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Exploring trade-offs in experimental design of a 2-fishery integrated tag-recapture and catch model for estimating mortality rates and abundance

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Abstract

The integrated tag-recapture and catch-at-age model for estimating mortality rates and abundance developed in CCSBT-ESC/0309/22 is extended to a two-fishery situation with a surface purse seine fishery and a longline fishery intended to resemble the southern bluefin tuna (SBT) situation. We also extended the model to allow for overdispersion in the tag return data. Tag reporting rates are assumed to differ between the two fisheries, and they are estimated from tag seeding data in the surface fishery and from observer data in the longline fishery. Simulations are used to investigate design issues for the tagging program currently being conducted on SBT as part of the CCSBT Scientific Research Program (SRP), in particular, to investigate levels of observer coverage and tag releases necessary to achieve reasonable precision in mortality rate and abundance estimates. The results suggest that the number of tags that have been released in recent years as part of the CCSBT SRP tagging program are adequate, but that increasing observer coverage from current levels could potentially lead to significant improvements in the precision of the fishing mortality rate estimates for the longline fishery, as well as smaller improvements in the estimate of population abundance. The results from the model with overdispersion in the tag returns suggest that in order to achieve coefficients of variation of 20% or less for the longline fishing mortality rates at ages 1 to 3, observer coverage must be at least 30% (and at least 20% for the model without overdispersion). Estimates of fishing mortality in the surface fishery are chiefly unaffected by the level of observer coverage in the longline fishery, provided fairly accurate estimates of surface fishery reporting rates and catch-at-age by fishery exist. It is important to note, however, that these results depend on the assumption of complete mixing. If this assumption is violated, then the level of observer coverage in the longline fishery would become more influential on the accuracy and precision of parameter estimates. Without good observer data, and thus good information on differential tag reporting and return rates between fishery components, there would be little power to test the assumption of non-mixing and, if necessary, develop spatially-explicit tag recovery models to account for heterogeneity in recapture probabilities. The results also demonstrate the importance of having reliable and precise estimates of the catch-at-age for each fishery when applying the estimation model presented here. This emphasizes the need to develop appropriate sampling and error models for the catch data; having representative and adequate observer coverage can help to accomplish this in the longline fishery.

Introduction

In CCSBT-ESC/0309/22, we developed an integrated Brownie and Peterson model for estimating abundance and mortality rates (fishing and natural) from multi-year tagging programs and estimates of the catch-at-age data. We explored the situation in which reporting rates are known in the catch-at-age data, and the situation in which reporting rates are estimated from observer data from a portion of the fleet. We showed that combining the catch-at-age data with the multi-year tagging data allows for population abundance to be estimated directly from the model and also provides additional information for estimating mortality rates. We also presented results from simulations on how the relative trade-off between effort put into tagging and observers affects the overall mortality and abundance estimates. The results suggested that observer levels of 20-30% (or even greater) may be required to achieve reasonable levels of precision in the parameter estimates, and raised concerns about whether the current tagging program being undertaken as part of the Council for the Conservation of Southern Bluefin Tuna Scientific Research Program (CCSBT SRP) (Anon. 2001a) will be able to meet its primary objective of being able to estimate mortality rates for southern bluefin tuna (SBT) with sufficient levels of precision to substantially improve the SBT stock assessment.

The results in CCSBT-ESC/0309/22 were based on consideration of a single fishery in which the only source of information for estimating reporting rates was from observers. However, juvenile SBT, which are the target of the SRP tagging program, are harvested both by purse seine and longline vessels. These gears have different age-specific selectivities, different levels of catch, and tag reporting rates are also likely to vary between the purse seine and longline fisheries (and in the case of the latter, there are multiple fleets in which reporting rates are also likely to vary). In addition, observers in the SBT purse seine fishery cannot provide any useful data by which to estimate reporting rates since captured fish are transferred without being removed from the water to cages for farming. Instead, tag seeding is being used to obtain estimates of reporting rates from this fishery component (Stanley and Polacheck 2003; Polacheck and Stanley 2004).

In the current paper, the estimation model in CCSBT-ESC/0309/22 is extended to a two-fishery situation with a purse seine fishery (referred to as the surface fishery) and a single longline fishery. We have reduced the multiple longline fleets to a single fishery with a uniform level of observer coverage and a uniform reporting rate both to simplify the presentation and because exploration of the possible trade-offs in observer coverage amongst different longline fisheries did not seem fruitful given the commitment of the CCSBT to have similar observer target levels in all fisheries. In our model, we allow for fishing mortality rates, as well as reporting rates, to differ between the two fisheries. Reporting rates are estimated from tag seeding data in the surface fishery and from observer data in the longline fishery. We present results on how the amount of effort put into tag releases and observers affects the mortality rate and abundance estimates. We have conditioned the simulations used to generate these results so that they qualitatively resemble the SBT situation.

The motivation for this papers stems from decisions made at the 2003 CCSBT Scientific Committee meeting (Anon. 2003). This meeting concluded that the current levels of observer coverage in the Japanese, Korean and Taiwanese longline fleets are not high enough to provide useful estimates of reporting rates, and thus fishing mortality rates, from these fleets. The overall implication of this conclusion for the ability of the SRP tagging program to meet its primary objectives were not certain because of the differential and much higher reporting rate in the Australian surface fishery, combined with the fact that the Australian surface fishery catches a substantial portion of the global catch of juvenile SBT. As such the Scientific Committee agreed to convene a Technical Group Meeting in conjunction with its next meeting to deal with this question. Among the terms of reference agreed to for this Technical Group are:

1. To evaluate the level of precision of mortality and abundance estimates that the current tagging program will be likely to provide at current levels of observer coverage and anticipated tag recovery rates (given current efforts directed at increasing them).
2. To evaluate the levels of observer coverage and tag recovery rates that would be required for the tagging program to provide acceptable levels of precision in key mortality and abundance estimates, and how these are influenced by model assumptions.

The results presented here will hopefully assist the Technical Group in its deliberations.

Methods

Estimation model

Underlying the integrated tag and catch model used here are the general population dynamics and catch equations commonly used in fisheries. These equations, presented in CCSBT-ESC/0309/22 and repeated below for fluidity, are expressed in terms of exponential and competing natural and fishing mortality rates. For a cohort of animals of a given age, the number that survive and the number that are caught are given by:

$$P_{i,\,t+1} = P_{i,\,t}\exp\{-F_{i,t} - M_{i,t}\} \tag{1}$$

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

where

$P_{i,t}$ = the number of individuals of age *i* at time *t*
$C_{i,t}$ = the catch of individuals of age *i* at time *t*
$F_{i,t}$ = the instantaneous fishing mortality rate for individuals of age *i* at time *t*
$M_{i,t}$ = the instantaneous natural mortality rate for individuals of age *i* at time *t*.

In the context of a tagging experiment, the above equations provide the basis for predicting the expected number of returns, assuming that the tagged fish constitute a representative sample of the population. In the current paper, we consider a multi-year tagging experiment involving only a single cohort of fish (tagged at consecutive ages). As such, age and year provide equivalent information, and we can simplify the notation by dropping the reference to year (i.e. the *t* subscript in the above equations) and expressing everything in terms of age.

In the two-fishery model presented here, we allow for natural mortality to differ between ages, and fishing mortality to differ between ages and fisheries. We also allow fishing mortality to differ between tagged fish in the year of tagging and untagged fish in that year (following the model presented in Hoenig et al. 1998). This is to allow for the fact that tagged and untagged fish will not be fully mixed directly after tagging, and also because in the SBT situation much of the tagging occurs near the end of the fishing season. This is done in order to prevent a large number of immediate returns, but will obviously mean that fishing mortality in that year will not be the same for tagged and untagged fish. As Hoenig et al. (1998) point out, technically, the model formulation assumes that the relative timing of fishing and natural mortality for tagged fish in the first year after tagging is the same as that for untagged fish and fully mixed tagged fish in subsequent years. However, this is not a critical assumption because the relative timing has only a minor effect on estimation of natural mortality, and furthermore, we are not interested in fishing mortality of newly tagged fish.

Reporting rates are estimated differently for the surface fishery than for the longline fishery. For the longline fishery, we assume observers are on board a percentage of vessels and that the reporting rate is 100% for fish caught on these vessels. Because on average the fishing mortality have been assumed to be the same for all longline vessels, the relative return rate between the observed catches and the unobserved catches provides an estimate of the reporting rate in the unobserved component (i.e. observer coverage is representative of the entire longline fleet). For the surface fishery, we assume reporting rates are estimated from independent data, such as tag seeding data, and that we have estimates of reporting rates, along with standard errors on the estimates, to use in our model.

We divide the tag returns and the corresponding catches into those coming from the surface fishery, the observed component of the longline fishery, and the unobserved component of the longline fishery. However, before proceeding we introduce the following notation:

Table 1. Data (to be inputted into the model).

N_a = number of tag releases of age a fish from a particular cohort
$R^{S}_{a,i}$ = tag returns of age i fish that were tagged at age a from the surface fishery
$R^{LL,obs}_{a,i}$ = tag returns of age i fish that were tagged at age a from the observed component of the longline fishery
$R^{LL,unobs}_{a,i}$ = tag returns of age i fish that were tagged at age a from the unobserved component of the longline fishery
$\hat{\lambda}^{S}_{i}$ = estimated tag reporting rate for fish recaptured at age i in the surface fishery
s_i = standard error of $\hat{\lambda}^{S}_{i}$
C^{S}_{i} = number of age i fish from the cohort of interest caught in the surface fishery
$C^{LL,obs}_{i}$ = number of age i fish from the cohort of interest caught in the observed component of the longline fishery
$C^{LL,unobs}_{i}$ = number of age i fish from cohort of interest caught in the unobserved component of the longline fishery
δ_i = proportion of age i fish in the observed component of the longline fishery
υ^{S}_{i} = coefficient of variation of age i catch data from the surface fishery
$\upsilon^{LL,obs}_{i}$ = coefficient of variation of age i catch data from the observed component of the longline fishery

Table 2. Parameters (to be estimated in the model).

λ_i^S = tag reporting rate for fish captured at age *i* in the surface fishery
λ_i^{LL} = tag reporting rate for fish captured at age *i* in the unobserved component of the longline fishery
M_i = instantaneous natural mortality rate for age *i* fish
F_i^S = instantaneous fishing mortality rate in the surface fishery for age *i* fish (excluding fish tagged at age *i*)
F_i^{LL} = instantaneous fishing mortality rate in the longline fishery for age *i* fish (excluding fish tagged at age *i*)
F_i^{*S} = instantaneous fishing mortality rate in the surface fishery for age *i* fish tagged at age *i*
F_i^{*LL} = instantaneous fishing mortality rate in the longline fishery for age *i* fish tagged at age *i*
P_1 = initial population size (at age 1) of tagged cohort
ω_a = Dirichlet variance parameter for the return probabilities of fish released at age *a*; *only used in model with overdispersion in tag returns*

Now define:

$$F_i^{*Tot} = F_i^{*S} + F_i^{*LL}$$
$$S_i^* = \exp\{-(F_i^{*Tot} + M_i)\}$$
$$f_i^* = \frac{F_i^{*Tot}}{F_i^{*Tot} + M_i}(1 - S_i^*)$$
$$F_i^{Tot} = F_i^S + F_i^{LL}$$
$$S_i = \exp\{-(F_i^{Tot} + M_i)\}$$
$$f_i = \frac{F_i^{Tot}}{F_i^{Tot} + M_i}(1 - S_i)$$

Note that S_i^* represents the survival rate of age *i* fish tagged at age *i*; S_i represents the survival rate of age *i* fish, excluding those tagged at age *i*; f_i^* represents the exploitation rate of age *i* fish tagged at age *i*; and f_i represents the exploitation rate of age *i* fish, excluding those tagged at age *i*[1].

