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Atlantic Halibut Fishing Mortality Estimated from Tagging on the Scotian Shelf and the Southern Grand Banks

Estimation, grâce au marquage, de la mortalité par pêche du flétan de l'Atlantique du plateau néo écossais et du sud des Grands Bancs

C. den Heyer, C. Schwarz, and K. Trzcinski

Population Ecology Division
Bedford Institute of Oceanography
PO Box 1006, Dartmouth
Nova Scotia Canada
B2Y 4A2

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ABSTRACT

In 2006, Fisheries and Oceans Canada (DFO) and the Atlantic Halibut Council (AHC) began the Halibut All Sizes Tagging (HAST) program to estimate exploitation rate and evaluate the distribution of halibut within the Scotian Shelf southern Grand Banks management unit. More than 2,000 halibut were double tagged with t-bar anchor tags, during the DFO-industry halibut surveys between 2006 and 2008. As of 26 August 2010, 409 of these halibut were recaptured and reported. The HAST study is an example of a band-recovery experiment. The models in this paper follow a similar development to Hoenig et al. (1998a&b), but also incorporate tag loss. We assume that survival after tagging and tag reporting are constant and that fishing mortality is equally spread over the year. We also estimate instantaneous fishing mortality for each cohort in the first year after release to allow newly tagged animals to mix with the population. Most tag loss occurs in the first year of release. Based on the multiyear models with incomplete mixing and two parameters to describe tag retention, tag loss is estimated at 17%/year in the first year and 9%/year in the second and subsequent years. Assuming 90% tag reporting and 80% survival from tagging, instantaneous natural mortality (M) for halibut that were greater than 81 cm was estimated to be 0.26 (SE=0.08), and instantaneous fishing mortality (F) was estimated to be 0.20 (SE=0.04) in 2007, 0.29 (SE=0.04) in 2008, and 0.21 (SE=0.04) in 2009.

RÉSUMÉ

En 2006, Pêches et Océans Canada (MPO) et l’Atlantic Halibut Council (AHC) ont entrepris un programme de marquage visant les flétans de toutes tailles, pour estimer le taux d’exploitation de l’espèce et en évaluer la distribution dans l’unité de gestion du plateau néo écossais et du sud des Grands Bancs. Plus de 2 000 flétans ont été marqués au moyen de deux étiquettes en T durant les relevés effectués par le MPO et l’industrie entre 2006 et 2008. Au 26 août 2010, 409 de ces flétans avaient été recapturés et signalés. L’opération de marquage des flétans de toutes tailles est un bon exemple d’expérience de récupération des données de marquage. Les modèles exposés dans ce document suivent une démarche semblable à celle de Hoenig et al. (1998 a et b) mais ils tiennent compte également de la perte des étiquettes. Nous supposons que la survie après le marquage et que les rapports de récupération d’étiquettes sont constants et que la mortalité par pêche est répartie également sur l’année. Nous estimons aussi la mortalité instantanée par pêche pour chaque cohorte dans la première année après le marquage pour tenir compte des poissons récemment marqués qui se sont mélangés à la population La plupart des pertes d’étiquettes se produisent dans la première année après la pose. Selon les modèles pluriannuels dans lesquels le mélange est incomplet et qui utilisent deux paramètres de maintien des étiquettes, la perte d’étiquettes est estimée à 17 % la première année et à 9 % par année la deuxième année et les années suivantes. En supposant que 90 % des étiquettes fassent l’objet de rapports et que 80 % des individus survivent au marquage, la mortalité naturelle instantanée (M) pour les flétans de plus de 81 cm était estimée à 0,26 (ET=0,08), et la mortalité instantanée par pêche (F) était estimée à 0,20 (SE=0,04) en 2007, à 0,29 (SE=0,04) en 2008 et à 0,21 (SE=0,04) en 2009.

INTRODUCTION

Atlantic Halibut, *Hippoglossus hippoglossus*, are a large long-lived sexually dimorphic flatfish typically found in the northwest Atlantic at depths between 200 and 450 m along the continental shelf and channel slopes. Atlantic Halibut has been exploited in Eastern Canadian waters for more than a century. The current Canadian management units, Scotian Shelf and Grand Banks (NAFO 3NOPs4VWX5Zc) and Gulf of St. Lawrence (NAFO 4RST), were established in 1987, based primarily on tagging studies and differences in growth rates (Stobo et al. 1988, Bowering 1986). Since 1988 the fishery has been managed by a total allowable catch (TAC), and in 1994 a legal size limit of ≥ 81 cm was fully established. In 1988, the TAC was set at 3200 t. The TAC remained at this level for six years during which landings declined. In 1994, the TAC was decreased to 1500 t and the following year it was further reduced to 850 t. Since 1995, the TAC and landings have steadily increased and in 2010 the TAC was set at 1700 t (Trzcinski et al. 2011).

Stock assessments of Scotian Shelf and southern Grand Banks Atlantic Halibut have been based on trends in abundance indices from DFO's research vessel (RV) groundfish surveys, DFO-Industry surveys and landings data. Because the halibut caught in the RV surveys tend to be small (30 – 70 cm), the RV surveys are considered to be an index of recruitment. Since 1998, the DFO-Industry halibut longline survey has been used to monitor adult abundance. In the 2009 halibut stock assessment, a modified Petersen equation was used to estimate fishing mortality from Halibut All Sizes Tagging (HAST) data (Trzcinski et al. 2010).

In 2006, Fisheries and Oceans Canada (DFO) and the Atlantic Halibut Council (AHC) began the HAST program to estimate exploitation rate and evaluate the distribution of halibut within the Scotian Shelf and Grand Banks management unit. Between 2006 and 2008, more than 2,000 halibut were double tagged with t-bar anchor tags during the halibut survey (May - July). Fishermen were compensated for releasing fish of legal size (≥ 81 cm) by the AHC. The AHC also provided cash rewards to encourage reporting of recaptured tags. An earlier tagging study where fisherman tagged undersized halibut throughout the year (< 81 cm yellow tag program 1995-2009) was not included in this analysis. There were also 12 pop-up satellite tags deployed on Atlantic halibut between 2008 and 2010 to investigate movement behaviour and habitat preference, but these data will be presented in another publication.

The HAST study is an example of a band-recovery experiment as exemplified by Brownie et al. (1985). While the Brownie et al. (1985) models are commonly applied to bird studies, Hoenig et al. (1998a) demonstrated how to re-parameterize the Brownie et al. (1985) models in terms of parameters commonly used in fisheries management (i.e. instantaneous survival (M) and fishing mortality (F)). The analysis in this paper follow a similar approach to Hoenig et al. (1998a&b), and includes estimates of fishery mortality, incomplete mixing, and tag loss.

METHODS

TAG RELEASE

Most of the Atlantic Halibut in this study were caught and tagged during the halibut survey. The halibut survey is conducted every year from May through June, follows a fixed station design and uses longline gear (Trzcinski at al. 2010). Halibut were tagged proportional to abundance as estimated from the catch rates in the halibut survey from 1999-2005. A target tagging distribution of tags for each NAFO area was calculated using a Delaunay triangulation spatial estimator of abundance based on fixed station catch rates. The allocation of tags was weighted by the area for each NAFO unit (i).

$$\text{Prop. Tags}_i = \text{Area}_i{*}\text{CPUE}_i \,/\, \Sigma\, \text{Area}_i{*}\text{CPUE}_i \quad (1)$$

If not enough halibut were caught and tagged in a particular NAFO area, additional halibut were caught during the halibut commercial index (which runs concurrently), or during commercial fishing.

Halibut were double-tagged with t-bar anchor tags applied 15 cm apart at the widest point near the dorsal fin on the dark or top side. Tagged halibut were returned to the water immediately and only halibut that had a high probability of survival were released. Observers recorded release information including date, location, tag numbers, total length and morphology codes that described fish health and hook injuries. It was not possible to assess the sex of the halibut at time of release. The data were entered into the DFO Industry Surveys Database (ISDB). Fishermen were compensated for releasing fish of legal size (≥ 81 cm) by the AHC.

