estimate of age 1 abundance for the 1989 cohort. To do so, we used the estimates of age 2 abundance for the 1989 cohort and age 1 natural mortality obtained from the model (which we will denote by $\hat{P}_{1989,1}$ and $\hat{M}_1$ respectively), and brought in external information on the catch of age 1 fish for the 1989 cohort, then solved equations (1) and (2) for both the fishing mortality rate and the population size at age 1 (we denote these by $\tilde{F}_{1989,1}$ and $\tilde{P}_{1989,1}$ to indicate that they are estimates, but not maximum likelihood estimates from the model). We calculated an approximate variance for $\tilde{P}_{1989,1}$ using the formula

$$Var\left(\tilde{P}_{1989,1}\right) \approx \left(\exp\left(\tilde{F}_{1989,1} + \hat{M}_1\right)\right)^2 Var\left(\hat{P}_{1989,2}\right),$$

where the variance of $\hat{P}_{1989,2}$ is obtained from the model output. This formula assumes that $\tilde{F}_{1989,1}$ and $\hat{M}_1$ are known without error; although this is not true, it provides a reasonable approximation for our purposes.

The parameter estimates obtained from the two models are very similar; the only parameters for which the error bars on the estimates (defined as plus or minus one standard deviation) do not overlap are $F_{1989,2}$ and $F_{1993,3}$. Natural mortality at age 1 is quite high (~0.4) and decreases to about 0.2 by age 5, but the uncertainty in the age 5 estimate is very high (Figure 1). Fishing mortality is generally close to zero for ages 1 and 2, and for ages 3 to 5 it appears to have increased with cohorts (or years) (Figure 2). These patterns are more apparent if we look at the separate age- and year-effect estimates from model 2; the results from model 2 suggest that selectivity at young ages is dome-shaped with the peak at age 3 (Figure 4, top), and that fishing mortality was a fairly smooth U-shaped function of time over the years of the analysis (Figure 4, bottom). Note that the estimate for 1991 is very high and uncertain (0.54±0.38), the reasons for which are discussed below when we examine the residuals, so it has been omitted from the graph. Population abundance appears to have decreased over time, from about 2.5-3 million age 1 fish in 1989 to just over 1 million age 1 fish in 1993 and 1994 (Figure 3).

The negative log-likelihood value for model 1 is 25295.0, and for model 2, which has 15 fewer fishing mortality parameters to be estimated than model 1, it is 25326.7 (Table 2). According to Akaike's information criterion (Akaike 1974), which takes the extra number of parameters in model 1 into account, model 1 provides a statistically better fit to the data than model 2. However, the breakdown of the likelihood into its components shows that the difference in the likelihoods is mainly due to model 1 fitting the catch at age data better; the other data sets, in particular the tag-return data, are fitted almost equally well by model 2 (Table 2).

Standardized residuals, as defined in the model section, were computed for the tag-return and catch data for both models. Not surprisingly given the comparison of the likelihood components between the two models, the residuals are very similar between the models for the tag-return data, but are worse for model 2 for the catch data (compare Tables 3 and 4). With regard to the tag-return residuals, an obvious feature is that the residuals for the returns at the same age as release are always very close to zero. This is due to having a unique F^* parameter for every observation corresponding to these residuals. While this is clearly a case of over-fitting, we showed in Appendix 5 and confirmed in our current analysis that the inclusion of F^*'s is necessary to get a good fit. More importantly, because tags tended to be released in the area of the surface fishery either near the beginning or end of the fishing season, the fishing mortality for fish tagged in the year of release would be expected to differ from that for the population as a whole and would also be expected to vary greatly for different releases depending upon the exact release time and location.

The standardized residuals pooled over tagging groups (Tables 3a and 4a) show no obvious outliers or patterns, except perhaps for a tendency for returns at age from the same cohort and release age to all be overestimated or underestimated (indicated by rows of mostly negative values or mostly positive values). Boxplots of the (unpooled) standardized return residuals broken down by a number of factors suggest that the returns for tagger groups 5 and, especially, 6 may be overestimated (Figure 5); otherwise, there is nothing to cause alarm (note that only model 1 results have been plotted because the model 2 results are so similar). The standardized catch residuals for model 1 suggest a very good fit (Table 3b); model 2 does not fit the catch data as well, with age 1 catches for cohorts 1992 to 1994 and age 2 catch for cohort 1989 being notably overestimated. Looking at the catch data (Table 1d), the age 1 catch was much higher in 1991 than in subsequent years of the analysis (almost 50 000 fish in 1991 versus <8000 fish in all other years and <500 in 1992 to 1996).[3] In order for model 2 to estimate an age 1 fishing mortality effect that fits both the large 1991 value and the small values in later years, it must reach a compromise and, thus, ends up underestimating the 1991 value and overestimating the others. However, having said this, the age 1 catch in 1991 is not underestimated to the degree we might expect; this is because, in response to the age 1 effect being estimated so low, the year effect for 1991 is estimated very high. There are only two catch observations contributing to the 1991 year effect – age 1 catch from the

[3] Historically, large numbers of age 1 SBT were caught off of Western Australia, but changes in the fishery resulted in 1991 being the last year of any substantive catches in this area (see Discussion).

1990 cohort and age 2 catch from the 1989 cohort – so the best model fit is achieved with a very high year effect for 1991, which gives a reasonable (although still somewhat underestimated) fit to the large age 1 catch value, but decidedly overestimates the age 2 value. Keep in mind that the model uses not only the catch data but also the tag-return data in estimating age- and year-specific fishing mortality effects; however, for 1991, only the catch data influence the fishing mortality estimates because the two tag-return observations for 1991 are from fish tagged in that same year so the F^* parameters for newly tagged fish apply instead of the fishing mortality parameters for the general population.

We re-fit both models only including data from cohorts 1991 to 1994 (which excludes any data from 1991 or prior). In this case, model 2 provides a significantly better fit than model 1 according to AIC.

To test the sensitivity of the results to the coefficient of variation assumed for the catch data and the standard error assumed for the reporting rate estimates we re-fit model 1, first, keeping σ_λ at 0.1 and varying υ_C and, second, keeping υ_C at 0.3 and varying σ_λ. In both situations, the point estimates of the parameters did not change significantly (all were within one standard deviation of each other), and the uncertainty in the estimates tended to increase as the variability in the data increased. For illustrative purposes, we have shown the results of varying υ_C (Figure 6) and varying σ_λ (Figure 7) on the fishing mortality rate estimates for the 1990 cohort and the age 1 population size estimates. We may have expected the increase in the standard deviation of the parameter estimates to be greater in response to increased uncertainty in the catch data or reporting rate estimates; however, the variance of the parameter estimates is determined by the variability of all data inputs and will tend to be dominated by the data set that is most variable, so changing one component may not necessarily have a large effect.

We also wanted to test the sensitivity of the results to the reporting rate estimates chosen as input to the model. As discussed in the data section, a number of reporting rate options are proposed in Appendix 19 based on a range of assumptions. Although we chose to use the option that is most highly information based, it is also yields the lowest reporting rates; thus, we re-fit model 1 using the option with the highest reporting rates (option 1 of Table 5a, Appendix 19) to evaluate the effect. Not surprisingly, the fishing mortality rates decreased and the population size estimates increased; however, the effect was greatest for the population size estimates (Figure 8). The changes were fairly uniform in that all fishing mortality estimates shifted down by relatively equal amounts, and all population size parameters shifted up by relatively equal amounts. Thus, if relative indices and trends in fishing mortality and abundance are of greater interest than actual magnitude, then the reporting rate option chosen does not matter as much. Note that the natural mortality rate estimates were largely unaffected by the reporting rate option used.