First consider the tag-recapture component of the model. The probability that an age *i* fish that was tagged at age *a* is returned from the surface fishery is:

[1] In the model developed here, the longline and surface fisheries are modelled as taking place throughout the year and their respective fishing mortalities constitute competing risks. In fact, for SBT, the surface and longline fisheries take place almost sequentially. While this detail could be added to the model without much difficulty, it would not be expected to change the general results presented in this paper. However, in an application in which fishing mortality rates are relatively high in one or both fisheries, it could have a small effect on the model predictions of the number of returns. In such situations, the modifications necessary for dealing with sequential fisheries might be worth including in the estimation model.

$$p_{a,i}^{S} = \begin{cases} \lambda_i^S \dfrac{F_i^{*S}}{F_i^{*Tot}} f_i^* & i = a \\ \lambda_i^S \dfrac{F_i^{S}}{F_i^{Tot}} S_a^* f_i & i = a+1 \\ \lambda_i^S \dfrac{F_i^{S}}{F_i^{Tot}} S_a^* \left(\prod\limits_{k=a+1}^{i-1} S_k \right) f_i & i > a+1 \end{cases} \tag{3}$$

The probability that an age *i* fish that was tagged at age *a* is returned from the observed component of the longline fishery is:

$$p_{a,i}^{LL,obs} = \begin{cases} \delta_i \dfrac{F_i^{*LL}}{F_i^{*Tot}} f_i^* & i = a \\ \delta_i \dfrac{F_i^{LL}}{F_i^{Tot}} S_a^* f_i & i = a+1 \\ \delta_i \dfrac{F_i^{LL}}{F_i^{Tot}} S_a^* \left(\prod\limits_{k=a+1}^{i-1} S_k \right) f_i & i > a+1 \end{cases} \tag{4}$$

The probability that an age *i* fish that was tagged at age *a* is returned from the unobserved component of the longline fishery is:

$$p_{a,i}^{LL,unobs} = \begin{cases} (1-\delta_i)\lambda_i^{LL} \dfrac{F_i^{*LL}}{F_i^{*Tot}} f_i^* & i = a \\ (1-\delta_i)\lambda_i^{LL} \dfrac{F_i^{LL}}{F_i^{Tot}} S_a^* f_i & i = a+1 \\ (1-\delta_i)\lambda_i^{LL} \dfrac{F_i^{LL}}{F_i^{Tot}} S_a^* \left(\prod\limits_{k=a+1}^{i-1} S_k \right) f_i & i > a+1 \end{cases} \tag{5}$$

These probability statements assume no mortality due to tagging and no tag shedding. If these assumptions are not met, additional parameters and potentially additional data will need to be introduced to account for these factors.

For tags released at a particular age, the numbers of returns by age from all sources (i.e. the surface fishery, the observed component of the longline fishery, and the unobserved component of the longline fishery), as well as those tags not returned, are expected to be multinomial with probabilities given in equations (3), (4) and (5). Thus, the likelihood equation for the tag return data corresponding to all release ages is:

$$L_R = \gamma \times \prod_a \left(\left(1 - p_{a,\bullet}^{Tot}\right)^{N_a - R_{a,\bullet}^{Tot}} \prod_{i \ge a} \left(\left(p_{a,i}^{S}\right)^{R_{a,i}^{S}} \left(p_{a,i}^{LL,obs}\right)^{R_{a,i}^{LL,obs}} \left(p_{a,i}^{LL,unobs}\right)^{R_{a,i}^{LL,unobs}} \right) \right) \tag{6}$$

where

$$\gamma = \prod_a \frac{N_a}{\left(N_a - R_{a,\bullet}^{Tot}\right)! \prod_{i \ge a} \left(R_{a,i}^{S}\,! R_{a,i}^{LL,obs}\,! R_{a,i}^{LL,unobs}\,!\right)},$$

$$R_{a,\bullet}^{Tot} = \sum_i \left(R_{a,i}^{S} + R_{a,i}^{LL,obs} + R_{a,i}^{LL,unobs}\right),$$

and

$$p_{a,\bullet}^{Tot} = \sum_i \left(p_{a,i}^{S} + p_{a,i}^{LL,obs} + p_{a,i}^{LL,unobs}\right).$$

Note that γ is a constant that can be left out when maximizing the likelihood.

Estimates of the fishing and natural mortality rates (F^*'s, F's and M's) can be obtained from the multi-year tagging data by maximizing the above likelihood. Note, however, that the information for estimating M_i comes from the differential between the expected returns at age $i+1$ of fish released at age *i* and those released at age $i+1$; thus, in an experiment with *n* consecutive release years, estimates can only be obtained for $n-1$ of the natural mortality rate parameters (regardless of the number of recapture years). Estimates of the reporting rates for the longline fishery (λ_i^{LL}'s) can also be obtained from the above likelihood using the differential between the return rates from the observed and unobserved catches, provided the ratios of observed to unobserved catches (δ_i's) are known.

There is not enough information in likelihood (6) to be able to estimate the reporting rates from the surface fishery. We assume instead that an estimate of the reporting rate at each age ($\hat{\lambda}_i^S$) and an associated standard error (s_i) has been obtained from independent tag seeding data, and that the estimate follows a standard beta distribution with mean λ_i^S and variance approximated by s_i^2. We chose a standard beta distribution because it gave a reasonably bell-shaped distribution that was constrained to lie between 0 and 1 (as desired for reporting rates). Thus, the likelihood component for the surface fishery reporting rate data is:

$$L_{\lambda^S} = \prod_i \frac{\Gamma(\alpha_i + \beta_i)}{\Gamma(\alpha_i)\Gamma(\beta_i)} \left(\hat{\lambda}_i^S\right)^{\alpha_i - 1} \left(1 - \hat{\lambda}_i^S\right)^{\beta_i - 1} \tag{7}$$

where

$$\alpha_i = \left(\frac{\lambda_i^S}{s_i}\right)^2 \left(1 - \lambda_i^S\right) - \lambda_i^S$$

and

$$\beta_i = \frac{\alpha_i \left(1 - \lambda_i^S\right)}{\lambda_i^S}.$$

Note that $\Gamma(\cdot)$ denotes the gamma function.

Now consider the catch component of the model. The probability that an age *i* fish from the cohort being studied is caught in the surface fishery is:

$$\pi_i^S = \begin{cases} \dfrac{F_i^S}{F_i^{Tot}} f_i & i = 1 \\ \dfrac{F_i^S}{F_i^{Tot}} \left(\prod_{k=1}^{i-1} S_k \right) f_i & i > 1 \end{cases} \tag{8}$$

The probability that an age *i* fish from the cohort of interest is caught in the observed component of the longline fishery is:

$$\pi_i^{LL,obs} = \begin{cases} \delta_i \dfrac{F_i^{LL}}{F_i^{Tot}} f_i & i = 1 \\ \delta_i \dfrac{F_i^{LL}}{F_i^{Tot}} \left(\prod_{k=1}^{i-1} S_k \right) f_i & i > 1 \end{cases} \tag{9}$$

The probability that an age *i* fish from the cohort of interest is caught in the unobserved component of the longline fishery is:

$$\pi_i^{LL,unobs} = \begin{cases} (1-\delta_i) \dfrac{F_i^{LL}}{F_i^{Tot}} f_i & i = 1 \\ (1-\delta_i) \dfrac{F_i^{LL}}{F_i^{Tot}} \left(\prod_{k=1}^{i-1} S_k \right) f_i & i > 1 \end{cases} \tag{10}$$

If we assume the numbers of fish caught at each age are known accurately (and that each fish has an equal probability of being caught), then the catch-at-age data, including those fish from the cohort not caught, are random multinomial, where each fish has a probability of being captured at age *i* in one of the fishery components (given by the expressions in (8), (9) and (10)) or else not captured. Usually, however, the catch-at-age data are not known accurately. In the case of SBT, the age distribution of the catch is 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 have chosen to model the error in the catch-at-age data that results from this sampling procedure as Gaussian, with a coefficient of variation (CV) that depends on the level of sampling. The CV is intended to capture variability in the catch-at-age data due to non-homogeneous spatial and temporal distribution of fish, as well as different size/age selectivities among vessels (i.e. if these factors are significant, then the CV of the catch-at-age data would be large because the age distributions derived from different samples could vary a lot).

To fit a model with both multinomial “process” error and Gaussian sampling error would require a relatively sophisticated approach, such as a Kalman filter. However, in most fishery situations, the number of fish in the cohort from which catches are being taken will be very large such that the multinomial error will be negligible compared to the Gaussian sampling error, and only the latter source of error needs to be considered. This is the approach taken in the current paper.

For the surface fishery, we assume that catches are routinely sampled and that there is an appropriate sampling design and estimation model that allows for the variance in the catch data to be well estimated. We have assumed that the CV of the catch data for each year (υ_i^S) is known and independent of the tag data. For the longline fishery, we assume that all fish caught in the observed component are sampled, but that no fish from the unobserved component are sampled. Thus, there is no age information for the unobserved catches, and only catch-at-age data from the observed component is included in the model. The CV for the longline catch data in a given year (υ_i^{LL}) will be determined by the level of observer coverage (since this determines the level of sampling).

The likelihood for the surface and observed longline catch data is:

$$L_C = \frac{1}{2\pi}\prod_i\left\{\frac{1}{\upsilon_i^S P_1\pi_i^S}\exp\left(-\frac{1}{2}\left(\frac{C_i^S - P_1\pi_i^S}{\upsilon_i^S P_1\pi_i^S}\right)^2\right)\right\}\times \\ \prod_i\left\{\frac{1}{\upsilon_i^{LL,obs} P_1\pi_i^{LL,obs}}\exp\left(-\frac{1}{2}\left(\frac{C_i^{LL,obs} - P_1\pi_i^{LL,obs}}{\upsilon_i^{LL,obs} P_1\pi_i^{LL,obs}}\right)^2\right)\right\} \tag{11}$$

The overall likelihood for the combined recapture and catch data can be obtained by multiplying likelihoods for the tag-recapture data, the tag-seeding data and the catch data together:

$$L_{Tot} = L_R \times L_{\lambda^S} \times L_C \tag{12}$$

The inclusion of the catch component in the overall likelihood allows for the initial cohort size P_1 to be estimated and also provides more information on the mortality rate estimates. Additionally, for our specific model which allows for non-mixing of tagged fish in the first year after release, the tag-recapture data does not provide an estimate of the fishing mortality at age 1 of untagged fish (F_1^S and F_1^{LL}); inclusion of the catch data provides these estimates. Thus, by maximizing (12), estimates of all parameters given in Table 2 can be estimated, with the exception that we can only estimate $n-1$ natural mortality rate parameters, where n is the number of consecutive release years.

In the current model formulation, there is not enough information to estimate the proportion of observer coverage in each year (the δ's). To do so, we would need to know the total observer catch in each year as well as the total overall catch in each year. Currently, the model only requires catch data from a single cohort (i.e. from a single age class in each year). Rather than bringing the total catch data into the model, we assume that the total catch numbers are known well enough that the δ's are estimated accurately, and we treat the δ's as being known without error in our model.