TAG REPORTING

Fishermen were asked to report the tag number or tag numbers, date, location, length and sex of tagged halibut caught during commercial fisheries or industry surveys. The AHC provided $100 reward for each fish reported with one or two tags, and the participant's name was entered into a quarterly lottery for $1000. Posters announcing the tagging program and the reward for returned tags were distributed throughout Atlantic Canada. Additional posters were sent to Iceland, Spain and the United States. Fishermen and observers were also provided tag envelopes to encourage collection of information on recapture location and date. For each tagged halibut reported, the participant was also sent a thank you letter, which included a map of the mark and recapture location, and a description of the net movement.

DATA MANAGEMENT

The Halibut Tagging Database includes release data extracted from ISDB and recapture data sent to DFO by fishermen and entered directly into the Halibut Tagging Database. ISDB data is double keypunched and has automated data entry checks. Nonetheless, a number of data errors were uncovered when the recapture data was entered and preliminary data analysis completed. The original datasheets were used to make corrections when possible. Further development of the Halibut Tagging Database will improve data checking at time of data entry.

The Halibut Tagging Database was queried on 26 August 2010 and all records for fish released in 2006-2008 were extracted. On some occasions tagged halibut were recaptured and re-released with both tags, only one tag, different tags or no tags. Re-releases were not included in this analysis. A small number of fish released with a single tag or with the archival pop-up tags were also excluded.

ESTIMATING CUMULATIVE TAG-LOSS

The cumulative tag-loss as a function of time at large was estimated using the methods of Seber and Felton (1981). The time at large for each recovered tag was divided into intervals and the number of recaptured fish with one or two tags. The cumulative tag-retention was estimated following Seber and Felton (1981) as:

$$\theta = \frac{2(dt)}{2(dt) + st} \qquad (2)$$

where *dt* is the number of fish with double tags, and *st* is the number of fish with a single tag (i.e. lost one tag). The cumulative tag-loss is the complement of this value.

MULTIYEAR MODEL WITH INCOMPLETE MIXING

The Hoenig et al. (1998b) model allows for incomplete mixing of newly tagged animals during the first year after release. Following the methods of Hoenig et al. (1998b), the expected number of fish released and recaptured can be expressed as shown in Table 1, where the expected number of recoveries given a constant instantaneous natural mortality (*M*), instantaneous fishing mortality for a cohort in the year of release (F_i^*), year-specific instantaneous fishing mortality (F_i), constant initial-tagging survival rate (ϕ), constant tag-reporting rate (λ) assuming that fishing takes place uniformly over the entire year with tagged-fish released assumed to be released half way through the calendar year of their release. In the incomplete mixing model it is not possible to estimate F_1 separately from F_1^*.

We have included two extensions to the Hoenig et al. (1998b) model. First, as the majority of tagging takes place in June and July, fish tagged and released in the first year are only subject to half of a year fishing and natural mortality. Second, tag-loss is considered in the model. We assume that survival after tagging and the tag reporting rate are constant over time. Also, our model assumes that fishing is equally spread over the year. This is not true for the halibut fishery, but Hoenig et al. (1998a) notes that estimates are relatively insensitive to this assumption.

The tag-retention parameter (θ_k^{2t}, the probability that a fish released with two tags will be recovered with *t* tags in the *k*th year after release) is computed assuming that tag retention rates are only a function of time since release and not of calendar year and that the probability of the tag loss of one tag is independent of the other tag. These are computed as following (again allowing for the first half year after release):

$$\theta_1^{22} = \left(\sqrt{R_1}\right)^2; \quad \theta_2^{22} = \left(\sqrt{R_1}\right)^2 R_2^2; \quad \theta_3^{22} = \left(\sqrt{R_1}\right)^2 R_2^2 R_3^2; \quad \ldots.$$

$$\theta_1^{21} = 2\left(\sqrt{R_1}\right)\left(1 - \sqrt{R_1}\right)$$

$$\theta_2^{21} = 2\left(\sqrt{R_1}\right)\left(1 - \sqrt{R_1}\right)R_2^1 + 2\left(\sqrt{R_1}\right)^2 R_2^1\left(1 - R_2^1\right)$$

$$\theta_3^{21} = 2\left(\sqrt{R_1}\right)\left(1 - \sqrt{R_1}\right)R_2^1 R_3^1 + 2\left(\sqrt{R_1}\right)^2 R_2^1\left(1 - R_2^1\right)R_3^1 + 2\left(\sqrt{R_1}\right)^2 R_2^2 R_3^1\left(1 - R_3^1\right)$$

The retention parameter R_i is the probability that a tag present at the start of the i^{th} year after release will be present at the end of the year. Notice that we have not accounted for the fact that fish are harvested throughout the year and so a fish harvested near the start of the calendar year has a higher probability of retaining tags than a fish harvested near the end of the calendar year. While the exact times of capture are available for most fish, these have not been used in this simple model as such refinements are not expected to change the result substantially. The complicated expressions for the probability of losing a single tag account for the loss of either tag on the fish and the potential timings of the loss. For example, a fish recaptured in the second year after release with a single tag could have lost the tag in the first year or the second year. These complicated expressions can be easily derived for the general case using matrices as shown in Cowen et al. (2009).

The plot of cumulative tag-loss over time (Fig. 1) indicates that most tag loss occurs in the first year after release. Consequently, models with 2 or 3 yearly retention parameters should be sufficient to account for the general shape of the cumulative tag-retention curve.

MODEL FITTING

Hoenig et al. (1998a) treated the possible outcomes from each release as a binomial distribution with the probabilities derived from the expected counts. Cormack and Jupp (1991) showed that equivalent inference can be obtained using a Poisson distribution and the observed recoveries, i.e. the likelihood function is constructed as:

$$L = \prod \frac{e^{-E_{ij}^{2t}} \left(E_{ij}^{2t}\right)^{Y_{ij}^{2t}}}{Y_{ij}^{2t}} \qquad (4)$$

where Y_{ij}^{2t} and E_{ij}^{2t} are the observed and expected number of fish released in year *i* with 2 tags and recovered in year *j* with *t* tags. Standard numerical techniques can be used to maximize the likelihood to obtain the maximum likelihood estimates and their standard errors.

Model assessment is performed in two ways. First the standardized residuals:

$$\varepsilon_{ij}^{2t} = \frac{Y_{ij}^{2t} - E_{ij}^{2t}}{\sqrt{E_{ij}^{2t}}} \qquad (5)$$

should have an approximate normal distribution and a plot of the standardized residuals versus the expected counts should show random scatter around the value of 0 with most standardized residuals between -2 and +2. Second, a measure of goodness of fit can be obtained as:

$$GOF = \frac{\left(Y_{ij}^{2t} - E_{ij}^{2t}\right)^2}{E_{ij}^{2t}} \qquad (6)$$

which should have an approximate chi-square distribution with degrees of freedom

$$df = \text{Number of Y values - 1 - Number of estimated parameters} \qquad (7)$$

As usual, the GOF statistic should be used with caution if some of the expected counts are small as this tends to inflate the GOF statistic. A measure of over-dispersion in the data can be estimated as:

$$\hat{c} = \frac{GOF}{df} \qquad (8)$$

and can be used to adjust the estimated standard errors (they need to be multiplied by $\sqrt{\hat{c}}$) to account for lack of fit in the data. Usually, an acceptable residual plot and values of $\hat{c}$ less than about 4 indicate acceptable fit.

Hoenig et al. (1998a) indicate that while estimation of the product of the initial tagging survival and reporting rate are theoretically possible, most tagging data sets are too sparse to estimate these quantities and so values for these parameters should be fixed based on outside studies. Twenty-three percent of 30 halibut captured by longline, ranging in size between 62 and 111 cm, died in a holding tank study designed to assess survivorship of undersized Atlantic Halibut exposed to typical fishing practices (Neilson et al. 1989). We used 0.8, 0.9, and 1.0 in our model fitting. Tag reporting is expected to be high because of the $100 cash reward and entry into the lottery supported by the AHC. Values of 0.9 and 1.0 were used in the model fitting.

A substantial number (n=469) of fish below the legal size limit (81 cm) were tagged and released. We analyzed a subset of the data (81+ cm) to exclude smaller fish that may have a lower probability of recapture (Table 2), possibly owing to size-selectivity of the fishery or may have a lower probability of immediate survival after tagging.