The model estimates of the reporting rates and the tag shedding parameters (see Annex A) have not been discussed. There is little information in the tag-return or catch data to draw these estimates away from their previously estimated values. As such, the model estimates of these parameters are quite similar to the estimates that are inputted. In fact, for the tag shedding parameters they are virtually identical because the standard errors being used for the shedding estimates (σ_ξ and σ_Ω) are so small that there is almost no flexibility in their estimation. The primary reason for including likelihoods for the reporting rate and shedding parameters is to acknowledge their uncertainty and thereby get more realistic variance estimates on the mortality rate and abundance estimates, not to improve the estimates of the reporting rate and shedding parameters themselves.

Estimates of the fishing mortality rate parameters for newly tagged fish (F^*'s) have not been presented. These parameters are not of general interest because they do not represent fishing mortality on the population as a whole. They are simply necessary in order to get realistic estimates of the parameters that are of interest.

Conclusions and Discussion

A comprehensive model for estimating mortality rates and abundance for southern bluefin tuna using tag-return data and catch data has been presented. Two versions of the model were fitted – one in which the age- and year- specific fishing mortality rates were unconstrained (model 1) and one in which they were constrained to have separable, multiplicative age and year effects (model 2). Both models led to similar parameter estimates and the same general conclusions. The results suggest that natural mortality at age 1 is quite high (~0.4) and decreases to about 0.2 by age 5; however, the uncertainty in the age 5 estimate is very high and we found that the estimate is sensitive to changes in either the model or the data inputs. Tagging cohorts at age 4 (in sufficient numbers) in addition to ages 1 to 3 could provide valuable information for better estimating natural mortality at older ages. Fishing mortality is generally close to zero for ages 1 and 2, is greatest at ages 3 and 4, and declines at age 5. The results also suggest that juvenile fishing mortality decreased in the first couple of years of the 1990s then increased fairly steadily from 1994 to 1997. Population abundance appears to have decreased from about 2.5-3 million age 1 fish in 1989 to just over 1 million age 1 fish in 1993 and 1994.

When fit to the data from cohorts 1989 to 1994, model 1 provided a better fit from a statistical point of view; however, from a practical point of view, model 2 may still be preferred given the fact that it led to very similar parameter estimates using substantially fewer parameters and it also provided better insight into trends in fishing mortality with age and years. However, the lack of fit of model 2 to some of the catch observations highlighted potential problems with separable models when fishing practices (e.g., selectivity) have changed over time. For example, we saw that the SBT fishery caught large numbers of age 1 fish in 1991 then dramatically decreased its catch of age 1 fish in subsequent years. Looking back at catch data prior to 1991 shows that age 1 fish were caught in even larger numbers over the history of the fishery, with over a million age 1 fish being caught in 1983. A large portion of the historic age 1 catches occurred off of Western Australia, but when joint venture fishing opportunities began in 1992 fishing off of Western Australia decreased substantially. It is important that such changes in selectivity over time are recognized and accounted for when estimating separate age and year effects. Because selectivity was relatively constant over most years included in our analysis, model 2 was still able to provide a reasonable fit. When we re-ran the analysis only including data from cohorts 1991 to 1994 in order to exclude any data from 1991 or prior, we found that model 2 provided a statistically better fit than model 1. These results suggest that a separable model is appropriate for SBT, and illustrate the importance of incorporating changes in selectivity.

Reporting rates and tag shedding rates were estimated from independent analyses for input to the model. We accounted for their uncertainty by including additional likelihood terms for the estimates and their standard errors (similar to putting a prior on the parameters in a Bayesian framework). Ideally, we would estimate reporting rates directly within the model (for example, using observer data as described in Appendix 7), but unfortunately the observer data for SBT are insufficient to let us do so. In the case of the shedding parameters, it is possible to directly incorporate their estimation into the model, as described in Appendix 14 (equations 10 and 11); however, this would require breaking the returns down not only by cohort, release age, return age and tagging group, but also according to whether one tag or both tags were returned. Many of the return counts will be very small when broken down to this level and will likely introduce estimation problems. Furthermore, the estimates of the shedding parameters will almost certainly be similar to those obtained from the independent analysis since the only information available for estimating them (i.e., comparing numbers of returns with one tag versus two) is the same in both cases.

Instead of modelling the reporting rate estimates directly, we modelled a variable representing the number of reported tag returns using a binomial distribution and an estimated effective sample size. It would have been more straightforward to model the reporting rate estimates themselves as having, say, a beta distribution (this was the approach taken in Appendix 9 for modelling the reporting rates in the surface fishery component of the 2-fishery model). However, the maximum likelihood estimates of the parameters of a beta distribution correspond to the mode, not the mean, so that the reporting rate estimates obtained using a beta likelihood are not equal to the reporting rate estimates inputted as data to the likelihood. In fact, they can be substantially different when the distribution is highly skewed. This result is undesirable because, in the absence of any other information, we do not want the reporting rate estimates to change. To resolve this problem, we used the binomial approach. Using a normal distribution for the reporting rates would also have resolved this problem but it would not have been a realistic choice because it does not constrain the estimates to be between 0 and 1. This is not necessarily a problem if the estimates are sufficiently away from these bounds and/or have small variances, but this is not true for many of the reporting rate estimates. We were able to use a bivariate normal distribution for the shedding parameters, even though they too should be constrained between 0 and 1, because their estimated variances were so small that the normal approximation was adequate.

The model assumes that catch numbers between ages within a year are independent. Although this is not true conditional on the total catch in a year (since catching more fish at one age means catching less fish at another age to achieve the same total), it is a reasonable assumption unconditionally. For example, consider the following argument: if the total catch within a year is random and follows a Poisson distribution, and the distribution of the age counts conditional on the total is multinomial, then the unconditional age counts are independent Poisson. At large catch sizes, these can be approximated as independent Gaussian, which is what we have done.

Even after taking measures to incorporate uncertainty in the reporting rates and shedding rates into the model, the standard errors of the mortality rate and abundance estimates may still to be underestimated. This is because the variance in the number of returns is likely to be greater than predicted by a multinomial distribution due to incomplete mixing and heterogeneity in the capture probabilities of fish. One way of accounting for overdispersion in the tag-return data is to model the data as Dirichlet-multinomial, as described in Appendix 9. To do so requires an assumption be made about the level of overdispersion, either assuming it is known or keeping it constant since it cannot be estimated otherwise. The necessity for, and potential gain from, incorporating overdispersion in the tag-return model for southern bluefin tuna is an area for further investigation.

References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, **19**: 716-723.

Anon. 2005. Report of the special management procedure technical meeting. Commission for the Conservation of Southern Bluefin Tuna. 15-18 February. Seattle, USA.

Hoenig, J.M., Barrowman, N.J., Pollock, K.H., Brooks, E.N., Hearn, W.S., and Polacheck, T. 1998. Models for tagging data that allow for incomplete mixing of newly tagged animals. Can. J. Fish. Aquat. Sci. 55: 1477-1483.