The model allows for the catch CV in each fishery to vary with year, and we assume that these CV's are known (there is not enough information with which to estimate them). If we were to assume a constant CV in all years for a given fishery, then, in theory, the CV should be estimable from the likelihood; however, we found in practice that its estimation is very poor (often converging to zero).

Overdispersion in tag return data

The tag-recapture component of the model presented above assumes a multinomial distribution for the tag returns; this is only valid if all fish of a particular age have the same probability of being caught. If there is unsystematic incomplete mixing of tagged and untagged fish[2] (e.g. if fish tagged in the same school and/or in close proximity on the same day have positively correlated recapture probabilities), then the numbers of returns at age will have more variability than a multinomial distribution would predict. Differential age/size selectivities among fishing vessels will also contribute to overdispersion if tagged fish are not homogeneously mixed within the untagged population. One way of incorporating this overdispersion is to model the tag return data as Dirichlet-multinomial. Essentially, the probabilities of return corresponding to releases at age *a* are modelled as Dirichlet random variables with variance parameter ω_a (see Appendix A). Then the numbers of returns conditional on the probabilities of return follow a multinomial distribution, and the unconditional numbers of returns follow the compound distribution referred to as the Dirichlet-multinomial (see Appendix A).

The likelihood for the tag return data when these data are modelled as Dirichlet-multinomial is:

$$L_R^{\omega} = \gamma^{\omega} \times \prod_a \left\{ \frac{\Gamma(\omega_a)}{\Gamma(N_a + \omega_a)} \prod_i \frac{\Gamma\left(\left(N_a - R_{a,\bullet}^{Tot}\right) + \omega_a\left(1 - p_{a,\bullet}^{Tot}\right)\right)}{\Gamma\left(\omega_a\left(1 - p_{a,\bullet}^{Tot}\right)\right)} \times \right.$$
$$\left. \prod_i \frac{\Gamma\left(R_{a,i}^{S} + \omega_a p_{a,i}^{S}\right)\Gamma\left(R_{a,i}^{LL,obs} + \omega_a p_{a,i}^{LL,obs}\right)\Gamma\left(R_{a,i}^{LL,unobs} + \omega_a p_{a,i}^{LL,unobs}\right)}{\Gamma\left(\omega_a p_{a,i}^{S}\right)\Gamma\left(\omega_a p_{a,i}^{LL,obs}\right)\Gamma\left(\omega_a p_{a,i}^{LL,unobs}\right)} \right\} \tag{13}$$

where

$$\gamma^{\omega} = \prod_a \frac{N_a\,!}{\left(N_a - R_{a,\bullet}^{Tot}\right)!\prod_i\left(R_{a,i}^{S}\,!R_{a,i}^{LL,obs}\,!R_{a,i}^{LL,unobs}\,!\right)},$$

and, as in equation (6),

$$R_{a,\bullet}^{Tot} = \sum_i \left(R_{a,i}^{S} + R_{a,i}^{LL,obs} + R_{a,i}^{LL,unobs}\right),$$

and

$$p_{a,\bullet}^{Tot} = \sum_i \left(p_{a,i}^{S} + p_{a,i}^{LL,obs} + p_{a,i}^{LL,unobs}\right).$$

[2] Unsystematic incomplete mixing is meant to refer to situations where there is still large amounts of mixing among tagged and untagged fish and the pattern of mixing has a large “random” component such that on average the probability of recapture of tagged and untagged fish are the same. This should be distinguished from the situation where there is a systematic and repeatable pattern of non-mixing between tagged and untagged fish -- for example, if all tagging was done late in the season in one location and fish in that location and time period only remain in one part of the stock’s overall range. Such systematic non-mixing will induce biases into the population and mortality estimates if it is not accounted for within the estimation model. A basic assumption of the estimation model used here is that the tagged fish constitute a representative sample of the population.

Note that γ^{ω} is a constant that can be left out of the likelihood.

The overall likelihood is now analagous to (12) except L_R^{ω} replaces L_R:

$$L_{Tot}^{\omega} = L_R^{\omega} \times L_{\lambda^S} \times L_C \tag{14}$$

The parameters that we estimate by maximizing the likelihood in (14) are the same as before, except now we also have overdispersion parameters (ω_a's) to estimate. Rather than estimating an overdispersion parameter for each release event (which would not likely be possible with the current model formulation), we constrain the ω_a's so that they lead to an increase in the variance of the returns at age of *x* times over that of multinomial returns. This can be accomplished by setting $\omega_a = \left(N_a - x\right)/(x-1)$ (refer to Appendix A). Now, instead of having several additional overdispersion parameters to estimate, we have just one, *x*.

Data and parameters used to condition the simulations

In generating data for the simulations, our aim was to choose input values that emulate the most recent years of SBT tag-recapture and catch data as closely as possible. SBT are generally tagged at ages 1 to 3, therefore in our simulations we assume that we tag a single cohort of fish in 3 consecutive years at ages 1, 2 and 3. Most SBT tags are returned within the first 5 years after release, so we generate 5 years of recapture data, along with 5 years of corresponding catch data.

The input values used to generate the tag-recapture and catch-at age data sets for our simulations are given in Table 3. The number of releases were determined by averaging the number of tags released at ages 1 to 3 as part of the CCSBT tagging program in years 2002, 2003 and 2004. We also looked at the effect of halving and doubling the number of releases.

The mortality rates were assumed to follow a negative linear trend with age; the slope and intercept were chosen to give values that closely resemble the mortality rate vector commonly used in past stock assessments. The reason for assuming a linear trend is that with only 3 release years, we can only estimate 2 mortality rate parameters. By constraining the mortality rates to be linear with age, we reduced the number of mortality rate parameters to 2 as required. Other constraints could have been imposed but a linear trend is consistent with previous assumptions about natural mortality rates for SBT.

The total fishing mortality rates (across fisheries) were based on total SBT catches from years 1998 to 2000. The average total catches in numbers of ages 1 to 5 fish over these 3 years were calculated to be 1959, 58208, 225015, 69982 and 26817 respectively. Thus, using the mortality rates discussed above and assuming an initial (age 1) population size of 2 million fish, we could calculate the age-specific fishing mortality rates required to give these catch numbers using equations (1) and (2). These are the F_i^{Tot} values reported in Table 3. We chose 2 million for P_1 because it is within the plausible range of values for SBT based on recent stock assessments (e.g. Hirmatsu and Tsuji 2001; Kolody and Polacheck 2001; Polacheck and Preece 2001), and it also resulted in reasonable fishing mortality rates. However, varying P_1 over the range of 1 to 4 million had a negligible effect on the results.

We expect the total fishing mortality rates for tagged fish in their first year after release (i.e. the F_i^{*Tot}'s) to be quite low for SBT because tagging generally occurs near the end of the surface fishery season. The values we chose were rather arbitrary (0.05 for all ages), but they do not have much influence on the results, with an exception being if one of the values is so close to zero that the simulated tagging data has no tag returns at that age. In such a case, not all parameters are estimable unless constraints/assumptions are imposed regarding the mortality rates and reporting rate for that age. Zero tag returns, especially at ages 1 and 2, may be an issue with real SBT tag-recapture data and, if so, would have to be dealt with appropriately.

To apportion the total fishing mortality between the surface fishery and longline fishery, we need to know the proportion of surface versus longline catches at each age. Using SBT catch data for years 1998 to 2000, we calculated the proportion of surface catches at each age in each year and then took the average of the 3 years; these values are reported as θ_i in Table 3. Then the fishery-specific F_i's and F_i^*'s were calculated by simply multiplying the total fishing mortalities by θ_i for the surface fishery and $(1-\theta_i)$ for the longline fishery.

The reporting rates used for the surface fishery were based on a preliminary analysis of data from a pilot tag seeding experiment conducted on SBT farm cages in 2002/2003 (Polacheck and Stanley 2004). This analysis suggested an average reporting rate of 0.65 with a standard error of 0.10. These values were assumed to apply in all years in the results presented here (i.e. for all ages in our single-cohort formulation). The reporting rates used for the unobserved component of longline fishery (0.10 for all ages) were based on longline reporting rate estimates from previous analyses of the 1990s SBT tagging data (which ranged between 0 and around 0.40 depending on the fleet) combined with concerns that promotional activities (particularly direct personal contact) encouraging fisherman to return tags has been less during the SRP than during the 1990s. However, the effect of increasing the reporting rates for the longline fishery was explored.

The CV for the catch-at-age data from the surface fishery was chosen to be 0.2 in all years. This figure is rather arbitrary but currently there are no estimates, or developed statistical models for obtaining estimates, of the error in the age composition of the surface catches. In addition, the actual CV is likely to vary among years. The CV of the catch-at-age data for the observer component of the longline fishery is assumed to be related to the level of observer coverage, because more observers means more catch sampling. A hypothetical relationship between the level of observer coverage and the CV of the catch data, which we believe to be reasonable for our purposes, is shown in Figure 1. The formula used to generate this curve is $\upsilon_i^{LL} = 0.75*(0.05)^{\sqrt{\delta_i}}$. Note that even with 100% observer coverage, the CV does not go to zero because there is still variability in the catch process (referred to previously as multinomial process error) and aging error in going from measured length distributions to estimated age distributions. This relationship is rather arbitrary; however, sufficient data and information are not available on the actual sampling protocols to develop a more realistic model.

We kept the level of observer coverage in the longline fishery the same in all years (i.e. at all ages) and, initially, set the level of be 0.1. This value was chosen because 10% observer coverage has been the goal set by CCSBT members in past years (Anon. 2001b). The CV of the observer catches that corresponds to this observer level is 0.29 (calculated using the relationship given in the previous paragraph). One of the primary goals of this paper is to investigate how the level of observer coverage affects our ability to estimate mortality rate and abundance parameters; thus, we also considered observer levels of 0.05, 0.2, 0.3 and 0.5, with corresponding catch CV's of 0.38, 0.20, 0.15 and 0.09 respectively.

In the model that incorporates overdispersion in the tag return data, we also need to specify how much extra variability we want in the tag returns compared to that of multinomial returns. We chose a factor of 3 (i.e., in the notation used in the Methods section, $x = 3$). Note that overdispersion in the tag return data is likely to be associated with higher variability in the longline catch data, especially at low levels of observer coverage (e.g. a large source of the variability in the catch data would come from large inter-vessel variability in the size/age composition of their catches, especially if catches from only a few vessels were sampled; this would be the case when observer coverage is low because observers would likely be constrained to a limited number of relatively long cruises). However, in the absence of information on this, the same CV/observer coverage relationship for the longline catch data was used in both the model with and without overdispersion in the tag returns.

Table 3. Parameter values for reference case simulation run.

	Age/year, *i*				
	1	2	3	4	5
P_i	2×10^6	–	–	–	–
N_i	2718	5807	1223	–	–
M_i	0.4	0.35	0.3	0.25	0.2
F_i^{*Tot}	0.05	0.05	0.05	–	–
F_i^{Tot}	0.001	0.053	0.340	0.183	0.103
θ_i	0.882	0.825	0.828	0.407	0.120
F_i^{*S}	0.044	0.041	0.041	–	–
F_i^{*LL}	0.006	0.009	0.009	–	–
F_i^{S}	0.001	0.044	0.282	0.075	0.012
F_i^{LL}	0.000	0.009	0.058	0.108	0.091
λ_i^{S}	0.65	0.65	0.65	0.65	0.65
s_i	0.10	0.10	0.10	0.10	0.10
υ_i^{S}	0.20	0.20	0.20	0.20	0.20
λ_i^{LL}	0.10	0.10	0.10	0.10	0.10
δ_i	0.10	0.10	0.10	0.10	0.10
υ_i^{LL}	0.29	0.29	0.29	0.29	0.29

Results

Multinomial tag returns

Using the values in Table 3, we simulated 100 multinomial tag-recapture and Gaussian catch-at-age datasets. We then obtained parameter estimates corresponding to each of the 100 datasets by maximizing the likelihood in (12). We refer to the simulations carried out using the values in Table 3 as the ‘reference case’ simulations.