RESULTS

Between 2006 and 2008, 2072 halibut were tagged and released. The data on 11 fish could not be used because either the release or recapture data could not be resolved. Consequently, 2061 tagged halibut were used in this analysis. The number of tags released in each NAFO area was roughly proportional to abundance in that area, with slightly more tag releases relative to estimated abundance in 4V and less in 4O (Table 3). As of 26 August 2010, 409 of the halibut tagged between 2006 and 2008 were recaptured, reported and entered into the halibut tagging database (Table 4).

Halibut tagging occurred primarily during the halibut survey in May, June and July (Table 5a). Tagged halibut were recaptured in all months (Table 5b), with the majority of recaptures in the summer (June, July and August). At the time of release halibut ranged in size from 49 cm to 207 cm. The median length was 97 cm (n = 2015, Fig. 2a). The time at large for tagged halibut ranged from less than 1 day to more than 3 years (n = 409, Fig. 2b). There was sufficient release and return information to calculate the net distance traveled for 377 halibut (Fig. 2c). The median net distance traveled was 29 km.

TAG LOSS

Estimates of cumulative tag-loss (Table 6, Fig. 1) increase and plateau after about 1 year at large. The estimated tag loss rate for 100-200 days-at-large is the exception to this rule, but it is based on only a small number of recaptured fish.

The parameter estimates for the combination of initial tagging survival, reporting rate, and for all data or only fish >81 cm are presented in Table 7. Residual plots from the models did not show any evident pattern, although the plots for the models fit to data from fish of all sizes were slightly more negative (Appendix 1). The estimated over-dispersion factor ($\hat{c}$) was approximately 2 indicating an acceptable fit. The largest residuals occurred in two cells with no evident pattern.

The tag retention parameters (R_i) are estimated based on the ratio of the number of fish returned with 1 tag and with 2 tags. Consequently, these estimates are unaffected by assumptions about the initial tagging survival or reporting rate. For example, if fewer fish survived tagging, then the total number of recoveries would be smaller, but the ratio between fish with 1 and 2 tags would be the same. Similarly, if the tag-reporting rate changed, then again the numbers of fish would change, but the ratio in numbers would not. The estimated initial annual tagging retention rate of 83% (Table 7, Models fit with halibut of all sizes) is comparable to the estimated cumulative tag-loss rate of around 19% in fish at large 200-400 days reported in Table 6. A set of models with 3 tag-retention parameters was also fit, but produced essentially the same estimates as the 2 tag-retention parameter models and so the results from these models are not shown.

Only the product of initial tagging survival and tag reporting rate appears in the expected counts in Table 1. Consequently, models with an initial tagging survival of 0.9 and a tag-reporting rate of 1.0 give the same estimates (and fit) for the natural and fishing mortality parameters as a model with an initial tagging survival of 1.0 and a tag-reporting rate of 0.9 (Table 7).

If only the reporting rate is changed (e.g. increased from 0.9 to 1.0), estimates of *M* increase and estimates of *F* decrease. For the same set of data, reducing the reporting rate “increases” the “actual” number of tags captured (e.g. if the reporting rate was 0.9 and 10 tags were reported, the actual number of tags captured was 11 = 10 / 0.9, but if the reporting rate was 1.0 and 10 tags were reported, the actual number of tags captured was 10). If the real number of tags captured increases (all else being equal) this implies that *F* must increase and *M* must decrease.

If only the initial tagging survival rate is changed (e.g. increased from 0.8 to 0.9), estimates of *M* increase and *F* decrease. An increase in the initial tagging survival rate implies that more tagged fish are available for capture. Consequently, to get the same number of tags back, the fishing mortality must decline, and because total mortality is again based on the subsequent ratio of recoveries, the estimated natural mortality must increase.

Whether the reporting rate or tagging survival changes, the model estimates adjust so that the estimate of total instantaneous mortality ($Z_i = M + F_i$) is approximately constant. This is not unexpected – the Brownie model was initially formulated to estimate the annual total survival rates which depends only on the ratio of number of tags recovered in year $t+1$ to those recovered in year t (all else being equal).

When the data were subset to fish 81+ cm at the time of tagging, the number of released fish is smaller (about 77 % of all fish), and the number of subsequent recaptures is also reduced (82 % of recoveries in all fish) (compare Tables 4a and 4b). Estimates of fishing mortality are approximately unchanged because the reduction in the number of tags returned (in the 81+ cm fish) approximately matches the reduction in the number of fish released, however estimates of natural mortality increased.

DISCUSSION

In previous halibut stock assessments, fishing mortality for one year was estimated using a modification of the Petersen equation to allow for incomplete mixing in the first 2 months post release (Trzcinski et al. 2010). The Petersen F estimate increases as the mixing period increases from zero to 6 months post release, with largest difference during the first couple of months. Stobo et al. (1988) also observed higher reporting rates in the second year post release suggesting that the recapture probability of halibut is reduced in the first year of release. Here we use the Hoenig et al. 1998b incomplete mixing model to estimate F* for the first year post release, which is approximately 6 months because of the seasonal distribution of tag releases. The Hoenig et al. 1998a model that assumes complete mixing was also run, but the results are not reported here because the complete mixing model did not fit as well (Appendix 2).

The previous F estimates for the 2006 and 2007 releases, 0.17 and 0.20 respectively, approximate the F_{2007} and F_{2008} of the multiyear model. The F estimates from the multiyear incomplete mixing model with a similar set of assumptions (RR=0.9, ITS=0.8) and data inputs (fish 81+ cm) are similar (0.20 (SE=0.04) in 2007, 0.29 (SE=0.04) in 2008). However, the incomplete mixing model estimates instantaneous natural mortality of halibut 81 cm+ at 0.26 (SE=0.08), which is more than double the input for the Petersen equation. In all of the models, fishing mortality in 2009 is slightly lower than 2008. The TAC has increased by 150 t in the last three years, but there has also been recent recruitment to the fishery (Trzcinski et al. 2011). The increasing population trends indicate that the population is capable of rebuilding under this fishing pressure and the current production regime. Our multiyear model also provides an estimate of F for 2010, based on recaptures reported by the end of August, but it is difficult to assess what fraction of the exploitation that represents.

Natural mortality is typically difficult to estimate. Halibut are a long-lived species. The oldest halibut seen on the Scotian Shelf and southern Grand Banks is a 50 year old male (Armsworthy and Campana, 2010). For long-lived fish, instantaneous natural mortality is typically assumed to less than 0.2, and in the recent framework stock assessment for the Scotian Shelf and the southern Grand Banks instantaneous natural mortality was assumed to be 0.1. In an earlier tagging study of halibut in the same area, Stobo et al. (1988) report 17% of the recaptures more than 5 years post release and one tag was recaptured 18 years post release, suggesting that tag retention is also high. The high natural mortality estimated during the tagging study may indicate an elevated natural mortality during that period. Alternatively, the tagging analysis may overestimate natural mortality if there were permanent emigration of tagged halibut out of the study area or if the initial tagging survival or reporting rates were overestimated.

The Brownie et al. (1985) models were originally developed to estimate annual survival with no partitioning of mortality among various components. Consequently, it is not surprising that estimated total instantaneous mortality ($F_i + M$) remains relatively constant among the models considered, even though the portioning of mortality among natural and fishing sources may vary. Estimates of annual survival are robust to different assumptions of initial tagging mortality or reporting rate as well. However, estimates of natural and fishing mortality are sensitive to the assumptions made about initial tagging survival and reporting rate. As seen in Table 7, estimates of natural mortality vary considerably among the models fit with little ability to distinguish among these models (the AICc values are essentially all the same).

In this study, the $100 reward for each return and lottery entry should be a large enough incentive to return tags and keep the reporting rate high, 90 to 100%. In order to estimate the actual reporting rate, an additional class of tags with higher (or lower) reward values that are assumed to have a 100% reporting rate would be needed (e.g. $1,000 reward).