Kolody, D., and Polacheck, T. 2001. Application of a statistical catch-at-age and length integrated analysis model for the assessment of southern bluefin tuna stock dynamics 1951-2000. Commission for the Conservation of Southern Bluefin Tuna. CCSBT-SC/0108/13.

Polacheck, T., W. Hearn, C. Millar, W. Whitelaw and C. Stanley. 1996. Estimation of natural and fishing mortality rates for juvenile southern bluefin tuna based on multi-year tagging of cohorts. Commission for the Conservation of Southern Bluefin Tuna. CCSBT/SC/96/11.

Polacheck, T., W. Hearn, C. Millar, W. Whitelaw and C. Stanley. 1997. Updated estimates of mortality rates for juvenile southern bluefin tuna from multi-year tagging cohorts 1997. Council for the Conservation of Southern Bluefin Tuna. CCSBT/SC/9707/26.

Polacheck, T., W. Hearn, C. Millar, W. Whitelaw and C. Stanley. 1998. Updated estimates of mortality rates for juvenile southern bluefin tuna from multi-year tagging cohorts 1998. Council for the Conservation of Southern Bluefin Tuna. CCSBT/SC/9807/20.

Polacheck, T., Preece, A. and Ricard, D. 2001. Assessment of the status of the southern bluefin tuna stock using virtual population analyses – 2001. Council for the Conservation of Southern Bluefin Tuna. CCSBT-SC/0108/20.

Preece, A., Polacheck, T., Kolody, D., Eveson, P., Ricard, D., Jumppanen, P., Farley, J., and Davis, T. 2001. Summary of the primary data inputs to CSIRO's 2001 stock assessment models. Commission for the Conservation of Southern Bluefin Tuna. CCSBT-SC/0108/21.

Preece, A., Cooper, S., and Hartog, J. 2004. Data post-processing for input to the 2004 stock assessments and comparisons of 2001 and 2004 assessment datasets. Commission for the Conservation of Southern Bluefin Tuna. CCSBT-ESC/0409/27.

Table 1. Summary of the four southern bluefin tuna data sets used as input to the model.

a) Tag-return data

Cohort	Release year	Release age	Number releases	Number returns by year 1991	1992	1993	1994	1995	1996	1997
1988	1991	3	810	63	8	16	7	1	5	1
1989	1991	2	3127	103	148	59	34	20	7	5
	1992	3	1097		57	18	11	9	3	2
1990	1991	1	3299	20	40	46	23	13	5	4
	1992	2	4646		88	159	101	33	12	8
	1993	3	2777			66	78	32	17	15
1991	1992	1	2144		1	21	56	37	11	7
	1993	2	2937			60	68	67	21	11
	1994	3	3640				77	145	30	40
1992	1993	1	4898			2	41	201	91	58
	1994	2	3158				29	167	76	52
	1995	3	2629					55	103	74
1993	1994	1	9003				4	110	401	364
	1995	2	5899					83	395	363
	1996	3	1511						115	201
1994	1995	1	8585					0	87	622
	1996	2	2518						77	339
	1997	3	526							91
1995	1996	1	82						0	3
	1997	2	592							15
1996	1997	1	884							1

b) Reporting rate estimates

Cohort	Reporting rate estimate, $\hat{\lambda}$						
	1991	1992	1993	1994	1995	1996	1997
1988	0.597	0.327	0.402	0.390	0.179	0.254	n/a
1989	0.654	0.543	0.471	0.457	0.192	0.275	0.596
1990	0.933	0.577	0.625	0.559	0.258	0.267	0.568
1991		0.887	0.750	0.600	0.388	0.250	0.537
1992			0.926	0.498	0.622	0.411	0.597
1993				0.522	0.592	0.474	0.639
1994					0.725	0.388	0.727
1995						0.321	0.775
1996							0.805

c) Tag shedding data (parameter estimates, standard errors and correlations)

Tagger Group	$\hat{\xi}$	σ_{ξ}	$\hat{\Omega}$	σ_{Ω}	ρ
1	0.974	0.007	0.039	0.004	0.005
2	0.961	0.012	0.049	0.006	0.008
3	1.000	0.000	0.067	0.004	0.000
4	1.000	0.000	0.093	0.006	0.000
5	0.934	0.040	0.089	0.023	0.028
6	0.967	0.022	0.160	0.016	0.016

d) Catch data

Cohort	Number fish caught						
	1991	1992	1993	1994	1995	1996	1997
1988	176057	77731	48640	24928	20560	15357	11443
1989	76744	150758	65802	32144	27442	18972	17492
1990	48450	33638	120232	72806	39073	24743	21673
1991		7624	38414	119166	61080	38646	27398
1992			404	10398	133300	76136	43001
1993				187	30789	171859	72177
1994					416	26276	203883
1995						422	32025
1996							1965

Table 2. Negative log-likelihood values for models 1 and 2. The total as well as breakdown into likelihood components is given.

Component	Model 1	Model 2
Tag-return	24691.0	24695.1
Reporting rates	360.0	361.5
Shedding rates	2.2	2.2
Catch	241.8	267.8
Total	25295.0	25326.7

Table 3. Standardized tag-return and catch residuals for the model with unconstrained fishing mortality rates (model 1).

a) standardized tag-return residuals, pooled over tagging groups[4]

	Release	Recapture age				
Cohort	age	1	2	3	4	5
1989	2		0.1	0.1	1.4	1.1
1989	3			-0.1	-1.9	-1.2
1990	1	0.0	0.4	-2.4	-2.5	-0.4
1990	2		0.1	1.3	1.8	0.2
1990	3			0.0	-0.3	0.3
1991	1	0.0	-0.1	2.4	0.5	0.9
1991	2		0.0	-2.0	-0.5	0.7
1991	3			0.0	0.4	-0.8
1992	1	0.0	0.7	1.3	1.5	0.6
1992	2		0.0	-1.3	-0.4	-0.4
1992	3			0.0	-0.9	-0.3
1993	1	0.0	-0.1	0.5	0.4	
1993	2		0.0	-1.1	-1.4	
1993	3			0.6	1.5	
1994	1	0.0	0.1	-1.7		
1994	2		0.3	2.4		
1994	3			0.0		

b) standardized catch residuals

Cohort	Age 1	Age 2	Age 3	Age 4	Age 5
1989		0.3	0.3	0.5	0.0
1990	0.3	-1.0	0.9	0.7	-0.1
1991	0.3	0.4	1.0	-1.0	0.1
1992	0.3	-1.8	0.8	0.3	0.6
1993	0.3	0.7	0.1	-0.1	
1994	0.3	-0.4	0.8		

[4] Pooled standardized residuals over tagging groups were calculated as

$$\sum_{t=1}^{6}\left(R_{k,t,a,i} - N_{k,t,a}\,\hat{p}_{k,t,a,i}\right) \Big/ \sqrt{\sum_{t=1}^{6} N_{k,t,a}\,\hat{p}_{k,t,a,i}\left(1-\hat{p}_{k,t,a,i}\right)}\ .$$

Table 4. Standardized recapture and catch residuals for the model with fishing mortality rates constrained to have separable age and year effects (model 2).

a) standardized tag-return residuals, pooled over tagger groups (see footnote to Table 3)