Effect of observer coverage

In addition to the reference case simulations, we also ran 100 simulations using each of the alternative levels of observer coverage being considered, namely, δ = 0.05, 0.2, 0.3 and 0.5 (with corresponding longline catch CV’s of $\upsilon^{LL} =$ 0.38, 0.20, 0.15 and 0.09). The means and standard deviations of the 100 maximum likelihood estimates for the parameters of key interest are given in Tables 4 and 5. Results for the remaining parameters can be found in Appendix B, Tables B1 and B2. The mean estimates of almost all parameters are within two standard errors of the true value, suggesting they are estimated without bias (standard error equals standard deviation divided by square root of sample size, where the sample size is 100 in our case). An exception is the estimate of the age 1 population size, P_1, which has a slight negative bias; however, the bias is small (<7%) and disappears as the level of observer coverage increases. There are also significant biases (statistically speaking) in some of the reporting rate estimates, but these biases are small in practical terms and they diminish as the level of observer coverage increases. The reporting rate estimates are not of primary interest, and since small biases in these estimates do not appear to induce biases in the mortality rate estimates, they are not of concern. Although insignificant, there is some suggestion of a small negative bias for both M_1 and M_5 (recall that natural mortality is constrained to be linear with age so it can be fully described by 2 parameters; we have chosen to parameterize the line in terms of M_1 and M_5). Interestingly, the bias for M_1 decreases as observer coverage increases, but the bias for M_5 increases.

Our ability to estimate almost all of the parameters improves as the level of observer coverage in the longline fishery increases (as seen by a decrease in standard deviation as observer coverage increases; Table 5). The degree of improvement differs between parameters and can be better evaluated by looking at the coefficient of variation (CV = standard deviation/mean) of the estimates as opposed to the standard deviation (Figure 1). As we would expect, the CV’s of the fishing mortality rate estimates for the longline fishery are most improved by increases in longline observer coverage, with improvements in CV ranging from 8% to 27% when observer coverage goes from 5% to 50%. We note that the CV of M_5 is large in all situations (~90%), whereas the CV of the initial cohort size P_1 is always small (~10%); we discuss these findings in the Discussion.

Table 4. Mean of key reference case parameter estimates (from 100 simulations) for various levels of observer coverage (δ). True parameter values are given below parameter names. The values for P_1 are expressed in millions.

	P_1	M_1	M_5	F_1^S	F_2^S	F_3^S	F_4^S	F_5^S	F_1^{LL}	F_2^{LL}	F_3^{LL}	F_4^{LL}	F_5^{LL}
δ	2.0	0.4	0.2	0.001	0.044	0.282	0.074	0.012	0.000	0.009	0.058	0.109	0.091
0.05	1.86	0.390	0.197	0.001	0.044	0.293	0.081	0.014	0.000	0.009	0.062	0.109	0.100
0.10	1.88	0.392	0.198	0.001	0.044	0.293	0.082	0.014	0.000	0.009	0.061	0.111	0.100
0.20	1.92	0.392	0.189	0.001	0.043	0.287	0.079	0.013	0.000	0.009	0.059	0.111	0.097
0.30	1.94	0.393	0.180	0.001	0.044	0.285	0.076	0.013	0.000	0.009	0.059	0.108	0.094
0.50	1.97	0.396	0.178	0.001	0.044	0.283	0.076	0.013	0.000	0.009	0.059	0.109	0.093

Table 5. Standard deviation of key reference case parameter estimates (from 100 simulations) for various levels of observer coverage (δ). The values for P_1 are expressed in millions.

δ	P_1	M_1	M_5	F_1^S	F_2^S	F_3^S	F_4^S	F_5^S	F_1^{LL}	F_2^{LL}	F_3^{LL}	F_4^{LL}	F_5^{LL}
0.05	0.23	0.057	0.176	0.000	0.007	0.050	0.023	0.006	0.000	0.003	0.016	0.032	0.051
0.10	0.22	0.056	0.177	0.000	0.007	0.046	0.023	0.007	0.000	0.003	0.013	0.030	0.042
0.20	0.20	0.056	0.174	0.000	0.007	0.045	0.020	0.007	0.000	0.002	0.010	0.027	0.043
0.30	0.18	0.052	0.165	0.000	0.008	0.044	0.019	0.006	0.000	0.001	0.008	0.023	0.037
0.50	0.16	0.054	0.168	0.000	0.008	0.040	0.018	0.005	0.000	0.001	0.006	0.023	0.034

Effect of number of releases

While the level of observer coverage is one factor of the experimental design that can be controlled, the number of releases is another. We repeated the reference case simulations except we first halved, and then doubled, the number of releases at each age. Again, the mean parameter estimates were unbiased for the most part, and any biases were small and not of concern; as such, we do not present the mean estimates. The CV's are of more interest (Figure 2). The general direction of the results is as expected — halving the number of releases degrades the estimates and doubling the number of releases improves the estimates, at least for parameters of interest (those shown in Figure 2). However, the response appears to be asymmetric; the loss in precision from halving the number of releases appears to be greater than the gain in precision from doubling the number of releases. It is also worth noting that changing the number of releases had a larger effect on the precision of the natural mortality rate estimates, M_1 and M_5, than changing the level of observer coverage.

These results were obtained using a 10% level of observer coverage since this is the reference level; however, the general relative effect of halving and doubling the number of releases on the precision of the parameter estimates remained the same at other levels of observer coverage.

Effect of other factors

We increased the longline reporting rate from the reference case value of 0.1 to 0.5 in all years, then reran the simulations. There was almost no improvement in the parameter estimates (Figure 4). This is expected because in the likelihood, the tag returns from the unobserved component of the longline fishery are scaled up by the estimated reporting rate to give an estimate of the actual number of tag recaptures. The reporting rates are determined by the return rate in the observer component, so that the age distribution of the returns always ends up the same for the unobserved component as the observed component. As such, it does not matter whether the reporting rate is 0.1 or 0.5; it is the accuracy of the observer tag return data that matters (as we saw in our previous simulations).

Preliminary analyses of data from recent tag seeding experiments suggested a value of 65% for the surface fishery reporting rates, so we used this value in our reference case simulations. However, in previous analyses of SBT tagging data , the reporting rate in the surface fishery has generally been assumed to be 100% (Polacheck et al. 1996, 1998). Thus, we ran simulations using 100% surface reporting rates (and assumed they were known without error) and found only a minimal improvement in the fishing mortality rate estimates for the surface fishery, and no improvement in the natural mortality rate and abundance estimates (Figure 5a). Furthermore, in the case of 65% reporting rates, we looked at the effect of changing the precision with which these rates are estimated; in particular we increased that standard error of the estimates from 0.10 to 0.30. This made virtually no difference to the results (Figure 5b). These results suggest that the return data from the surface fishery are already sufficiently informative that neither an increase in the magnitude of the reporting rates, nor an increase in the precision of the reporting rate estimates, has much effect.

Lastly, we considered the effect of changing the CV of the catch-at-age data in the surface fishery from 0.2 in all years to 0.05, and also 0.30, in all years. The estimates of fishing mortality at ages 1 and 2 in the surface fishery were most affected, with the CV of the age 1 estimates decreasing by over 20% when the catch CV was improved from 0.30 to 0.05 (Figure 6).

Dirichlet-multinomial tag returns

We repeated all of the simulations done in the case of multinomial tag returns using the model with Dirichlet-multinomial tag returns.

We first present the results from the simulations looking at the effect of changing the level of observer coverage. The means and standard deviations of the estimates for the parameters of key interest are summarized in Tables 6 and 7; those for the remaining parameters can be found in Tables B3 and B4 of Appendix B. The CV's of the key parameter estimates are shown in Figure 7. Comparing these results with the analogous results for the case of multinomial tag returns (i.e., Tables 4, 5, B1 and B2, and Figure 1), we see that:

- Again, the mean estimates are all within one standard deviation of the true value, with the exception of the increased-variance factor, x, for the Dirichlet distribution, which is consistently underestimated (see Tables B1 and B2 of Appendix B).
- The slight biases seen in the abundance and mortality rate estimates in the case of multinomial returns no longer appear to exist.
- The standard deviations (and hence CV's) of the estimates are larger for all parameters (and significantly so for some parameters, in particular for the fishing mortalities at older ages in both fisheries).
- Again, the standard deviations (and hence CV's) of almost all parameter estimates decline as the level of observer coverage increases, and for a given parameter, the amount that the CV declines is roughly the same. For example, the declines in the CV's are still largest for the fishing mortality rates in the longline fishery and they are in the range of 10 to 30% when the observer level increases from 5% to 50%.

Qualitatively, the results from varying any of the factors were very similar in the model with Dirichlet-multinomial returns as the model with multinomial tag returns. The parameters were almost always estimated with less precision (i.e. their CV's were larger) with Dirichlet-multinomial returns, but the relative changes in CV's and general observations made did not change significantly between the models.

Table 6. Mean of key reference case parameter estimates (from 100 simulations) for various levels of observer coverage (δ) when overdispersion is incorporated in tag return data. True parameter values are given below parameter names. The values for P_1 are expressed in millions.

	P_1	M_1	M_5	F_1^S	F_2^S	F_3^S	F_4^S	F_5^S	F_1^{LL}	F_2^{LL}	F_3^{LL}	F_4^{LL}	F_5^{LL}
δ	2.0	0.4	0.2	0.001	0.044	0.282	0.074	0.012	0.000	0.009	0.058	0.109	0.091
0.05	1.94	0.398	0.193	0.001	0.045	0.297	0.084	0.015	0.000	0.009	0.059	0.111	0.106
0.10	1.95	0.397	0.198	0.001	0.044	0.288	0.084	0.015	0.000	0.009	0.059	0.111	0.104
0.20	2.00	0.400	0.219	0.001	0.044	0.299	0.084	0.016	0.000	0.009	0.060	0.117	0.116
0.30	2.02	0.411	0.205	0.001	0.044	0.298	0.082	0.015	0.000	0.009	0.060	0.114	0.114
0.50	1.99	0.399	0.190	0.001	0.045	0.289	0.078	0.013	0.000	0.009	0.058	0.112	0.103

Table 7. Standard deviation of key reference case parameter estimates (from 100 simulations) for various levels of observer coverage (δ) when overdispersion is incorporated in tag return data. The values for P_1 are expressed in millions.