In theory, tagging experiments provide information about the product of initial tagging survival rate and the reporting rate if these are constant over time. However, Hoenig et al. (1998a) indicate that data requirements would be large to get estimates with any precision– indeed the AICc values in Table 7 indicate virtually the same model fit with all combinations examined in this study. Consequently, estimates of initial tagging survival need to be obtained from experiments outside the tagging study, e.g. cage study such as done by Neilson et al. (1989) designed to assess survivorship of undersized Atlantic Halibut exposed to typical fishing practices. Twenty-three percent of 30 halibut captured by longline, ranging in size between 62 and 111 cm, died in the holding tanks. Mean survival time was lower for smaller halibut (62 – 81 cm) than all halibut held. Similarly, for the otter trawl captured (29 – 96 cm), larger halibut had higher survival times. As our tagging protocol selects for individuals without serious injury and halibut of all sizes or 81+ cm at the time of release, 80% initial tagging survival should be considered a minimum estimate.

This analysis makes a number of assumptions: i) every fish has the same chance of being caught and its tag reported (homogeneity of catchability), ii) every fish has the same survival rate (homogeneity of survival), and iii) natural mortality is constant across ages and time. Natural mortality likely varies among fish with larger (older) fish having a lower natural mortality. Pollock and Raveling (1982) discuss the impacts of heterogeneity upon estimates in the Brownie et al. (1985) model. Heterogeneity in survival rates among animals results in relatively unbiased estimates of annual survival for the average survival rate. In this case, because of gear selectivity, this would be the average survival rate of animals subject to catch for tagging. However, heterogeneity in survival tends to result in overdispersion in the number of animals recovered, and the estimated standard error needs to be adjusted (using the over-dispersion factor). While estimates of annual survival will remain relatively unbiased, it is not clear what impact heterogeneity has on estimates of natural and fishing mortality given that heterogeneity in survival occurs in both natural mortality (size based) and fishing mortality (size and selectivity based).

Pollock and Raveling (1982) found that heterogeneity in catchability also results in relatively unbiased estimates of annual survival as long as heterogeneity in catchability was not related to heterogeneity in survival. In our case, this may not be true with larger fish having a lower natural mortality but higher fishing mortality. However, Pollock and Raveling (1982) also found that unless the tagging study was very large, the size of the biases will be modest relative to the standard errors of the estimates. Here, the uncertainty in the estimates associated with the values chosen for initial tagging survival and reporting rates may overwhelm these biases.

Heterogeneity may also be introduced by spatial variability. Tags were applied approximately proportional to abundance (across broad NAFO divisions) so that the proportion of tagged fish to the population abundance is approximately equal throughout the study area. Effort is also likely to be approximately distributed proportional to abundance, but this has not been assessed. In this study, natural mortality includes both actual mortality and permanent emigration. There is considerable evidence that halibut move substantial distances (McCracken 1958, Stobo et al. 1988, Trzcinski et al. 2010), but the majority of tagged fish were recaptured with 30 km of the release point, so permanent emigration is expected to be small.

The precision of the estimates of fishing and natural mortality are relatively poor (CV for M approximately 100%; CV for F *approximately* 50%). Estimates of mortality are strongly influenced by assumptions about initial tagging survival and tag reporting rates. Generally, precision can be improved by increasing the number of tags applied or increasing the recovery rate, although the latter would be difficult considering the high reporting rate of this study.

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Table 1. Expected number of recoveries given N_i fish tagged and released in year *i* and recovered in year *j* assuming a constant instantaneous natural mortality *M*, year-specific instantaneous fishing mortality F_i under complete mixing and F_i^* under incomplete mixing, constant immediate tagging survival ϕ, constant tag reporting rate λ and a probability that a fish released with 2 tags will have *t* tags retained (*t*=1, 2) in the k^{th} year after release (*k*=1, …) θ_k^{2t}. The extension to recovery years 4 and 5 follows the same pattern. Fishing is assumed to occur uniformly over the calendar year. Incomplete mixing of tags in the second half of the calendar year of release is allowed.

	Expected recoveries in year		
	1	**2**	**3**
1	$\frac{N_1\phi\lambda(0.5F_1^*)\theta_1^{2t}}{0.5F_1^*+0.5M}\left(1-e^{-0.5F_1^*-0.5M}\right)$	$\frac{N_1\phi\lambda F_2\theta_2^{2t}}{F_2+M}\left(1-e^{-F_2-M}\right)e^{-.5F_1^*-.5M}$	$\frac{N_1\phi\lambda F_3\theta_3^{2t}}{F_3+M}\left(1-e^{-F_3-M}\right)e^{-.5F_1^*-F_2-1.5M}$
2		$\frac{N_2\phi\lambda(0.5F_2^*)\theta_1^{2t}}{0.5F_2^*+0.5M}\left(1-e^{-0.5F_2^*-0.5M}\right)$	$\frac{N_2\phi\lambda F_3\theta_2^{2t}}{F_3+M}\left(1-e^{-F_3-M}\right)e^{-.5F_2^*-.5M}$
3			$\frac{N_3\phi\lambda(0.5F_3^*)\theta_1^{2t}}{0.5F_3^*+0.5M}\left(1-e^{-0.5F_3^*-0.5M}\right)$

Table 2. Proportion of tagged halibut recaptured within one year of release in 10 groups based on length at time of release (cm). The standard error (SE) for the proportion recaptured is also reported.

Length (cm)	Number Recaptured	Proportion Recaptured	SE
(51.8,67.4]	9	0.10	0.03
(67.4,82.9]	29	0.08	0.01
(82.9,98.4]	78	0.15	0.02
(98.4,114]	45	0.14	0.02
(114,130]	41	0.17	0.02
(130,145]	29	0.18	0.03
(145,161]	16	0.18	0.04
(161,176]	12	0.24	0.06
(176,192]	5	0.29	0.11
(192,207]	1	0.20	0.18

Table 3. The number of halibut tagged and released as part of the all-sizes tagging program by NAFO between 2006 and 2008 (n=2061).

NAFO	Proportion Allocated	2006	2007	2008	Total	Proportion of Total
3N	0.22	93	54	54	201	0.10
3O	0.13	32	57	58	147	0.07
3Ps	0.19	30	237	143	410	0.20
4V	0.19	103	264	185	552	0.27
4W	0.16	165	132	166	463	0.22
4X	0.12	103	84	101	288	0.14

Table 4a. Summary of recovery data. Each cell has two entries. The first entry is the number of fish with a single tag recovered; the second entry is the number of fish with both tags recovered. All fish released had two tags. Pooled over all lengths at release, all areas released, areas recovered, etc. Year classes are calendar years.

Year of Release	Number Released	Year of Recovery				
		2006	2007	2008	2009	2010
2006	526	1 / 15	13 / 25	9 / 17	7 / 12	4 / 4
2007	828		5 / 13	34 / 75	23 / 35	12 / 12
2008	707			3 / 18	12 / 43	11 / 6

Table 4b. Summary of recovery data. Each cell has two entries. The first entry is the number of fish with a single tag recovered; the second entry is the number of fish with both tags recovered. All fish released had two tags. Only fish released that are 81+ cm but pooled over all areas released, areas recovered, etc. Year classes are calendar years.

Year of Release	Number Released	Year of Recovery				
		2006	2007	2008	2009	2010
2006	420	1 / 14	12 / 23	7 / 14	4 / 8	3 / 2
2007	622		5 / 12	33 / 64	16 / 30	7 / 6
2008	550			2 / 14	10 / 34	10 / 6

Table 5a. The number of halibut tagged and released as part of the all-sizes tagging program by month between 2006 and 2008 (n=2061).

Month	Years			Total
	2006	2007	2008	
4	0	0	99	99
5	11	164	71	246
6	254	0	441	695
7	218	653	96	967
8	43	11	0	54

Table 5b. The number of halibut recaptured as part of the all-sizes tagging program by month between 2006 and 2008 (n=409).

Month	Year					Total
	2006	2007	2008	2009	2010	
1	0	5	13	17	6	41
2	0	4	14	11	17	46
3	0	6	6	15	7	34
4	0	1	5	4	7	17
5	0	2	6	16	0	24
6	1	5	35	25	8	74
7	1	10	35	21	3	70
8	3	9	16	11	1	40
9	5	4	11	5		25
10	3	5	2	2		12
11	2	3	8	2		15
12	1	2	5	3		11

Table 6. Estimated cumulative tag-loss.