	Release	Recapture age				
Cohort	age	1	2	3	4	5
1989	2		0.1	0	1.6	1.9
1989	3			-0.1	-1.9	-0.9
1990	1	0.0	0.5	-2.5	-2.5	-0.4
1990	2		0.1	1.2	1.8	0.3
1990	3			0.0	-0.5	0.2
1991	1	0.0	0.4	2.2	0.6	0.8
1991	2		0.0	-2.1	-0.5	0.7
1991	3			0.0	0.2	-1.0
1992	1	0.0	0.9	1.3	1.5	0.5
1992	2		-0.1	-1.4	-0.3	-0.4
1992	3			0.0	-1.1	-0.6
1993	1	0.0	0.2	0.7	0.1	
1993	2		0.0	-0.8	-1.6	
1993	3			0.4	2.6	
1994	1	0.0	-0.4	-1.8		
1994	2		0.4	2.4		
1994	3			0.0		

b) standardized catch residuals

Cohort	Age1	Age2	Age3	Age4	Age5
1989		-2.5	-0.1	0.6	0.9
1990	1.0	-1.0	0.5	0.4	-0.2
1991	1.0	1.0	0.3	-1.2	-0.8
1992	-2.7	-1.5	1.4	0.3	0.5
1993	-3.1	0.3	1.2	-0.7	
1994	-2.9	-0.7	1.3		

Figure 1. Comparison of natural mortality rate (*M*) estimates and their standard deviations (SD) by age for the model with unconstrained fishing mortality rates (model 1) and the model with fishing mortality rates constrained to have separable age and year effects (model 2). Black circle = model 1 results; blue triangle = model 2 results.

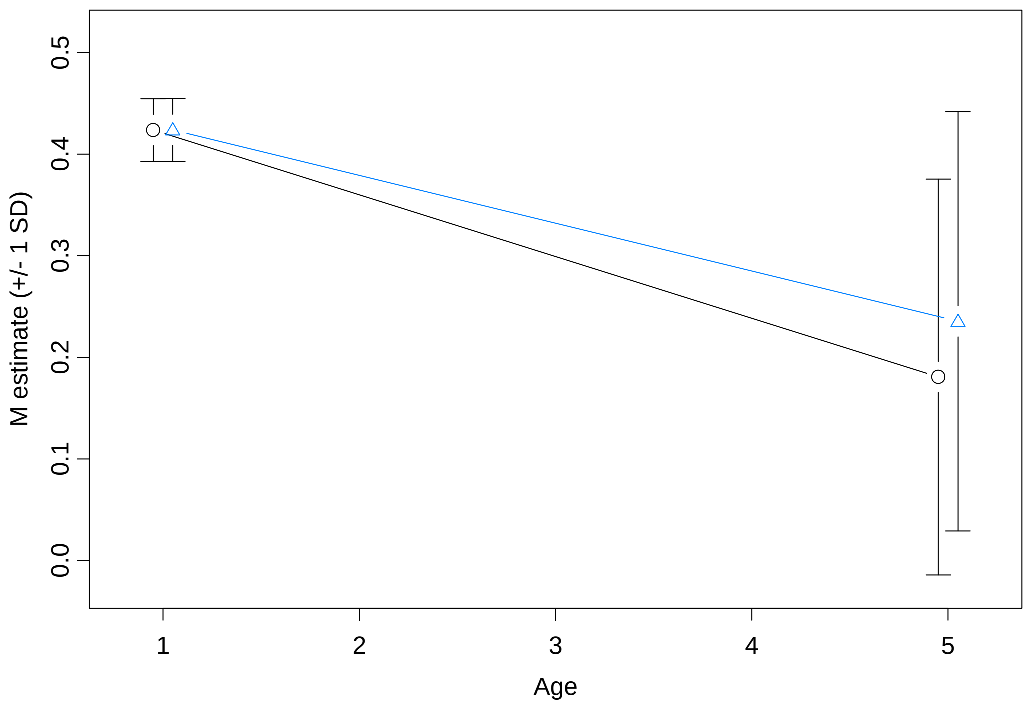


Figure 2. Comparison of fishing mortality rate (*F*) estimates and their standard deviations (SD) by cohort and age for the model with unconstrained fishing mortality rates (model 1) and the model with fishing mortality rates constrained to have separable age and year effects (model 2). Black circle = model 1 results; blue triangle = model 2 results.