δ	P_1	M_1	M_5	F_1^S	F_2^S	F_3^S	F_4^S	F_5^S	F_1^{LL}	F_2^{LL}	F_3^{LL}	F_4^{LL}	F_5^{LL}
0.05	0.30	0.097	0.211	0.000	0.010	0.066	0.033	0.010	0.000	0.004	0.023	0.050	0.074
0.10	0.30	0.104	0.215	0.000	0.009	0.065	0.032	0.011	0.000	0.003	0.018	0.039	0.065
0.20	0.28	0.087	0.223	0.000	0.009	0.063	0.029	0.010	0.000	0.002	0.015	0.043	0.075
0.30	0.24	0.086	0.218	0.000	0.008	0.060	0.027	0.009	0.000	0.002	0.012	0.038	0.065
0.50	0.25	0.086	0.204	0.000	0.009	0.059	0.024	0.008	0.000	0.001	0.010	0.035	0.056

Discussion

The estimation framework and simulation results presented in this paper provide insights into design issues for the tagging program currently being conducted as part of the CCSBT SRP, in particular into appropriate levels of observer coverage and tag releases. Observer coverage to date has generally been minimal (<5%) (Anon. 2003). The results suggest that increasing observer coverage can lead to significant improvements in the precision of the fishing mortality rate estimates for the longline fishery, as well as smaller improvements in the estimate of population abundance. The number of tags that have been released in recent years as part of the CCSBT SRP tagging program appear to be adequate. Doubling the number of releases at each age led to only marginal improvements in any of the parameter estimates. On the contrary, halving the number of releases noticeably degraded some of the parameter estimates; thus, we would caution against reducing the number of releases without further investigation.

An advantage to having a multi-component fishery is that, if the catches by component are known well, then reporting rates only need to be estimated well in one component in order to get reasonable estimates of reporting rates (and hence other parameters) in other components (Hearn et al. 2003). This relies on the assumption that recapture rates of tagged fish (i.e. number of tags per unit of catch) are the same in all components (i.e. complete mixing). Then, knowing the reporting rate in one component means the recapture rate is known in that component, so that the number of tags that should have been returned in another component to achieve the same recapture rate can be calculated. We see evidence of this in our simulations because the reporting rates in the surface fishery are estimated very well so that even when the level of observer coverage is only 5% in the longline fishery, the reporting rates (and hence fishing mortality rates) in the longline fishery can still be estimated reasonably well. In essence, the observer data are not contributing substantially to the estimation of reporting rates; instead, the reporting rates for the longline fishery are being derived in most part from extrapolation from the surface fishery return rates. On the contrary, if we were to assume that there is no information about reporting rates in the surface fishery (e.g. no tag seeding data), then our ability to estimate the reporting rates in the longline fishery, as determined by the level of observer coverage, would have a larger influence on the reporting rate and fishing mortality rate estimates in the surface fishery (see Figure 8). The degree of influence will be greater when the surface catches are known with high precision (Figure 8a) versus when they are known with less precision (Figure 8b). It is interesting to note that when there is no information on reporting rates in the surface fishery, the level of observer coverage becomes more influential not only on the estimation of the surface fishery parameters, but also on the estimation of the initial population size parameter.

There are several disadvantages of basing reporting rates for the longline fishery on extrapolation from the surface fishery instead of obtaining independent estimates from observer data. Firstly, extrapolation from the surface fishery precludes the ability to test for significant non-mixing. Low return rates of tags in one fishery component could be the result of either low reporting rates or the fact that tagged fish did not mix with the portion of the stock being fished by this fishery component. These two possibilities are unresolvable without direct information on the reporting rates in the different fishery components. This issue is particularly of concern for SBT longline fisheries given the large spatial/temporal scales on which these fisheries operate and the spatially-restricted nature of the current tagging operations. For example, if low tag return rates are found for longline vessels fishing off South Africa, this could be due to low reporting rates or the fact that low numbers of tagged fish actually mixed with fish off South Africa. The implications of these two alternatives could be large in terms of estimates of mortality rates and population size; simply assuming complete mixing when it does not exist will bias these estimates. Furthermore, if non-mixing exists, then the extrapolated reporting rates will be biased, which will compound the biases already introduced into the mortality rate and population size estimates due to non-mixing. Moreover, the use of extrapolated reporting rates prevents the application of more spatially-explicit tag recovery models to account for heterogeneity in recapture probabilities as a result of non-mixing.

The model with multinomial tag returns assumes complete mixing of tagged and untagged fish, and that the fate of each tagged fish is independent of the fate of other tagged fish. The first of these assumptions may be violated in the case of SBT because their distribution is often patchy and juvenile fish tend to form schools. The second assumption is also likely to be violated for SBT because tagging generally occurs over a limited geographic area and a limited time period, and multiple fish from the same school are often tagged. If fish tagged from the same school or within close time and proximity of each other have a tendency to behave similarly, then their recapture probabilities would be positively correlated. Either non-mixing or dependence between tagged fish would mean that the return data are overdispersed. We attempted to incorporate overdispersion into our model by modelling the tag return data as Dirichlet-multinomial, which allows for extra variability compared to that of a multinomial distribution. We parameterized the Dirichlet-multinomial distribution so that the amount of extra variability was a constant factor, regardless of the number of releases. It may be argued that if the overdispersion stems mainly from non-independence among tagged fish, then tagging more fish will reduce this source of variance (assuming more releases would mean fish from a larger number of schools and a larger geographical and temporal range would be tagged). In such a case, the overdispersion should be modelled as a function of the number of releases. Determining the sources of overdispersion, their relative magnitudes, and the most appropriate way to model them is an issue requiring further investigation.

In modelling the catch-at-age data as Gaussian, we argued that the multinomial process error should be negligible compared to the sampling error (assumed to Gaussian), so that only the latter source of error needed to be considered. However, if fish are not distributed homogeneously in space or time, or if there is large variability in the size/age selectivities of vessels, then the process error would be overdispersed relative to a multinomial distribution. Furthermore, the sampling error would be larger (i.e. the CV of the Gaussian distribution would be larger). In this case, it is not clear if the process error would still be negligible compared to the sampling error, nor is it clear how the relationship between the CV of the sampling error and the level of sampling (i.e. the level of observer coverage for the longline fishery) should be modelled. More observer data should still mean a reduction in the sampling error (i.e. a smaller CV), but the amount of reduction will depend on the nature of the increased observer coverage. If all of the additional observer data comes from only a few vessels/cruises, then the gain will be much less than if it comes from a large number of vessels/cruises operating over a wide geographic range. Developing an appropriate error model for the catch-at-age data is an important area for future work because it is critical for understanding the statistical properties of the parameter estimates obtained from the tagging and catch model.

In all of our results, the natural mortality rate at age 1, M_1, is estimated with reasonable precision, even in the model with overdispersion (CV around 20-25%). On the other hand, the natural mortality rate at age 5, M_5, is estimated with very low precision (CV over 100% in the case of overdispersion), and a histogram of the estimates for any set of simulations shows that the estimate of M_5 usually equals either the lower bound (0.01) or upper bound (0.4) set for this parameter. While this causes some concern, it is important to recall that natural mortality has been constrained to be a linear function of age, so that the natural mortality rate estimates for ages 2 to 4 will have CV's intermediate to those at ages 1 and 5. For example, we calculated the natural mortality estimates at all ages for the reference case simulations and found their CV's to be 0.14, 0.14, 0.28, 0.52 and 0.89 for ages 1 to 5 respectively.

The initial population size (P_1) was estimated well in all cases (CV less than 20%), even when many of the fishing and natural mortality rate parameters were not. At first this seems counter-intuitive. However, on further consideration, it can be explained by the presence of high positive correlations between natural mortality and fishing mortality (see discussion below). If natural mortality is overestimated for a particular set of data, then fishing mortality is also likely to be overestimated since fishing and natural mortality are positively correlated. An overestimation of natural mortality would mean the probability of catching a fish is underestimated, whereas an overestimation of fishing mortality would mean the probability of catching a fish is overestimated; thus, the two counteract each other such that the probability of catching a fish may be estimated without any bias. A similar argument holds if natural mortality was underestimated. For estimating population size, it is the estimate of the probability of catching a fish that matters, not the actual estimates of natural and fishing mortalities (since, in simplistic terms, catch equals population size times probability of catching a fish, so if we know the catch and the probability of catch well, then we know the population size well).

High correlations exist between many of the parameter estimates (see Appendix B, Table B5). As already mentioned, there are some high positive correlations between the natural mortality and fishing mortality estimates, especially at older ages. This is expected because an increase in natural mortality means that less fish are still alive in the population; thus, in order to achieve a particular level of catch, fishing mortality must increase (i.e. the percentage of the population caught must increase) as natural mortality increases. For the same reason, the fishing mortality rates between ages and fisheries are often highly positively correlated. For example, if fishing mortality at age i increases, then there are less fish of age i+1 alive in the population the next year; thus, in order to achieve a particular level of catch at age i+1, the fishing morality at age i+1 would have to increase if fishing mortality at age i increased. Finally, there are high negative correlations between the initial population size and the fishing mortality estimates. These can be explained in a similar fashion, because to have achieved a particular level of catch, the population size must have been larger if the fishing mortality had been high than if it had been low.

The results presented here are for a tagging experiment involving a single cohort. In practice, it would likely be feasible and cost efficient to tag two or more cohorts in any given year, and this is done in the case of SBT. This could improve the information available for estimating reporting rates since we assume that reporting rates differ only by year, and not age. Perhaps more importantly, if mortality rates are assumed to vary only with age and not year, then having data from more cohorts could potentially improve our ability to estimate natural mortality rates, which we have seen is quite poor. In order to evaluate the potential benefit of including more cohorts, we ran some simulations using data for two consecutive cohorts, both with 3 consecutive release years and 5 recapture years (i.e. cohort 1 was tagged in years 1, 2 and 3 at ages 1, 2 and 3 and recaptured in years 1 to 5; cohort 2 was tagged in years 2, 3 and 4 at ages 1, 2 and 3 and recaptured in years 2 to 6). We allowed fishing mortality rates to vary with age, year and fishery; natural mortality rates to vary with age; and reporting rates to vary with year and fishery. A small improvement was seen in the estimate of M_1 (3-4% decrease in CV) and a slightly larger improvement in the estimate of M_5 (5-10% decrease in CV). Further improvements would be expected with the inclusion of even more cohorts, and data from multiple cohorts should be available from the current SBT tagging program.

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Acknowledgements

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Figure 1. The assumed relationship between level of observer coverage and accuracy (i.e. the coefficient of variation) of the catch-at-age data for the longline fishery.