Time at Large (Days)	Recovered Fish with Double Tags	Recovered Fish with a Single Tag	Estimated Cumulative Tag-Loss
(0,100]	36	3	0.04
(100,200]	16	11	0.26
(200,400]	99	46	0.19
(400,600]	46	30	0.25
(600,800]	42	29	0.26
(800,1200]	30	21	0.26
(1200,2000]	5	4	0.29

Table 7. Summary of parameter estimates using the incomplete-mixing model under several scenarios for the initial tagging survival (ITS) and tag reporting rate (RR) and two subsets of fish released. First entry in estimates of F represents F* (instantaneous fishing mortality during the first 6 months after release) and the second entry represents F for complete mixing.

		Parameter Estimates[1]							
		F^*_{2006}	F^*_{2007}	F^*_{2008}	F^*_{2009}	F^*_{2010}			
Model	M	F_{2006}	F_{2007}	F_{2008}	F_{2009}	F_{2010}	R_1[6]	R_2	AICc[4]
M(dot), F(t), F*(t), R(2),		0.092	0.061	0.092	NA[3]	NA[3]			
ITS=0.8, RR=0.9 ALL fish	0.184	NA[2]	0.149	0.218	0.174	0.092[5]	0.83	0.91	-1739.4
M(dot), F(t), F*(t), R(2),		0.086	0.055	0.083	NA	NA			
ITS=0.8, RR=1.0 ALL fish	0.203	NA	0.134	0.198	0.157	0.084	0.83	0.91	-1739.5
M(dot), F(t), F*(t), R(2),		0.085	0.055	0.082	NA	NA			
ITS=0.9, RR=0.9 ALL fish	0.205	NA	0.132	0.196	0.156	0.083	0.83	0.91	-1739.6
M(dot), F(t), F*(t), R(2),		0.076	0.050	0.073	NA	NA			
ITS=0.9, RR=1.0 ALL fish	0.222	NA	0.119	0.178	0.141	0.076	0.83	0.91	-1739.6
M(dot), F(t), F*(t), R(2),		0.076	0.050	0.073	NA	NA			
ITS=1.0, RR=0.9 ALL fish	0.222	NA	0.119	0.178	0.141	0.076	0.83	0.91	-1739.6
M(dot), F(t), F*(t), R(2),		0.069	0.045	0.066	NA	NA			
ITS=1.0, RR=1.0 ALL fish	0.237	NA	0.107	0.161	0.127	0.069	0.83	0.91	-1739.6
M(dot), F(t), F*(t), R(2),		0.117	0.078	0.092	NA[3]	NA[3]			-1322.8
ITS=0.8, RR=0.9 81+ cm	0.264	NA[2]	0.195	0.289	0.211	0.112[5]	0.81	0.91	
M(dot), F(t), F*(t), R(2),		0.105	0.071	0.083	NA	NA			
ITS=0.8, RR=1.0 81+ cm	0.289	NA	0.175	0.263	0.193	0.103	0.81	0.91	-1323.0
M(dot), F(t), F*(t), R(2),		0.104	0.070	0.082	NA	NA			
ITS=0.9, RR=0.9 81+ cm	0.292	NA	0.173	0.261	0.190	0.102	0.81	0.91	-1323.0
M(dot), F(t), F*(t), R(2),		0.093	0.064	0.074	NA	NA			
ITS=0.9, RR=1.0 81+ cm	0.314	NA	0.156	0.237	0.173	0.094	0.81	0.91	-1323.2
M(dot), F(t), F*(t), R(2),		0.093	0.064	0.074	NA	NA			
ITS=1.0, RR=0.9 81+ cm	0.314	NA	0.156	0.237	0.173	0.094	0.81	0.91	-1323.2
M(dot), F(t), F*(t), R(2),		0.083	0.058	0.067	NA	NA			
ITS=1.0, RR=1.0 81+ cm	0.335	NA	0.141	0.216	0.157	0.086	0.81	0.91	-1323.4

[1] Standard errors were computed, but are not reported here and are approximately (after adjusting for $\hat{c}$) 0.10 for M; 0.04 for F_i; 0.06 for R_i.

[2] No estimate is available for the instantaneous fishing mortality in year 1 for complete mixing (see text)

[3] No estimates are available for the initial instantaneous fishing mortality for incomplete mixing for these years because releases terminated in 2006

[4] Because subset of data was used for the analysis of fish in the 81+ cm size category, AICc should not be compared between these two analyses.

[5] F_{2010} is based on tags recovered up to the end of August and so does not represent a full fishing year.

[6] R_1 is the annual tag retention rate in the first year of release on an annual basis. It is prorated for the first ½ year after release in the model.

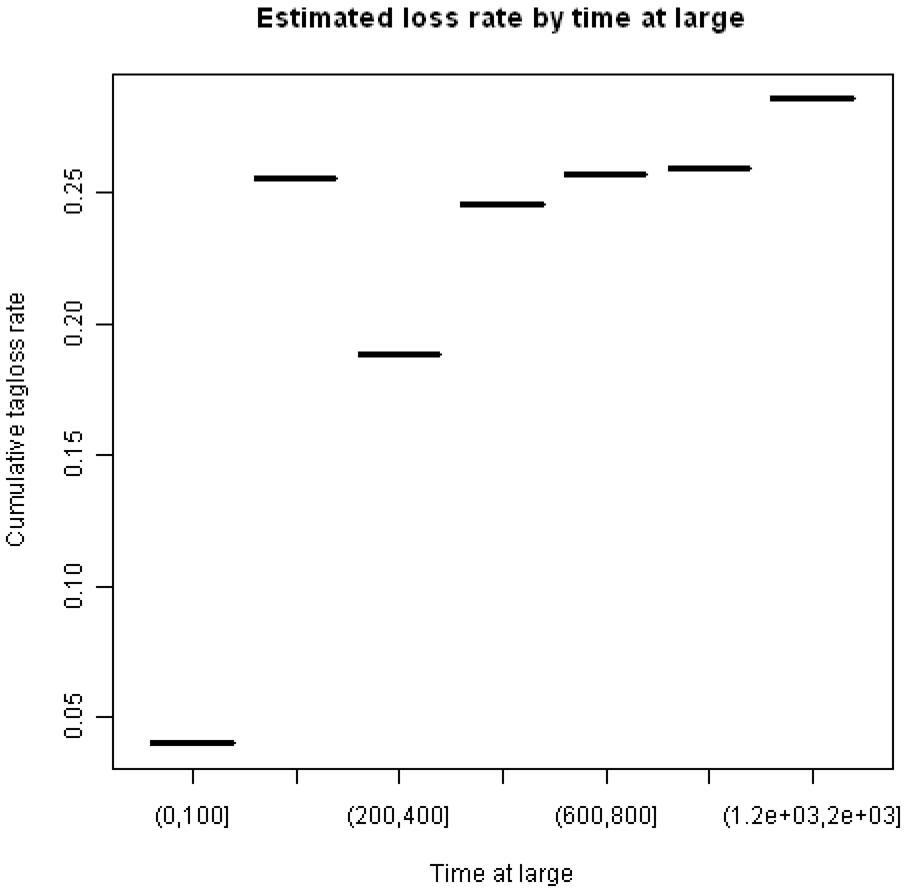


Figure 1. Estimated cumulative tag-loss by time-at-large.

