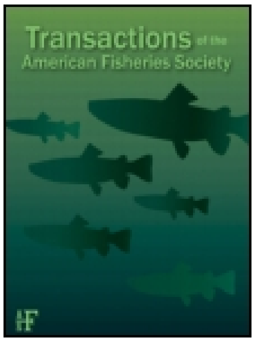

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ARTICLE

# Fishing and Natural Mortality Rates of Atlantic Halibut Estimated from Multiyear Tagging and Life History

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***Abstract***

**Fishing mortality and natural mortality rates for Atlantic Halibut *Hippoglossus hippoglossus* on the Scotian Shelf and southern Grand Banks were estimated from a multiyear tagging study. Models that were used to estimate mortality rates incorporated tag loss. Between 2006 and 2008, 1,913 Atlantic Halibut were double-tagged with t-bar anchor tags; as of 26 August 2010, 368 of these fish had been recaptured. We estimated instantaneous fishing mortality (*F*) separately for each cohort in the first year (on average, 6 months) after release to allow newly tagged animals to mix with the population. A two-parameter model was used to describe tag loss. Tag loss was estimated at 13% per year in the first year and 10% per year in the second and subsequent years. Using the multiyear model with incomplete mixing and assuming 90% tag reporting and 80% survival from tagging, average instantaneous natural mortality (*M*) of Atlantic Halibut was estimated to be 0.22 and *F* was estimated to be 0.15 in 2007, 0.24 in 2008, and 0.18 in 2009. These estimates of *F* were comparable to those from the stock assessment population model. However, the estimates of *M* were higher than inferred estimates of *M* based on life history and growth. Estimates of *F* and *M* were sensitive to the minimum size of Atlantic Halibut at the time of release. An increase in *F* with size is consistent with fishery size selectivity resulting from either gear selectivity or the distribution of fishing effort where there is spatial heterogeneity in the size composition. We suggest that *M* may have been overestimated because of emigration from the study area.**

The impact of a fishery on an exploited population is typically measured as the fishing mortality rate. Regulatory agencies often attempt to manage a fishery by setting a target fishing mortality and limiting catch by using assessment models based on total fishery catches and stock size survey indices, models based on information from tagging and telemetry studies, or some combination of these two approaches (Brownie et al. 1985; Hoenig et al. 1998a, 1998b; Fu et al. 2001; Maunder 2001). Other direct methods of estimating fishing mortality and natural mortality include depletion methods (Leslie and Davis 1939; DeLury 1947) and cohort tracking (Gulland 1965; Murphy 1965; Smith and Botsford 1998). Beverton and Holt life history invariants (Charnov 1993; Jensen 1996; Lester et al. 2004) and the growth model developed by Pauly (1980) provide indirect estimates of natural mortality (reviewed by Hewitt et al. 2007 and Brodziak et al. 2011) that are used when there are not enough

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data to estimate natural mortality directly. These estimates are often incorporated into stock assessment models that assume a constant natural mortality. Recently, methods have been developed to use additional information to separate natural mortality and fishing mortality in stock assessment models (Fournier et al. 1998; Hampton and Fournier 2001), integrate tagging estimates of natural mortality into stock assessment models (Maunder 1998, 2001; Hampton and Fournier 2001), improve estimates of natural mortality by using food web models (Gaichas et al. 2010), and allow for time-varying estimates of natural mortality (Fu et al. 2001; Chouinard et al. 2005; Mohn and Rowe 2012).

The Atlantic Halibut *Hippoglossus hippoglossus* is a large, long-lived, sexually dimorphic flatfish that is typically found in the northwest Atlantic at depths between 200 and 450 m along the continental shelf and channel slopes. Atlantic Halibut have been heavily exploited in eastern Canadian waters for more than a century. Prior to 1840, Atlantic Halibut were abundant and were considered a nuisance bycatch, but over the span of 40 years Atlantic Halibut became a marketable product and underwent a series of localized depletions, resulting in commercial extinction before the turn of the century (Grasso 2008). Atlantic Halibut are just one of many groundfish species to suffer a dramatic decline in the northwest Atlantic. As a result of intense and prolonged fishing effort, northwest Atlantic ecosystems today are very different from those of the sixteenth century, when Europeans began exploiting whales, cod, and other groundfish species (Heymans 2003; Lotze and Milewski 2004; Rosenberg et al. 2005).