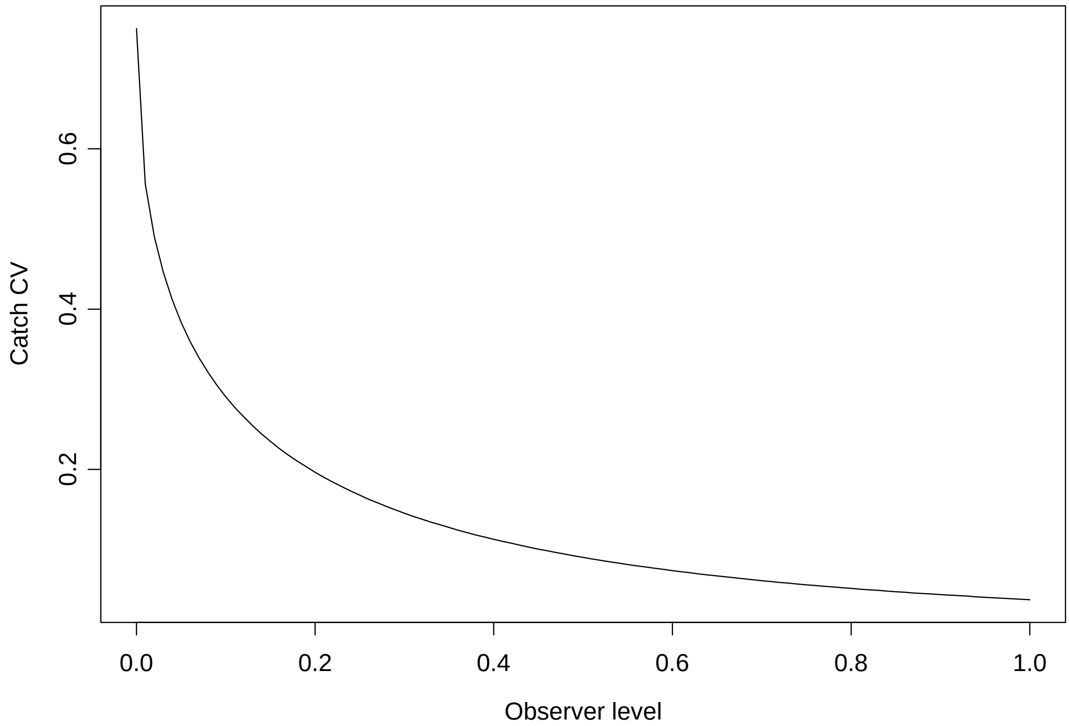


Figure 2. Effect of varying the level of observer coverage on the coefficient of variation (CV) of the key parameter estimates.

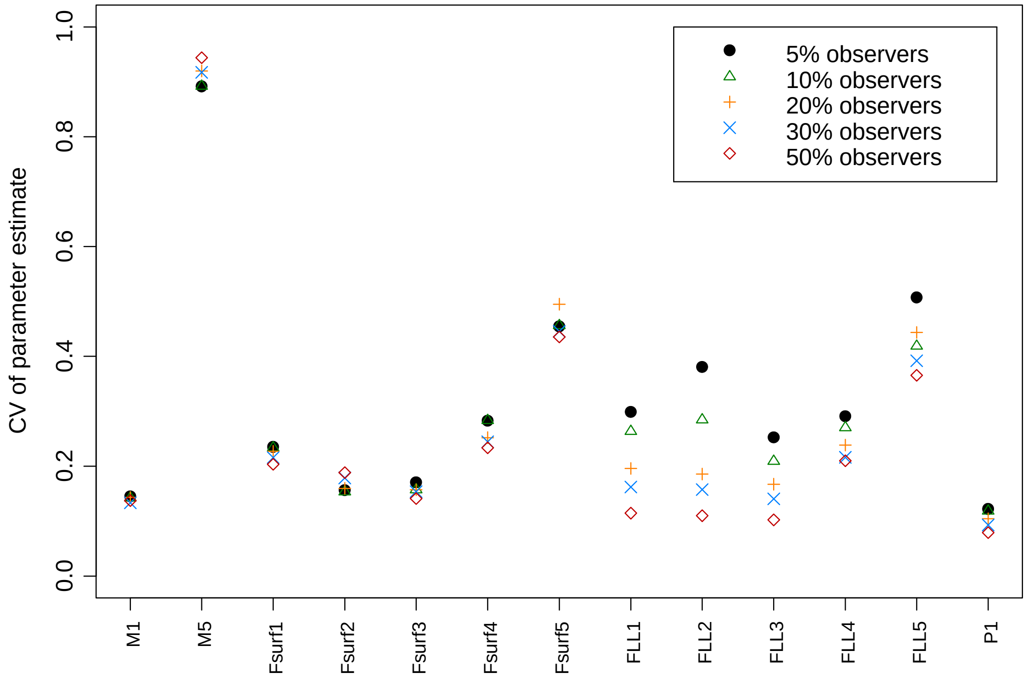


Figure 3. Effect of varying the number of releases (N) on the coefficient of variation (CV) of the key parameter estimates when the level of observer coverage is 0.10. N refers to the reference case number of releases.

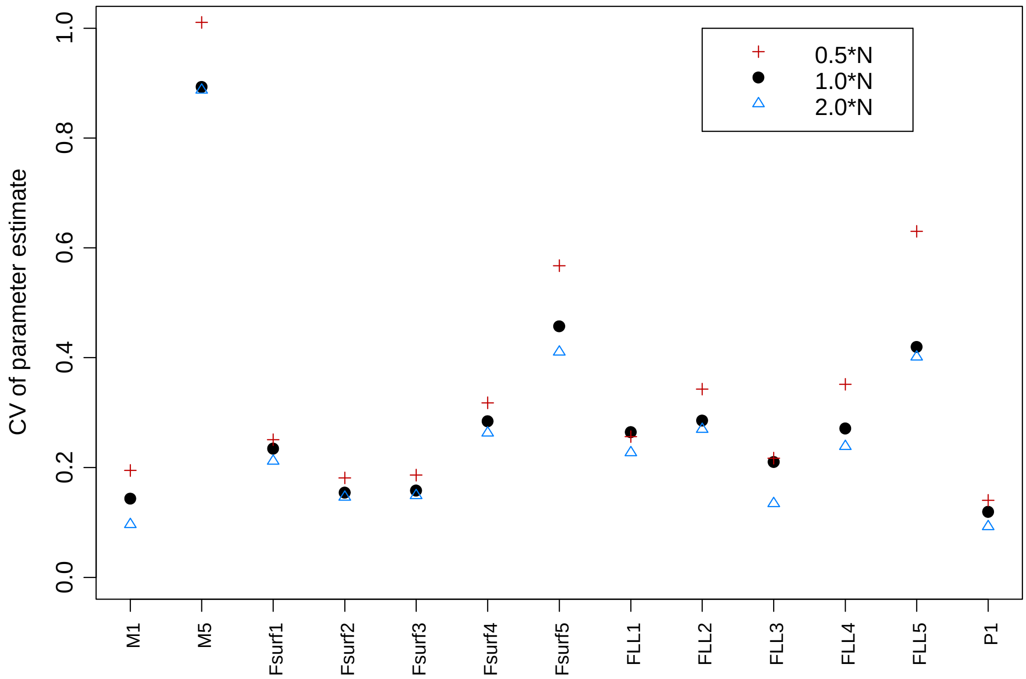


Figure 4. Effect of varying the reporting rate in the unobserved component of the longline fishery (LL rep rate) on the coefficient of variation (CV) of the key parameter estimates.

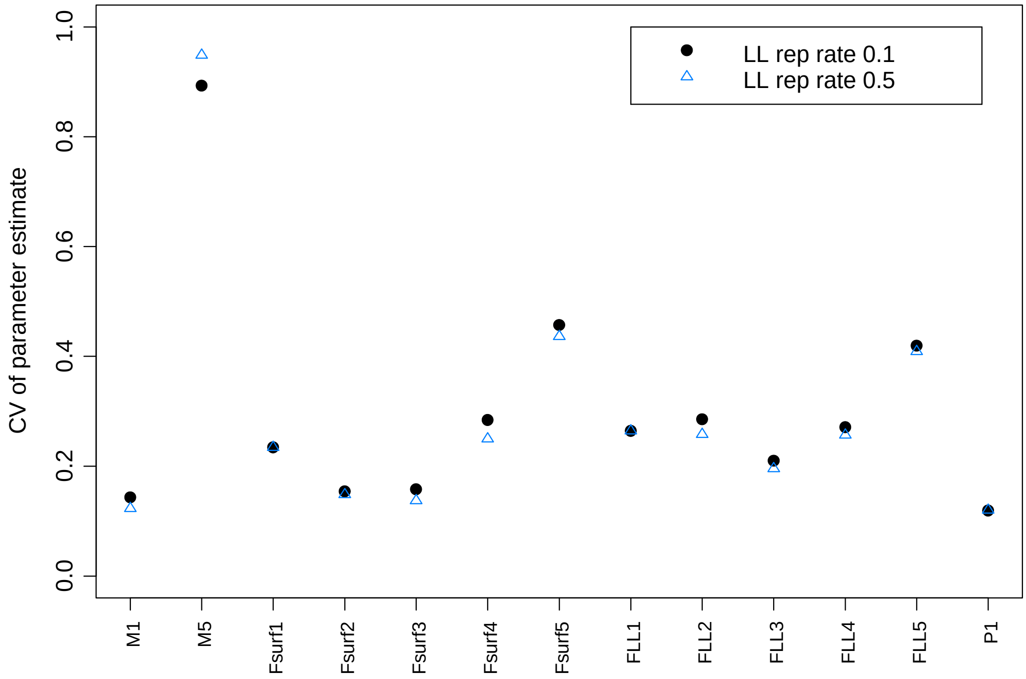
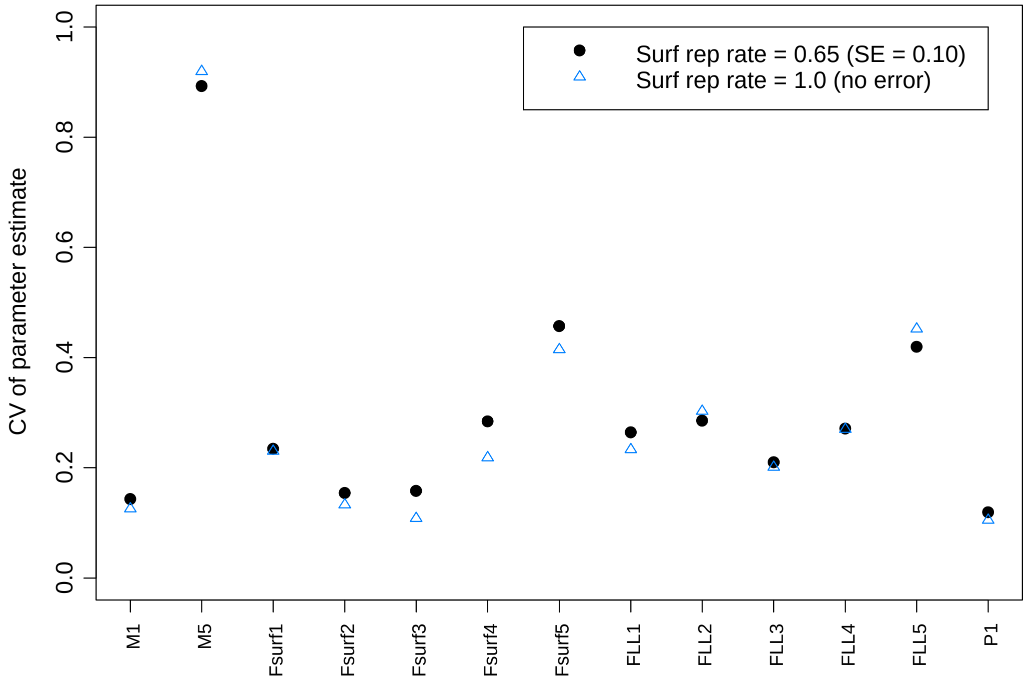


Figure 5. Effect of varying a) the magnitude of the reporting rates in the surface fishery (surf rep rate); and b) the standard error (SE) of the reporting rate estimates for the surface fishery, on the coefficient of variation (CV) of the key parameter estimates.

a)



b)