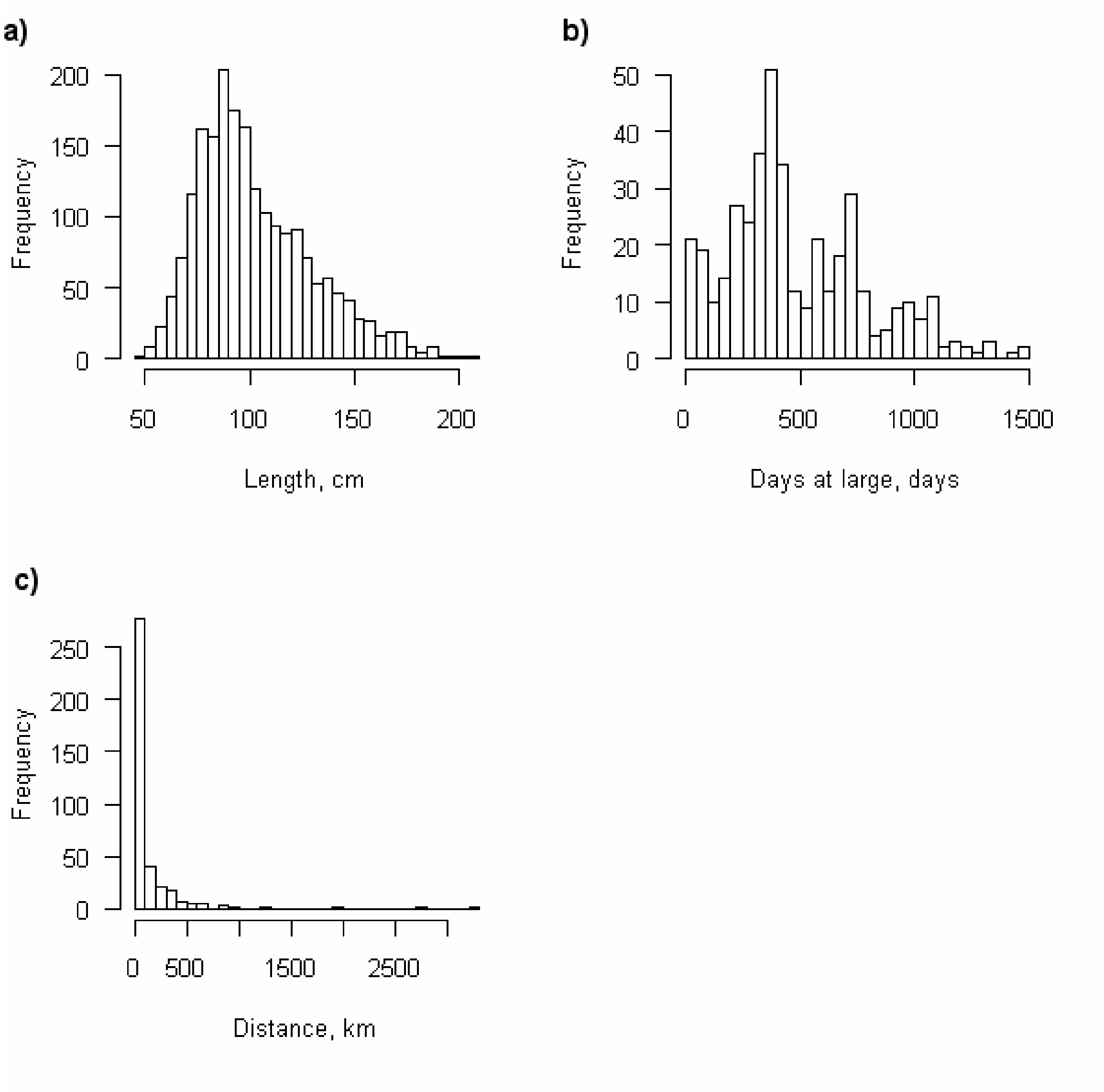
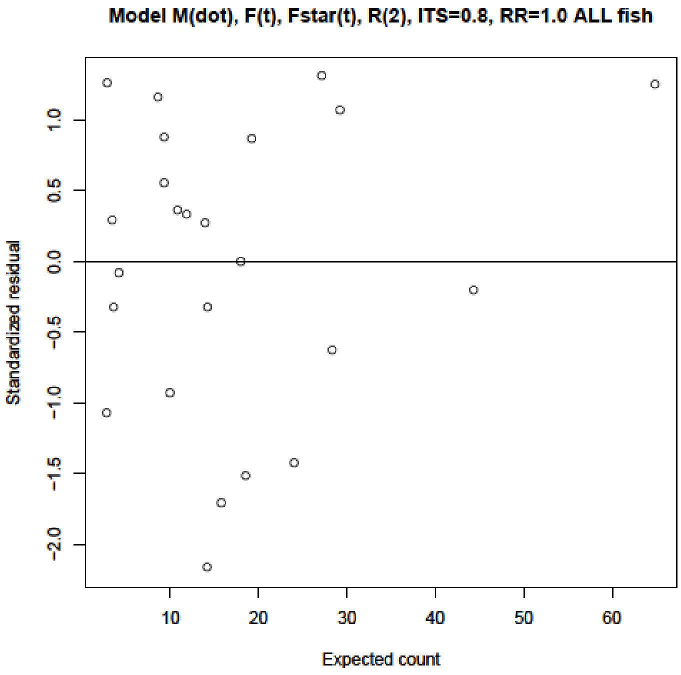
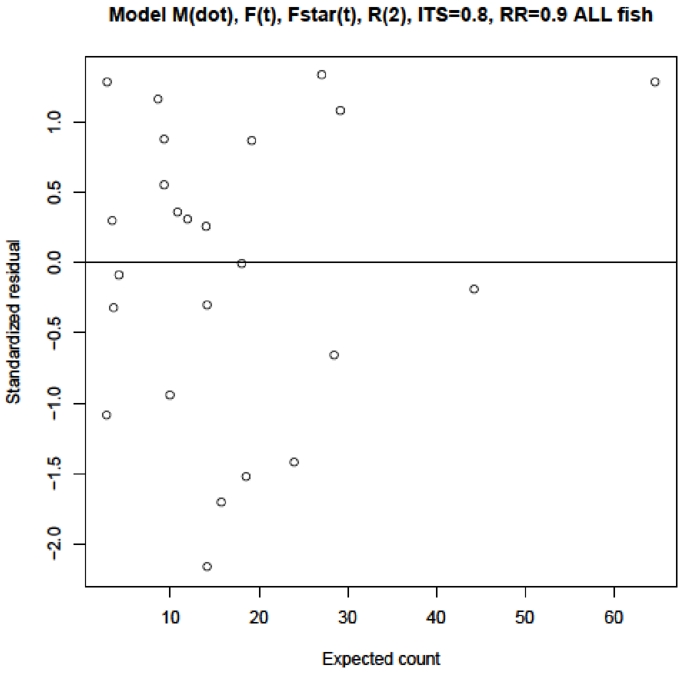
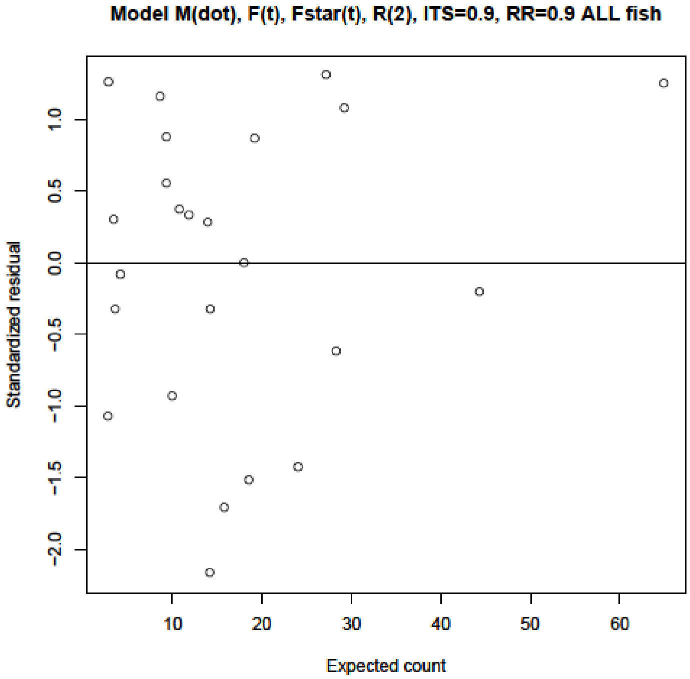