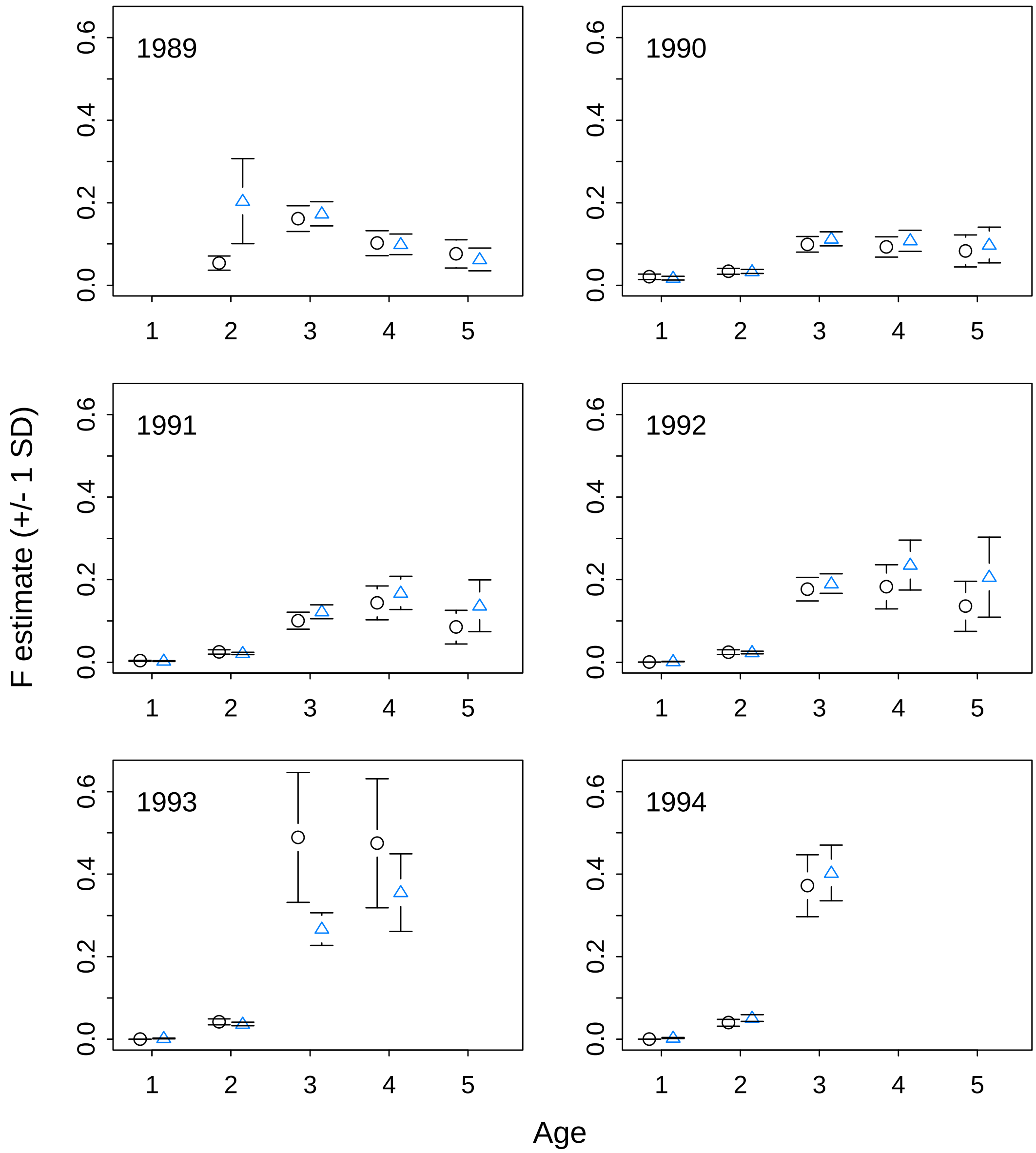


Figure 3. Comparison of population size (*P*) at age 1 estimates and their standard deviations (SD) by cohort for the model with unconstrained fishing mortality rates (model 1) and the model with fishing mortality rates constrained to have separable age and year effects (model 2). Black circle = model 1 results; blue triangle = model 2 results. For the 1989 cohort, only a direct estimate of *P* at age 2 is obtained from the models, so the age 1 estimates shown are post-calculated (see text).

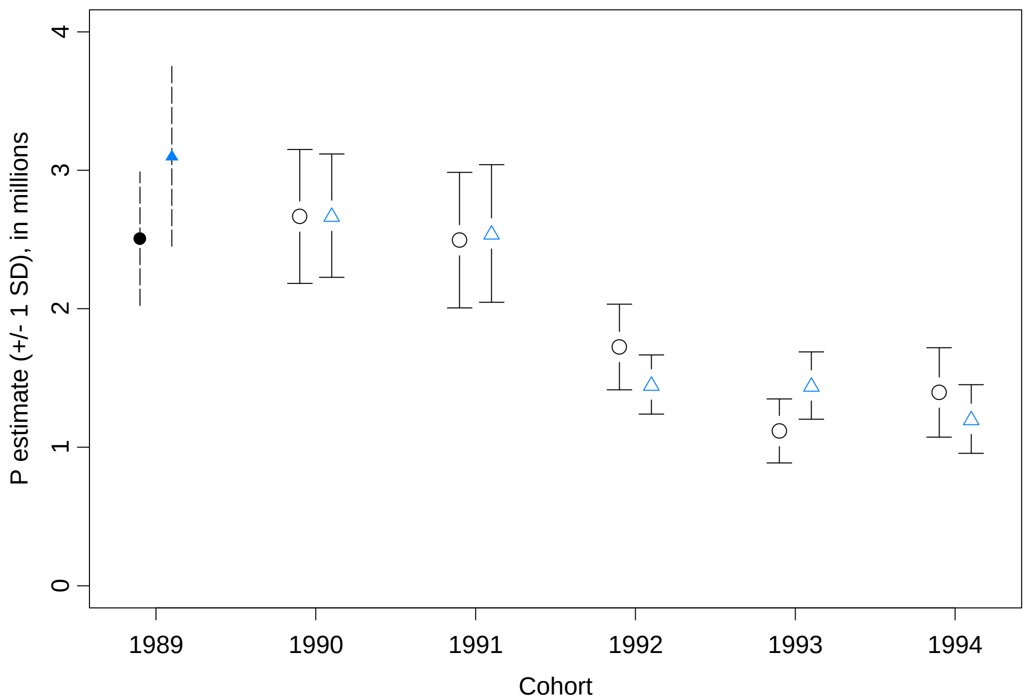


Figure 4. Estimates (± 1 standard deviation) of the age-specific fishing mortality rate effect (upper panel) and the year-specific fishing mortality effect (lower panel) for the model with separable fishing mortality rates (model 2). Note that the estimates should be interpreted as relative indices; the age effect at age 5 has been fixed at 1.0 (see text). The estimate of the year-specific component for 1991 has been omitted because it is based on very little data and has large uncertainty associated with it (refer to text).

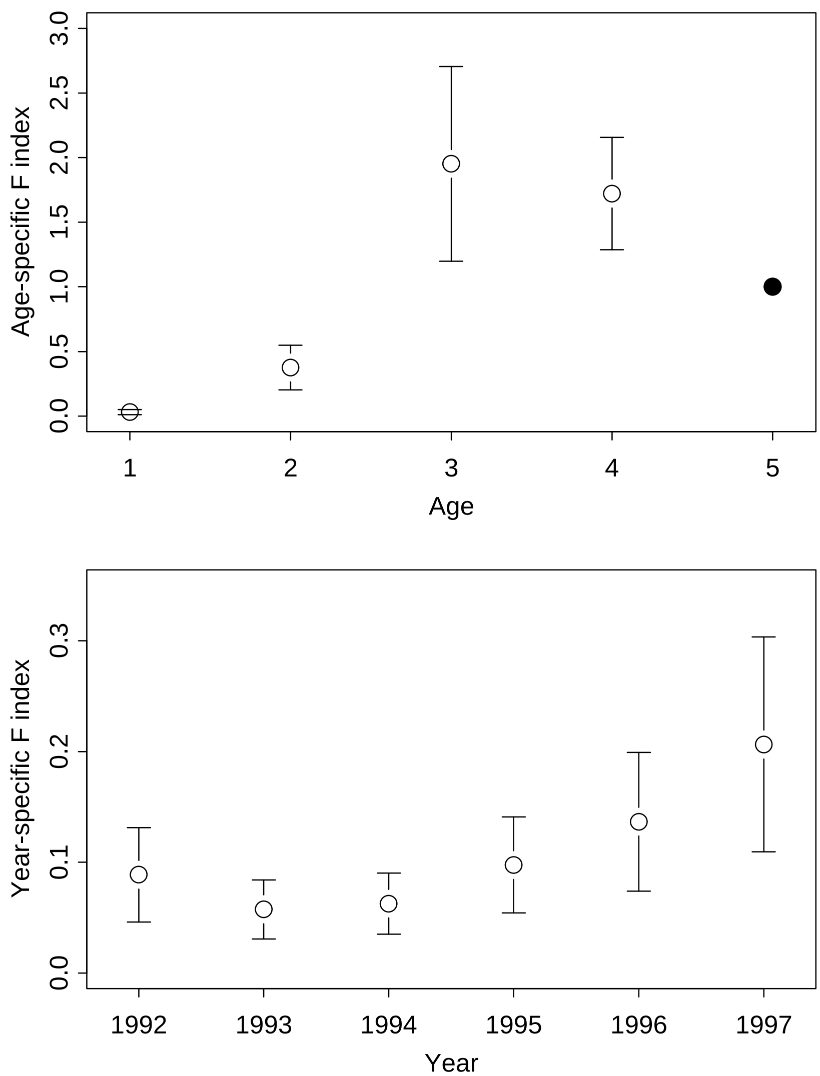


Figure 5. Boxplots of standardized recapture residuals broken down by various factors for the model with unconstrained fishing mortality rates (model 1).