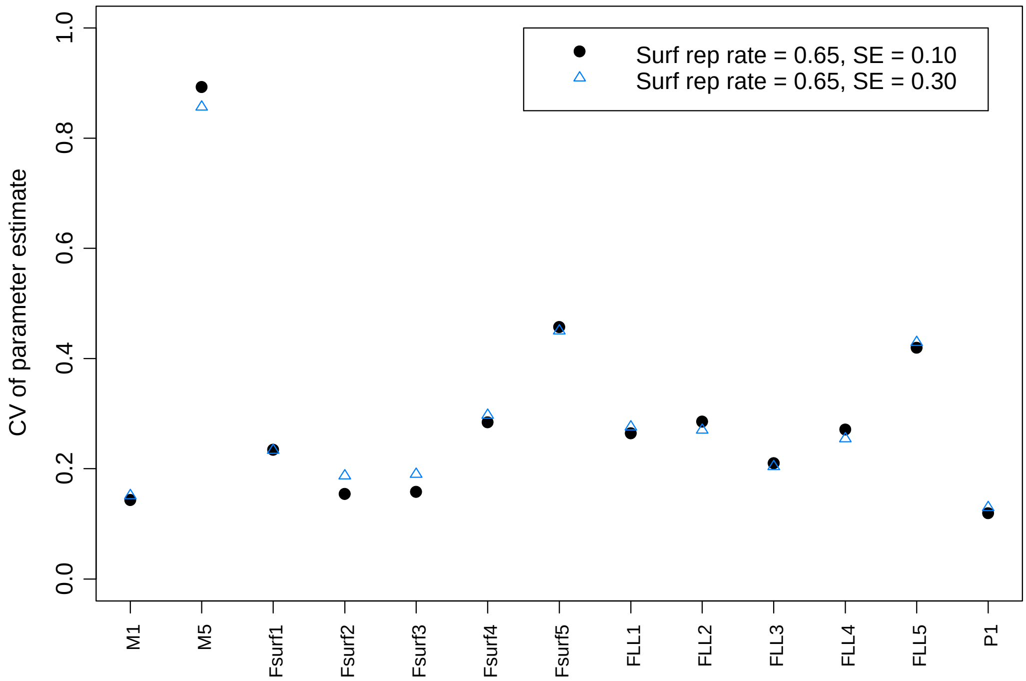


Figure 6. Effect of varying the coefficient of variation of the catch-at-age data in the surface fishery (CV_surf) on the coefficient of variation (CV) of the key parameter estimates.

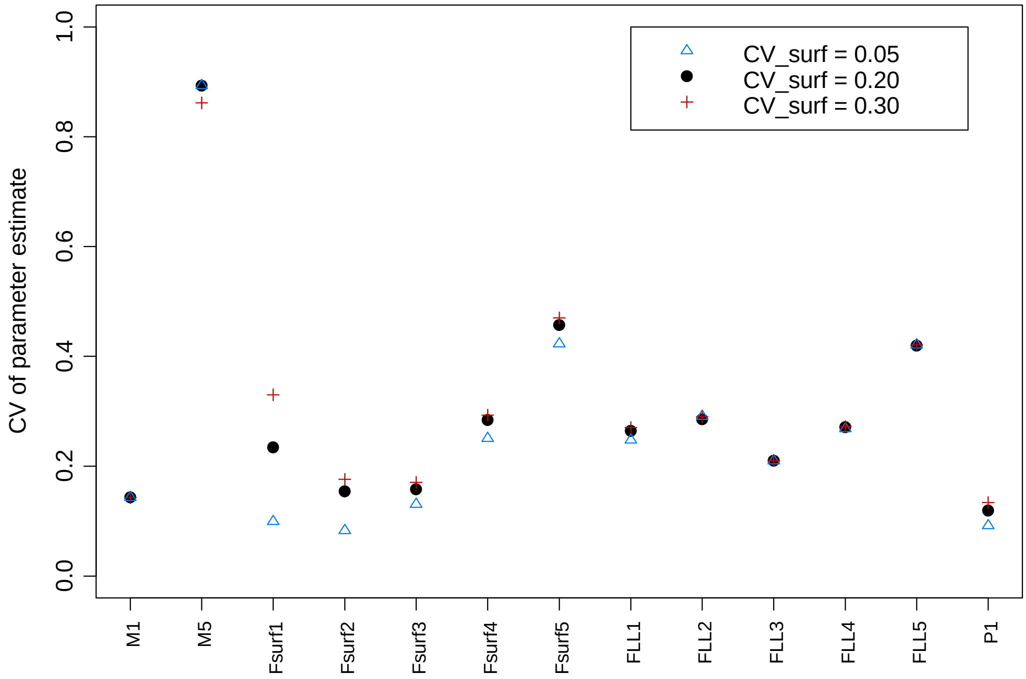


Figure 7. Effect of varying the level of observer coverage on the coefficient of variation (CV) of the key parameter estimates for the model with overdispersion in the tag return data.

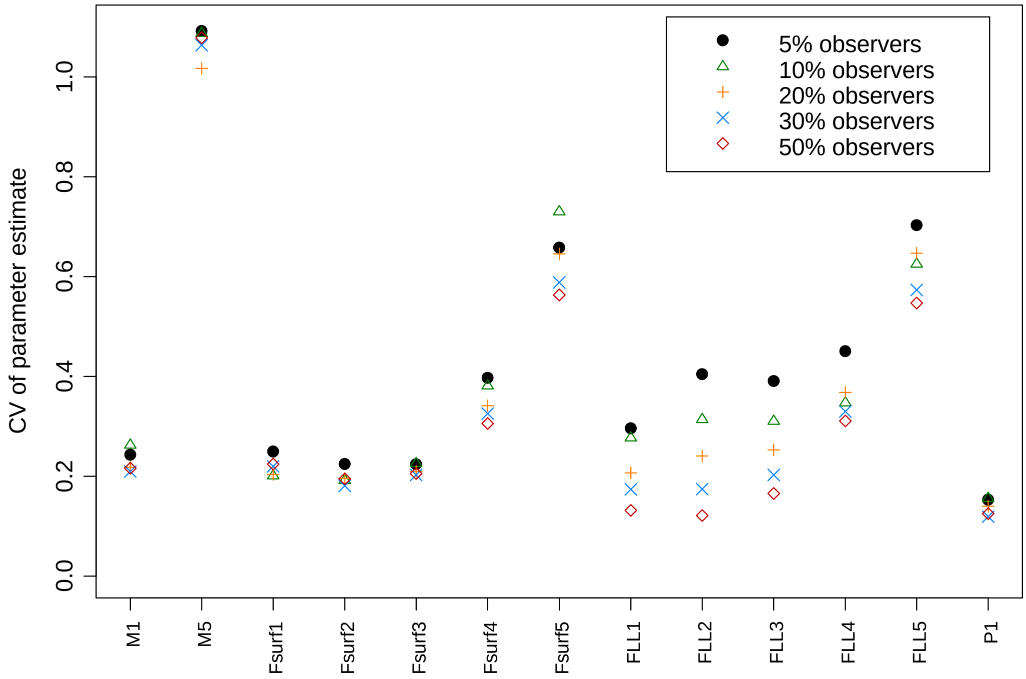
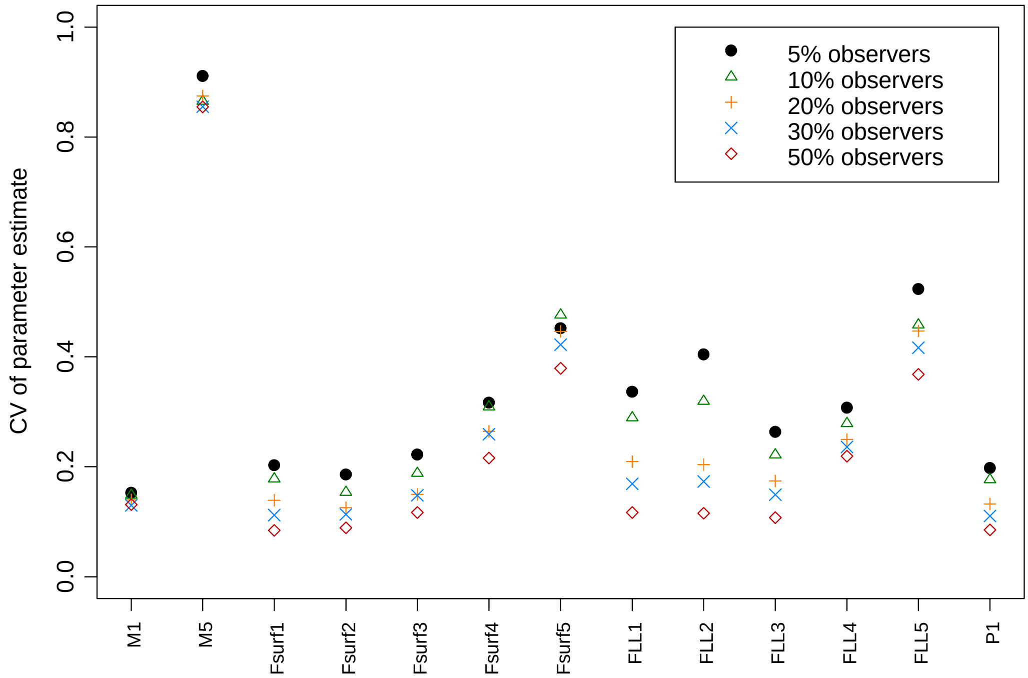
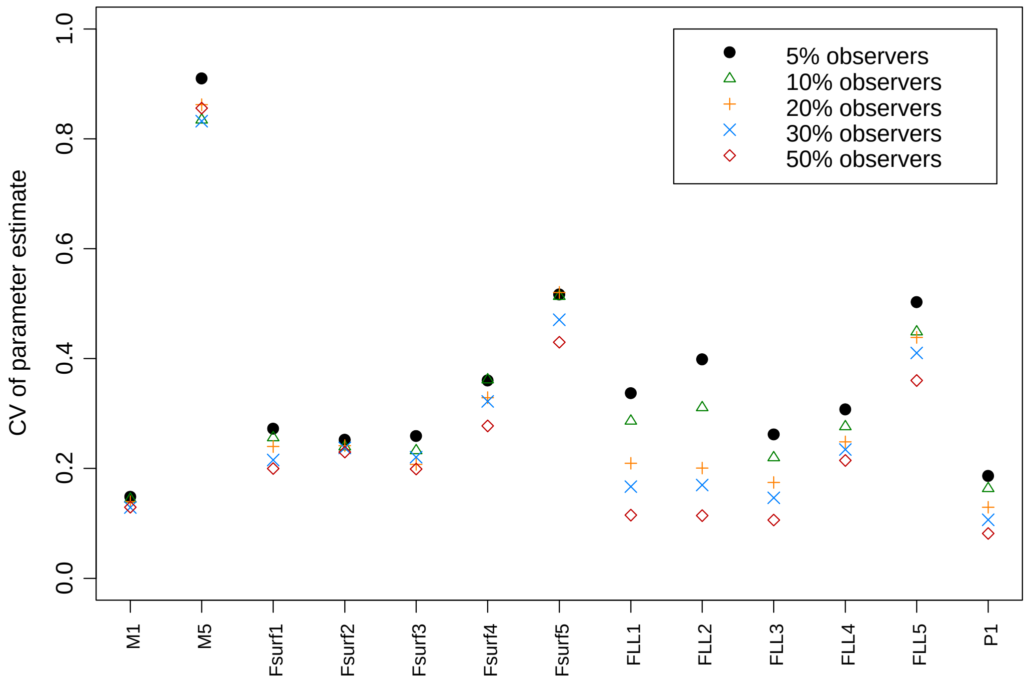


Figure 8. Effect of varying the level of observer coverage on the coefficient of variation (CV) of the key parameter estimates when there is no information about reporting rates for the surface fishery and a) the surface catch data are known with high precision (CV=0.05); b) the surface catch data are know with less precision (CV=0.20). Results are shown for model with multinomial tag returns.



a)

b)



Appendix A.