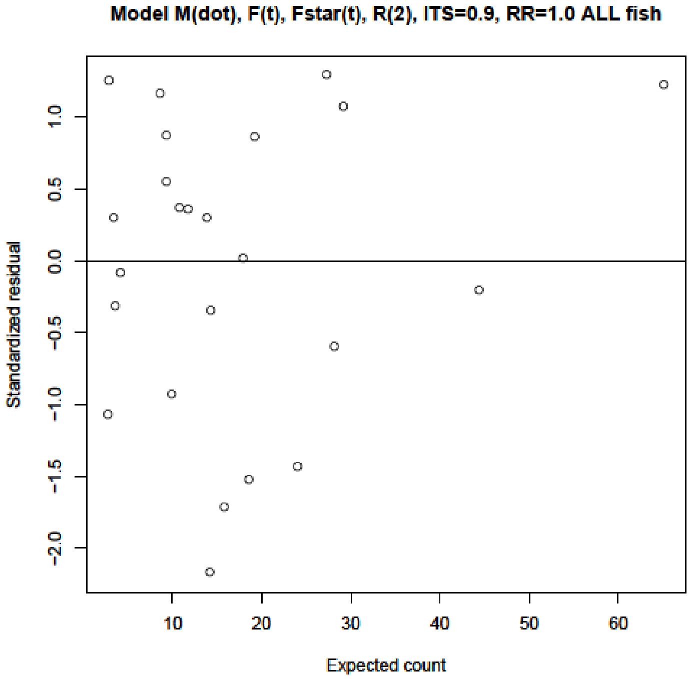
Figure 2. Histograms of a) halibut length at time of release, b) days at large between release and recapture and c) the net distance traveled between release and recapture.

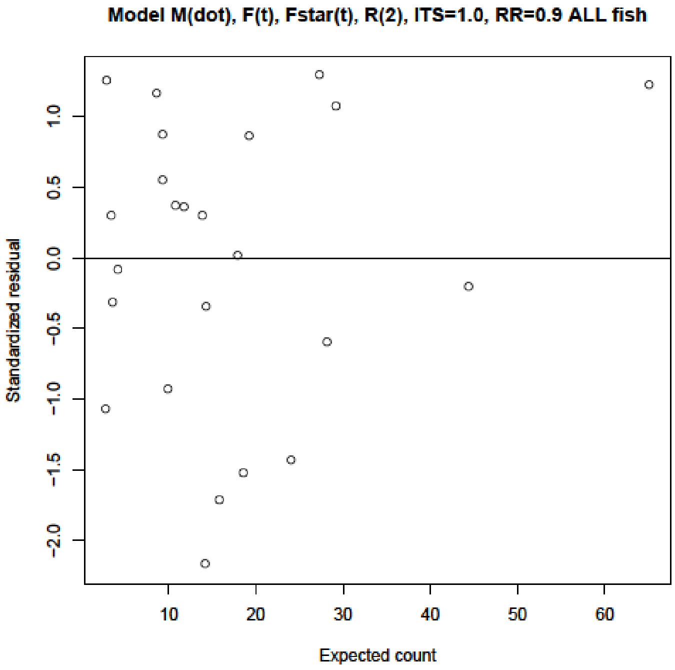
Appendix 1. Residual plots of incomplete mixing models.

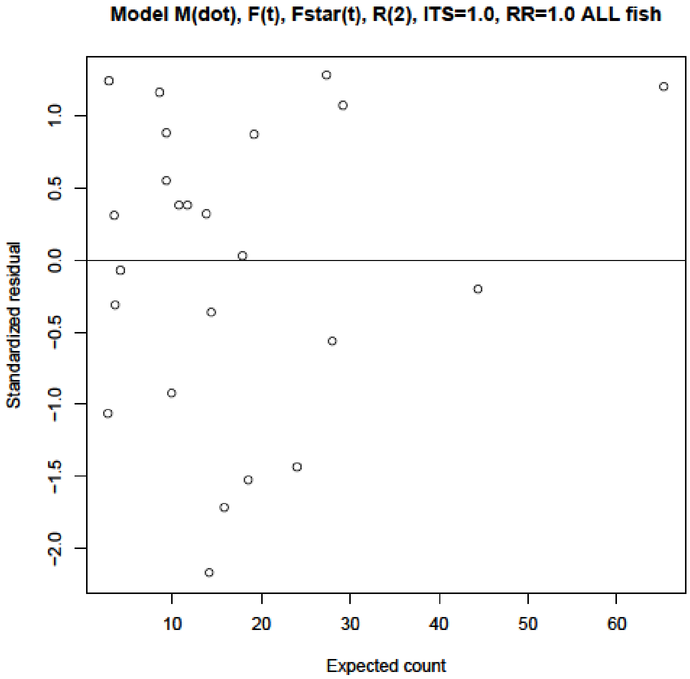


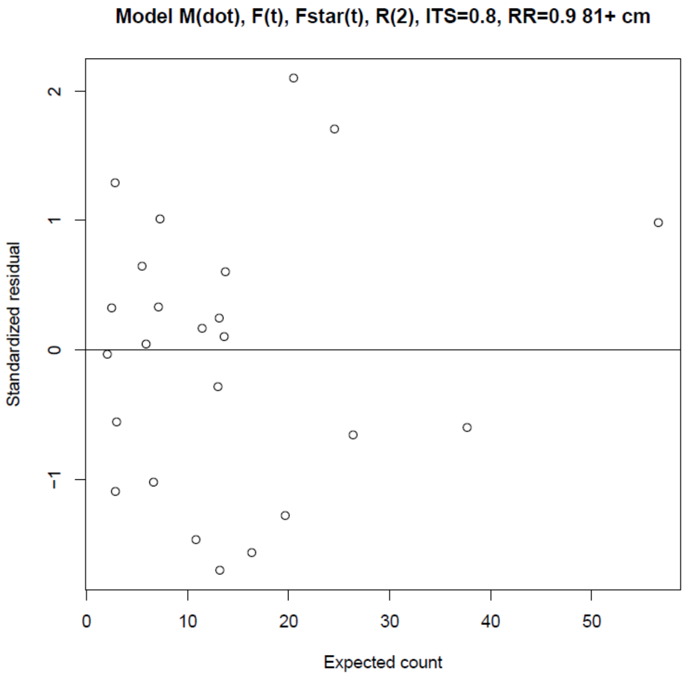



Model M(dot), F(t), Fstar(t), R(2), ITS=0.9, RR=0.9 ALL fish
Standardized residual
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
10
20
30
40
50
60
Expected count

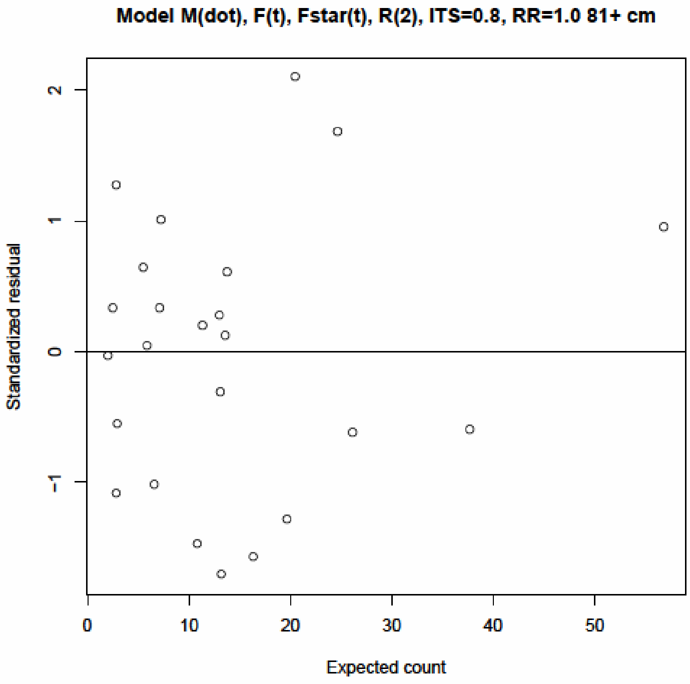

Model M(dot), F(t), Fstar(t), R(2), ITS=0.9, RR=1.0 ALL fish
Standardized residual
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
10
20
30
40
50
60
Expected count


Model M(dot), F(t), Fstar(t), R(2), ITS=1.0, RR=0.9 ALL fish
Standardized residual
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
10
20
30
40
50
60
Expected count