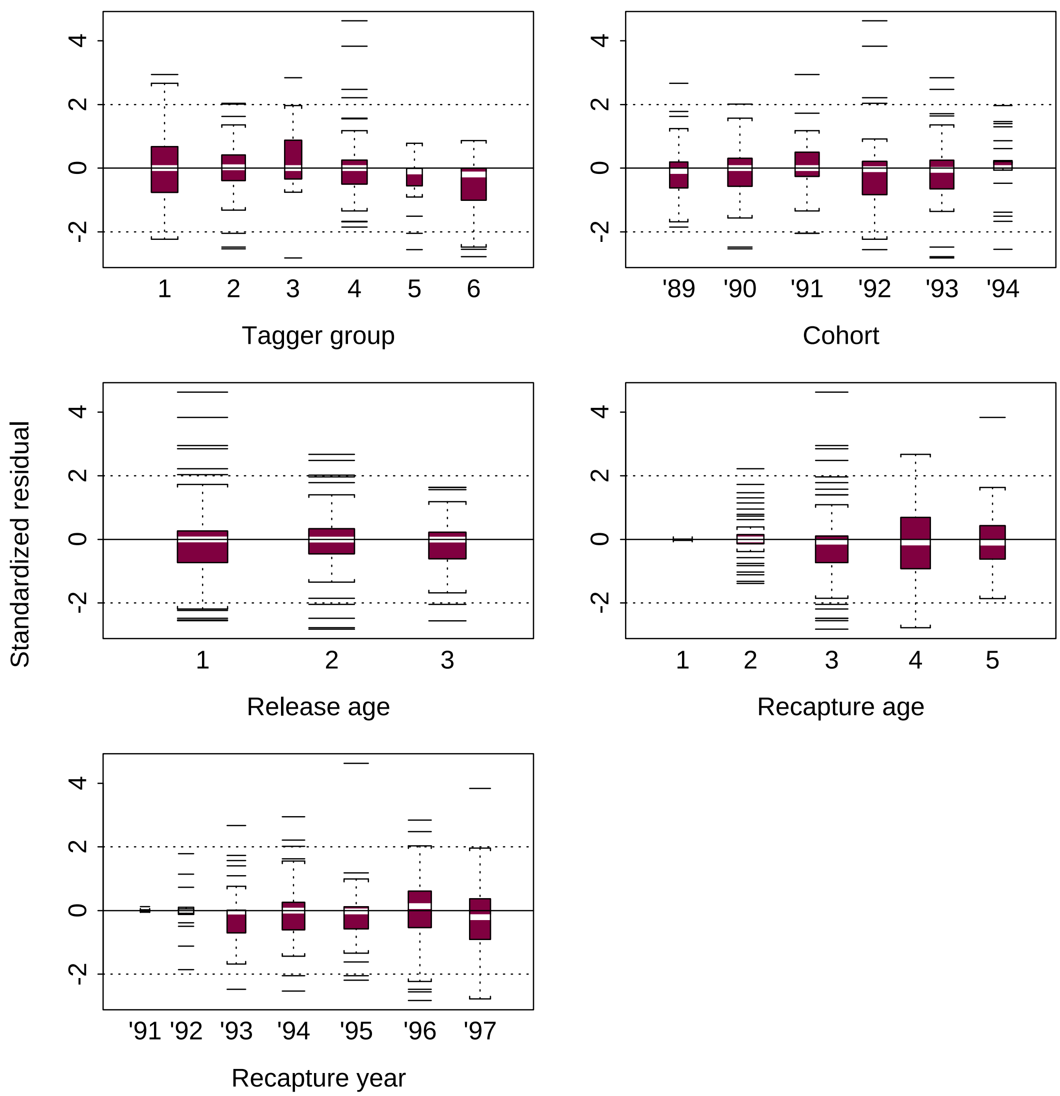
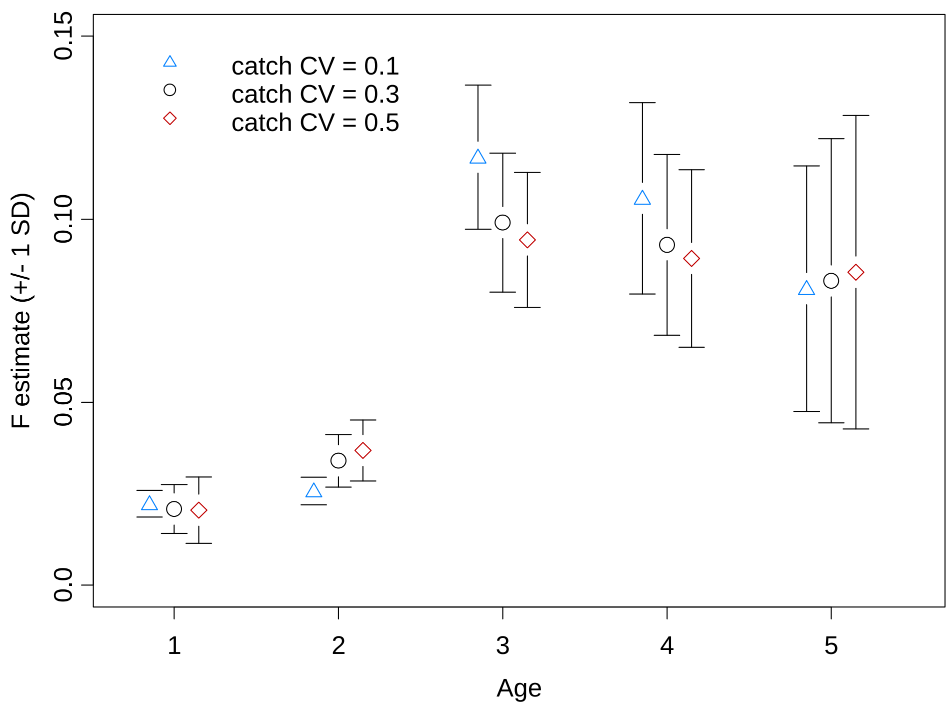


Figure 6. Effect of varying the coefficient of variation of the catch data ("catch CV") on the fishing mortality rate estimates for the 1990 cohort (top) and the age 1 population size estimates (bottom).