The notation and parameterizations used in this Appendix were chosen to be representative of the estimation model with overdispersion presented in the main body of the paper. Thus, in the presentation below, *N* represents the number of tag releases at a particular age, $R_1, \ldots, R_{k-1}$ represent the number of tag returns at ages 1 to $k-1$, and R_k represents the number of tags that were not returned by age *k*. The π's are the random Dirichlet probabilities of return at age and the *p*'s are their expected values (in our estimation model with overdispersion, the *p*'s are analogous to the return probabilities given in equations (3)-(5)).

The Dirichlet distribution

The Dirichlet distribution is used to describe the variation in a set of proportions that sum to 1. The probability density of a set of proportions $\underline{\pi} = \{\pi_1, \ldots, \pi_k\}$ with parameter set $\underline{p} = \{\omega, p_1, \ldots, p_k\}$ is given by:

$$\Pr(\underline{\pi}) = \frac{\Gamma(\omega)}{\prod_{i=1}^{k}(\omega p_i)} \prod_{i=1}^{k} \pi_i^{\omega p_i - 1}$$

where $0 < p_i < 1$ for all *i* and $\sum_{i=1}^{k} p_i = 1$.

The mean and variance of the proportions are:

$$E[\pi_i] = p_i$$

and

$$V[\pi_i] = \frac{p_i(1-p_i)}{\omega + 1}.$$

Note that the Dirichlet distribution with $k = 2$ reduces to the beta distribution.

The Dirichlet-multinomial distribution

The multinomial distribution describes a situation in which *N* independent random trials are conducted and the outcome of each trial can fall into one of *k* categories; the probability of falling into category *i* is π_i ($\sum_{i=1}^{k} \pi_i = 1$). The final category counts $\underline{R} = \{R_1, \ldots, R_k\}$, where $\sum_{i=1}^{k} R_i = N$, have a multinomial distribution with probability density:

$$\Pr(\underline{R}) = \frac{N!}{\prod_{i=1}^{k} R_i!} \prod_{i=1}^{k} \pi_i^{R_i}$$

When the category probabilities are themselves viewed as random variables following a Dirichlet distribution, then the multinomial probability density given above describes the *conditional* distribution of the category counts *given* the probabilities, which we denote by

$\Pr\left(\underline{R} \mid \underline{\pi}\right)$. Then the *unconditional* distribution of the category counts is given by the compound distribution called the Dirichlet-multinomial with probability density:

$$\Pr\left(\underline{R}\right) = \int_{\underline{\pi}} \Pr\left(\underline{R} \mid \underline{\pi}\right) \Pr\left(\underline{\pi}\right) \, d\underline{\pi}$$

The integral is *k*-dimensional over all values of $\underline{\pi}$ such $0 \le \pi_i \le 1$ and $\sum_{i=1}^{k} \pi_i = 1$. It is easy to show that the resulting distribution is:

$$\Pr\left(\underline{R}\right) = \frac{N!}{\prod_{i=1}^{k} R_i!} \prod_{i=1}^{k} \frac{\Gamma\left(R_i + \omega p_i\right)}{\Gamma\left(\omega p_i\right)}$$

The mean and variance of the category counts are:

$$E\left[R_i\right] = N\, p_i$$

and

$$V\left[R_i\right] = \left(\frac{N+\omega}{\omega+1}\right) N\, p_i (1 - p_i) .$$

Recall that the variance of the category counts for the multinomial distribution is $N\, p_i (1 - p_i)$ so that the variance for the Dirichlet-multinomial is a factor of $\left(N+\omega\right) / \left(\omega+1\right)$ times larger.

Appendix B. Additional results

Table B1. Mean of remaining reference case parameter estimates (from 100 simulations) for various levels of observer coverage (δ). True parameter values are given below parameter names.

	F_1^{*S}	F_2^{*S}	F_3^{*S}	F_1^{*LL}	F_2^{*LL}	F_3^{*LL}
δ	0.044	0.041	0.041	0.006	0.009	0.009
0.05	0.045	0.044	0.043	0.005	0.008	0.010
0.10	0.045	0.044	0.043	0.006	0.009	0.007
0.20	0.045	0.043	0.042	0.006	0.009	0.008
0.30	0.045	0.042	0.043	0.006	0.009	0.008
0.50	0.045	0.041	0.042	0.006	0.009	0.008

	λ_1^S	λ_2^S	λ_3^S	λ_4^S	λ_5^S	λ_1^{LL}	λ_2^{LL}	λ_3^{LL}	λ_4^{LL}	λ_5^{LL}
δ	0.65	0.65	0.65	0.65	0.65	0.10	0.10	0.10	0.10	0.10
0.05	0.648	0.631	0.632	0.622	0.623	0.189	0.141	0.103	0.110	0.107
0.10	0.644	0.633	0.633	0.624	0.626	0.146	0.117	0.101	0.101	0.101
0.20	0.644	0.638	0.641	0.631	0.621	0.134	0.107	0.097	0.098	0.100
0.30	0.644	0.644	0.641	0.627	0.623	0.143	0.101	0.096	0.101	0.093
0.50	0.643	0.650	0.645	0.630	0.624	0.142	0.112	0.097	0.097	0.100

Table B2. Standard deviation of remaining reference case parameter estimates (100 simulations) for various levels of observer coverage (δ).

δ	F_1^{*S}	F_2^{*S}	F_3^{*S}	F_1^{*LL}	F_2^{*LL}	F_3^{*LL}
0.05	0.008	0.009	0.043	0.005	0.005	0.008
0.10	0.008	0.009	0.043	0.005	0.004	0.007
0.20	0.008	0.010	0.042	0.004	0.003	0.005
0.30	0.007	0.009	0.043	0.003	0.002	0.004
0.50	0.006	0.009	0.042	0.002	0.002	0.004

δ	λ_1^S	λ_2^S	λ_3^S	λ_4^S	λ_5^S	λ_1^{LL}	λ_2^{LL}	λ_3^{LL}	λ_4^{LL}	λ_5^{LL}
0.05	0.084	0.084	0.074	0.084	0.091	0.165	0.091	0.041	0.033	0.038
0.10	0.082	0.083	0.074	0.083	0.089	0.137	0.067	0.026	0.032	0.032
0.20	0.082	0.084	0.076	0.083	0.090	0.116	0.051	0.028	0.023	0.029
0.30	0.082	0.078	0.072	0.082	0.087	0.119	0.042	0.024	0.023	0.029
0.50	0.082	0.076	0.073	0.084	0.086	0.116	0.057	0.028	0.027	0.038

Table B3. Mean of remaining reference case parameter estimates not in Table 5 (from 100 simulations) for various levels of observer coverage (δ) when overdispersion is incorporated in tag return data. True parameter values are given below parameter names.

	F_1^{*S}	F_2^{*S}	F_3^{*S}	F_1^{*LL}	F_2^{*LL}	F_3^{*LL}	x
δ	0.044	0.041	0.041	0.006	0.009	0.009	3.0
0.05	0.045	0.043	0.045	0.007	0.010	0.011	1.86
0.10	0.045	0.044	0.044	0.006	0.009	0.008	1.89
0.20	0.046	0.044	0.045	0.006	0.009	0.009	1.81
0.30	0.047	0.043	0.044	0.007	0.009	0.008	1.86
0.50	0.046	0.042	0.043	0.007	0.009	0.009	1.82

	λ_1^S	λ_2^S	λ_3^S	λ_4^S	λ_5^S	λ_1^{LL}	λ_2^{LL}	λ_3^{LL}	λ_4^{LL}	λ_5^{LL}
δ	0.65	0.65	0.65	0.65	0.65	0.10	0.10	0.10	0.10	0.10
0.05	0.643	0.640	0.641	0.631	0.613	0.185	0.134	0.122	0.120	0.110
0.10	0.643	0.636	0.653	0.624	0.622	0.175	0.126	0.111	0.109	0.106
0.20	0.643	0.636	0.642	0.627	0.621	0.119	0.125	0.104	0.104	0.097
0.30	0.643	0.646	0.648	0.623	0.611	0.133	0.121	0.108	0.109	0.096
0.50	0.649	0.642	0.651	0.632	0.617	0.126	0.113	0.104	0.103	0.099

Table B4. Standard deviation of remaining reference case parameter estimates (100 simulations) for various levels of observer coverage (δ) when overdispersion is incorporated in tag return data.

δ	F_1^{*S}	F_2^{*S}	F_3^{*S}	F_1^{*LL}	F_2^{*LL}	F_3^{*LL}	x
0.05	0.012	0.011	0.018	0.012	0.008	0.016	0.35
0.10	0.012	0.011	0.016	0.008	0.006	0.010	0.42
0.20	0.013	0.012	0.016	0.005	0.005	0.010	0.31
0.30	0.015	0.011	0.017	0.005	0.004	0.008	0.42
0.50	0.013	0.008	0.015	0.004	0.003	0.007	0.34

δ	λ_1^S	λ_2^S	λ_3^S	λ_4^S	λ_5^S	λ_1^{LL}	λ_2^{LL}	λ_3^{LL}	λ_4^{LL}	λ_5^{LL}
0.05	0.083	0.089	0.084	0.084	0.097	0.170	0.087	0.070	0.060	0.065
0.10	0.083	0.088	0.084	0.080	0.094	0.162	0.090	0.055	0.046	0.053
0.20	0.082	0.083	0.085	0.083	0.092	0.119	0.092	0.043	0.039	0.046
0.30	0.081	0.091	0.079	0.091	0.104	0.126	0.094	0.046	0.043	0.042
0.50	0.085	0.084	0.095	0.082	0.099	0.127	0.083	0.056	0.047	0.049

Table B5. Correlations between key parameter estimates for the reference case simulations (those with magnitude ≥ 0.5 are shaded).

	M_1	M_5	F_1^S	F_2^S	F_3^S	F_4^S	F_5^S	F_1^{LL}	F_2^{LL}	F_3^{LL}	F_4^{LL}	F_5^{LL}	P_1
M_1	1.0	-0.27	-0.07	0.15	0.24	0.14	0.05	-0.04	0.08	0.20	0.17	0.07	0.13
M_5		1.00	-0.04	-0.01	0.16	0.50	0.71	-0.01	-0.01	0.26	0.54	0.71	0.02
F_1^S			1.00	0.50	0.51	0.42	0.31	0.35	0.36	0.44	0.34	0.23	-0.69
F_2^S				1.00	0.64	0.52	0.4	0.36	0.49	0.56	0.49	0.38	-0.69
F_3^S					1.00	0.76	0.61	0.38	0.45	0.68	0.66	0.57	-0.69
F_4^S						1.00	0.82	0.28	0.37	0.70	0.80	0.77	-0.57
F_5^S							1.00	0.23	0.27	0.61	0.81	0.86	-0.40
F_1^{LL}								1.00	0.32	0.35	0.27	0.20	-0.48
F_2^{LL}									1.00	0.34	0.32	0.27	-0.51
F_3^{LL}										1.00	0.68	0.56	-0.63
F_4^{LL}											1.00	0.78	-0.52
F_5^{LL}												1.00	-0.36
P_1													1.00