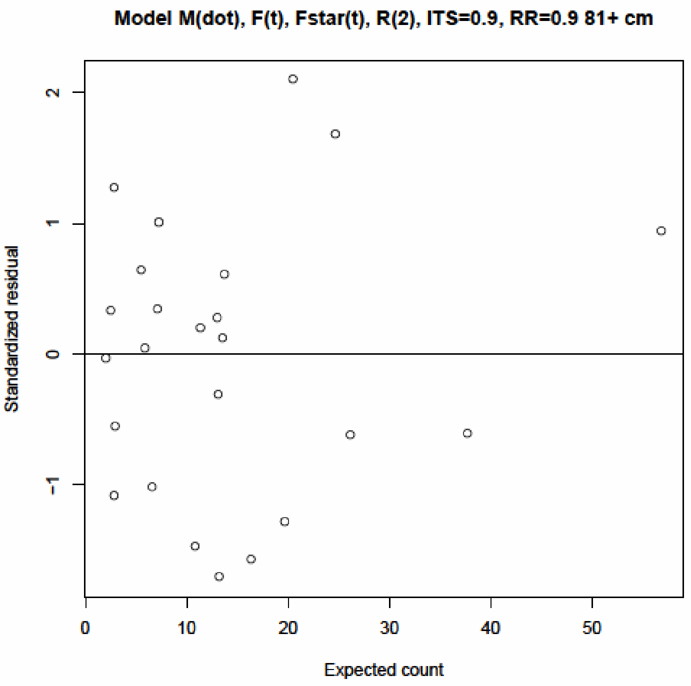

Model M(dot), F(t), Fstar(t), R(2), ITS=1.0, RR=1.0 ALL fish
Standardized residual
1.0
0.5
0.0
−0.5
−1.0
−1.5
−2.0
10
20
30
40
50
60
Expected count

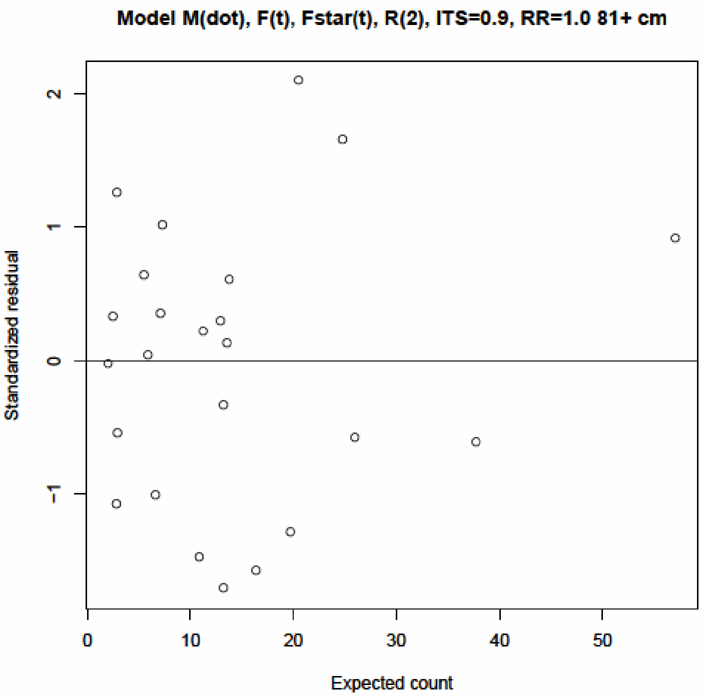


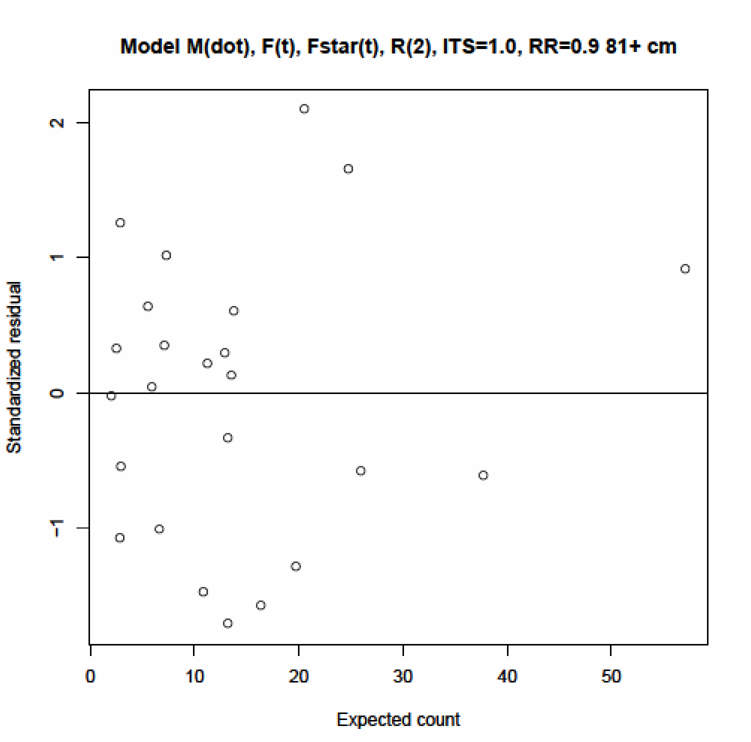
Model M(dot), F(t), Fstar(t), R(2), ITS=0.8, RR=0.9 81+ cm

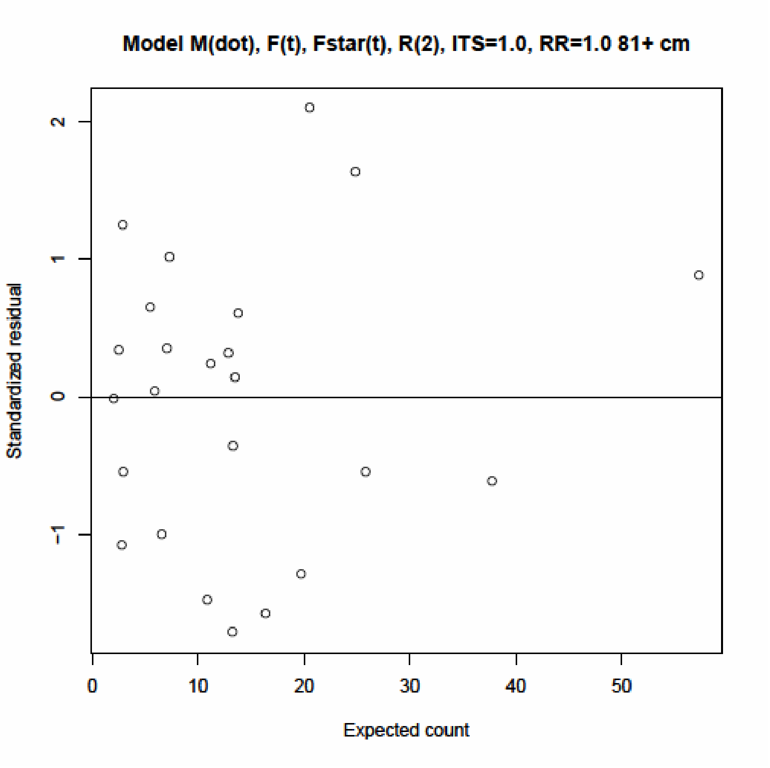


Model M(dot), F(t), Fstar(t), R(2), ITS=0.8, RR=1.0 81+ cm


Model M(dot), F(t), Fstar(t), R(2), ITS=0.9, RR=0.9 81+ cm
Standardized residual
2
1
0
−1
0
10
20
30
40
50
Expected count


Model M(dot), F(t), Fstar(t), R(2), ITS=0.9, RR=1.0 81+ cm
Standardized residual
2
1
0
−1
0
10
20
30
40
50
Expected count


Model M(dot), F(t), Fstar(t), R(2), ITS=1.0, RR=0.9 81+ cm
Standardized residual
2
1
0
−1
0
10
20
30
40
50
Expected count


Model M(dot), F(t), Fstar(t), R(2), ITS=1.0, RR=1.0 81+ cm
Standardized residual
2
1
0
−1
0
10
20
30
40
50
Expected count

Appendix 2. Example residual plot from complete mixing model.