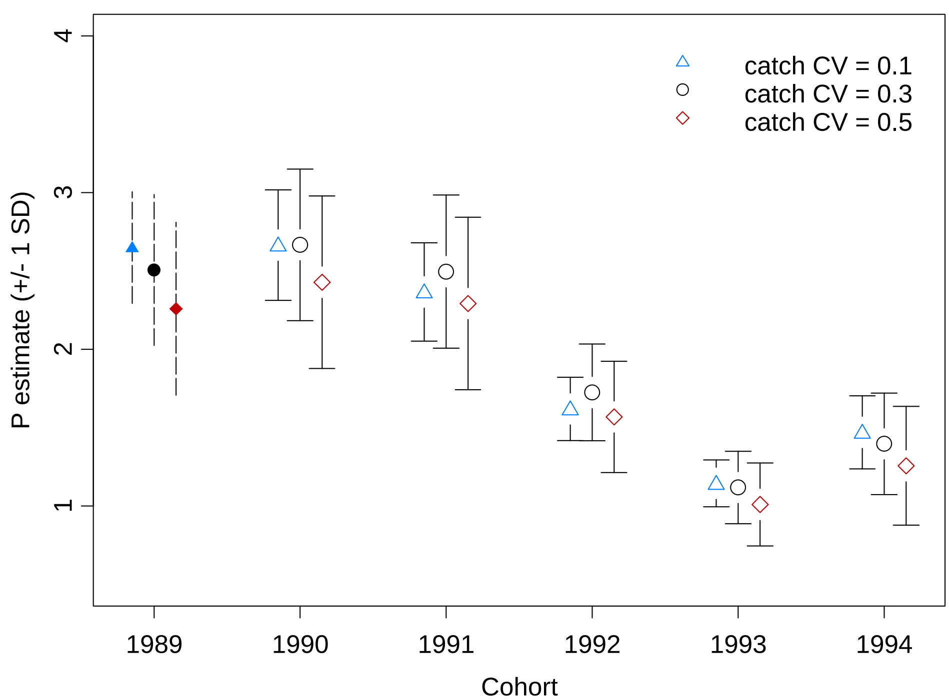
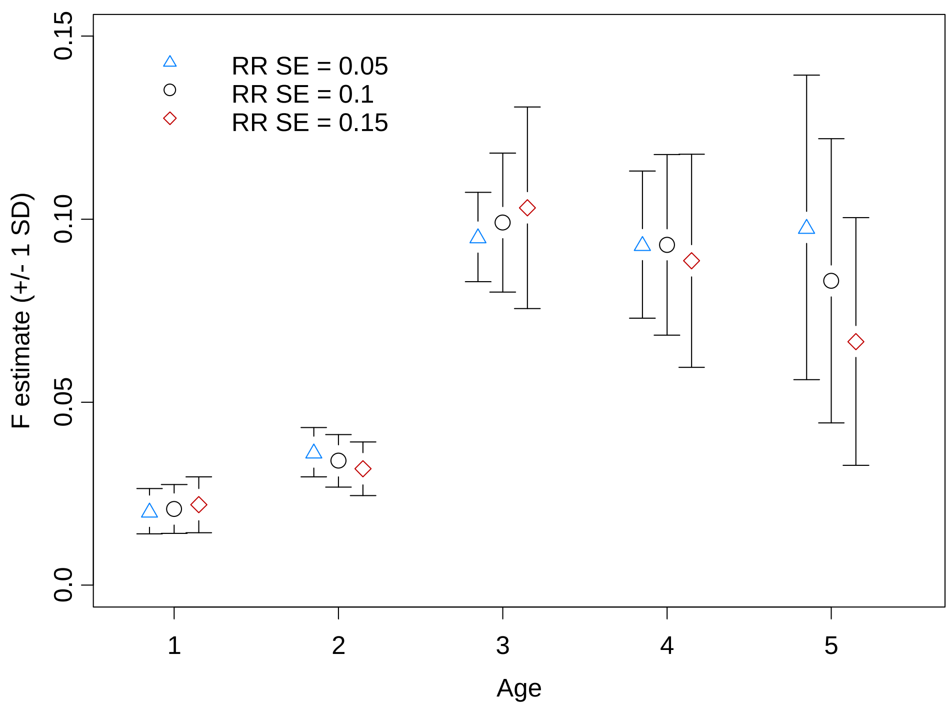


Figure 7. Effect of varying standard error of reporting rate estimates (“RR SE”) on the fishing mortality rate estimates for the 1990 cohort (top) and the age 1 population size estimates (bottom).



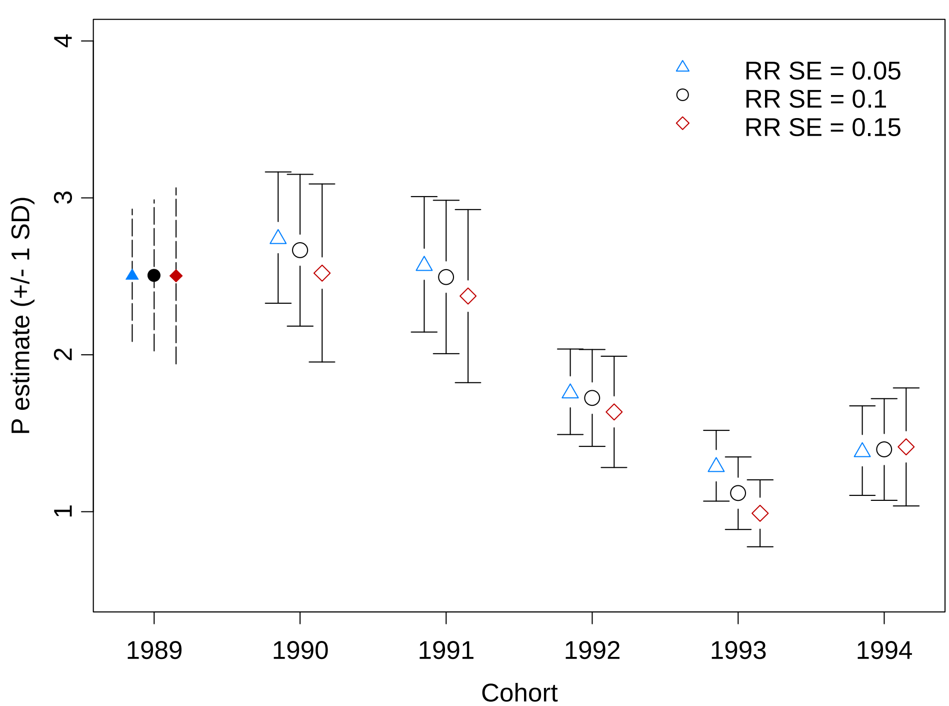
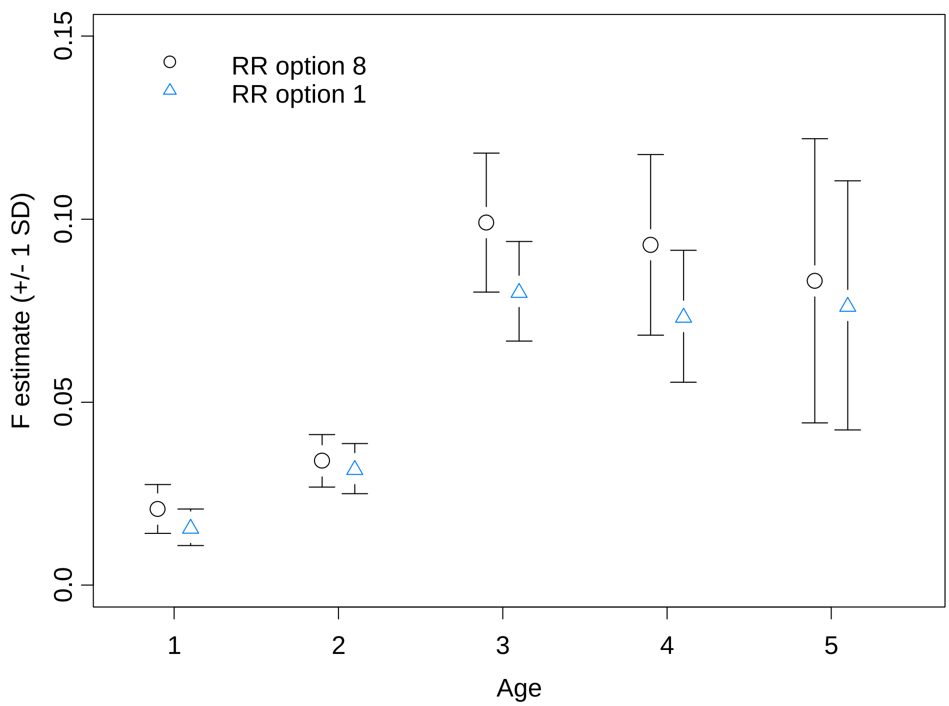
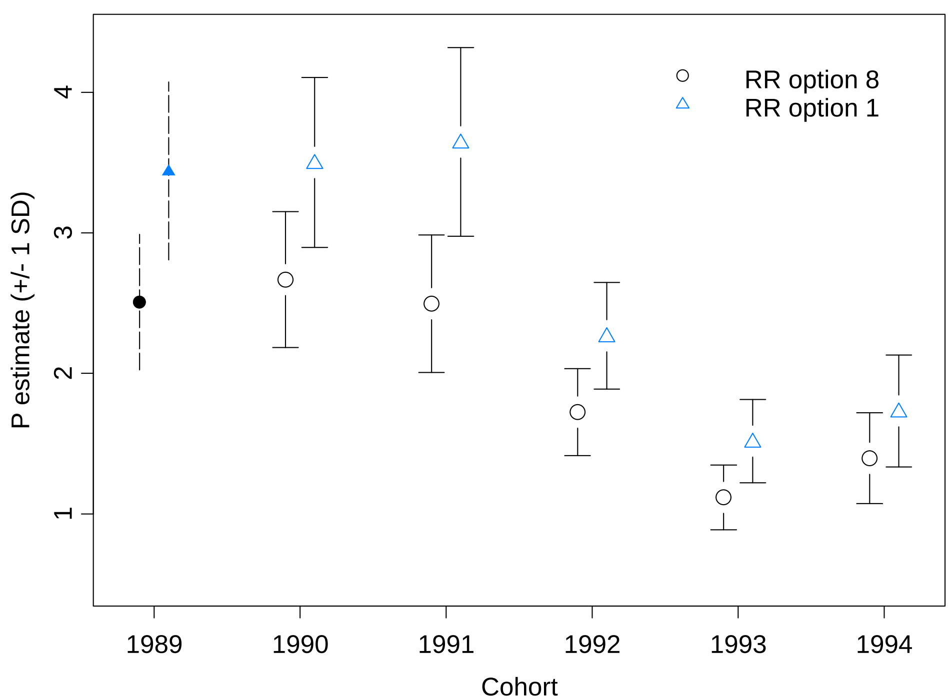


Figure 8. Effect of using reporting rate option 1 (high reporting rates) versus reporting rate option 8 (low reporting rates) on the fishing mortality rate estimates for the 1990 cohort (top) and the age 1 population size estimates (bottom).





Annex A

Table A1. Parameter estimates obtained from model with unconstrained fishing mortality rates (model 1). Standard error estimates are given in parentheses below the point estimates. Note that values for the population size at the initial age of tagging, P_{A_k} , are in millions, and that $A_k = 1$ for all cohorts except 1989, for which $A_k = 2$. The F^* estimates of fishing mortality for newly tagged fish are not of primary interest and are not shown.

M_1	M_5
0.424	0.181
(0.031)	(0.195)

Cohort	F_1	F_2	F_3	F_4	F_5	P_{A_k}
1989	–	0.054	0.162	0.102	0.076	1.62
		(0.017)	(0.031)	(0.030)	(0.034)	(0.31)
1990	0.021	0.034	0.099	0.093	0.083	2.67
	(0.007)	(0.007)	(0.019)	(0.025)	(0.039)	(0.48)
1991	0.003	0.025	0.101	0.144	0.085	2.50
	(0.001)	(0.005)	(0.021)	(0.041)	(0.041)	(0.49)
1992	0.000	0.024	0.177	0.183	0.136	1.72
	(0.000)	(0.006)	(0.029)	(0.054)	(0.061)	(0.31)
1993	0.000	0.042	0.489	0.475	–	1.12
	(0.000)	(0.007)	(0.158)	(0.156)		(0.23)
1994	0.000	0.040	0.372	–	–	1.40
	(0.000)	(0.008)	(0.075)			(0.32)

Cohort	λ_1	λ_2	λ_3	λ_4	λ_5
1989	–	0.679	0.558	0.455	0.476
		(0.093)	(0.088)	(0.087)	(0.088)
1990	0.930	0.632	0.570	0.528	0.306
	(0.105)	(0.088)	(0.094)	(0.090)	(0.078)
1991	0.887	0.741	0.531	0.464	0.276
	(0.100)	(0.098)	(0.094)	(0.091)	(0.073)
1992	0.926	0.571	0.620	0.413	0.570
	(0.100)	(0.091)	(0.086)	(0.082)	(0.091)
1993	0.520	0.563	0.315	0.662	–
	(0.100)	(0.092)	(0.085)	(0.090)	
1994	0.725	0.480	0.695	–	–
	(0.100)	(0.084)	(0.104)		

Tagger Group	ξ	Ω
1	0.974	0.039
	(0.005)	(0.003)
2	0.961	0.049
	(0.008)	(0.004)
3	1.000	0.067
	(–)	(0.003)
4	1.000	0.092
	(–)	(0.004)
5	0.921	0.096
	(0.029)	(0.016)
6	0.951	0.179
	(0.016)	(0.011)

Table A2. Parameter estimates obtained from model with fishing mortality rates constrained to have separable age and year effects (model 2). Standard error estimates are given in parentheses below the point estimates. Note that values for the population size at the initial age of tagging, P_{A_k}, are in millions, and that $A_k = 1$ for all cohorts except 1989, for which $A_k = 2$. The F^* estimates of fishing mortality for newly tagged fish are not of primary interest and are not shown.

M_1	M_5
0.424	0.236
(0.031)	(0.206)

	Age				
	1	2	3	4	5
F_A	0.032	0.377	1.952	1.722	1.0
	(0.020)	(0.172)	(0.754)	(0.435)	--

	Year						
	1991	1992	1993	1994	1995	1996	1997
F_Y	0.541	0.089	0.058	0.063	0.098	0.137	0.206
	(0.378)	(0.043)	(0.027)	(0.028)	(0.043)	(0.063)	(0.097)

	Cohort					
	1989	1990	1991	1992	1993	1994
P_{A_k}	2.01	2.67	2.54	1.45	1.45	1.2
	(0.42)	(0.45)	(0.50)	(0.21)	(0.24)	(0.25)

Cohort	λ_1	λ_2	λ_3	λ_4	λ_5
1989	–	0.682	0.542	0.49	0.565
		0.092	0.076	0.070	0.075
1990	0.930	0.637	0.524	0.492	0.298
	0.105	0.079	0.071	0.064	0.053
1991	0.887	0.770	0.461	0.431	0.208
	0.100	0.086	0.063	0.056	0.040
1992	0.926	0.582	0.595	0.352	0.466
	0.100	0.076	0.063	0.048	0.065
1993	0.520	0.627	0.529	0.718	–
	0.100	0.072	0.061	0.068	
1994	0.725	0.397	0.677	–	–
	0.100	0.060	0.075		

Tagger Group	ξ	Ω
1	0.974	0.039
	(0.005)	(0.003)
2	0.961	0.049
	(0.008)	(0.004)
3	1.000	0.067
	(–)	(0.003)
4	1.000	0.092
	(–)	(0.004)
5	0.921	0.097
	(0.029)	(0.016)
6	0.951	0.179
	(0.016)	(0.011)