The Atlantic Halibut fishery has been managed by a total allowable catch (TAC) since 1988, and in 1994 a minimum legal size limit of 81 cm was fully implemented. The current stock assessment of Scotian Shelf and southern Grand Banks Atlantic Halibut is based on trends in abundance indices and size composition from Department of Fisheries and Oceans Canada's (DFO) research vessel groundfish surveys, DFO–industry longline surveys, and landings data (Trzcinski et al. 2011). The assessment uses a catch-at-length model assuming natural mortality of 0.1 and shows a peak in fishing mortality in the early 1990s. After reductions in the TAC in the mid-1990s, fishing mortality has varied around 0.2, and spawning stock biomass has increased steadily. In recent years, it appears that a recruitment pulse has contributed to the increased productivity of this stock (Trzcinski et al. 2011).

Here, we use data from the Atlantic Halibut All-Sizes Tagging (HAST) Program (den Heyer et al. 2012) to estimate fishing mortality and natural mortality between 2006 and 2009. The HAST Program is an example of a band-recovery experiment (e.g., Brownie et al. 1985). Although the Brownie et al. (1985) models are commonly applied to bird studies, Hoenig et al. (1998a) demonstrated how to re-parameterize those models in terms of parameters that are commonly used in fisheries management (i.e., instantaneous survival and fishing mortality). Following an approach similar to that of Hoenig et al. (1998a, 1998b), we estimated natural mortality and fishing mortality while assuming incomplete mixing of tags and tag loss. We also compare the estimates of natural mortality from the tagging study with indirect estimates of natural mortality based on life history and growth parameters, and we compare the estimates of fishing mortality with estimates from the assessment model.

## METHODS

### Direct Estimates of Fishing Mortality and Natural Mortality Rates from Tagging

*Tagging*.—Most of the Atlantic Halibut in this study were caught and tagged during the halibut survey, which is conducted every year in May–June and follows a fixed-station design using longlines with Mustad number-14 circle hooks set for 6–12 h (Trzcinski et al. 2011). Fishermen were compensated for releasing fish of legal size ($\geq$81 cm) by the Atlantic Halibut Council (AHC), a consortium representing the fishing industry and collaborators on this research project. The tagging effort was allocated to North Atlantic Fisheries Organization (NAFO) divisions (Figure 1) in proportion to abundance estimated from catch rates in the halibut survey between 1999 (when the survey was fully established) and 2005. The survey catch rates were expanded to estimate abundance in a management unit by using a Delaunay triangulation spatial estimator (den Heyer et al. 2012). The allocation of tags (Table 1) was weighted by the area

TABLE 1. Number of Atlantic Halibut that were tagged and released in each North Atlantic Fisheries Organization (NAFO) division between 2006 and 2008 ($n$ = 1,913) as part of the All-Sizes Tagging Program.

| NAFO division | Proportion allocated | Release year | | | Total number released | Proportion of total |
|---|---|---|---|---|---|---|
| | | 2006 | 2007 | 2008 | | |
| 3N | 0.22 | 93 | 54 | 54 | 201 | 0.11 |
| 3O | 0.13 | 32 | 57 | 58 | 147 | 0.08 |
| 3Ps | 0.19 | 30 | 237 | 143 | 410 | 0.25 |
| 4V | 0.19 | 103 | 116 | 185 | 404 | 0.21 |
| 4W | 0.16 | 165 | 132 | 166 | 463 | 0.24 |
| 4X | 0.12 | 103 | 84 | 101 | 288 | 0.15 |

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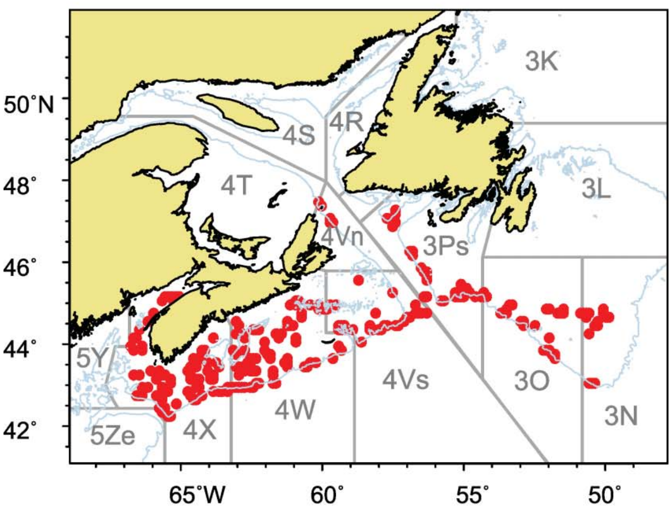
a) Releases



b) Returns

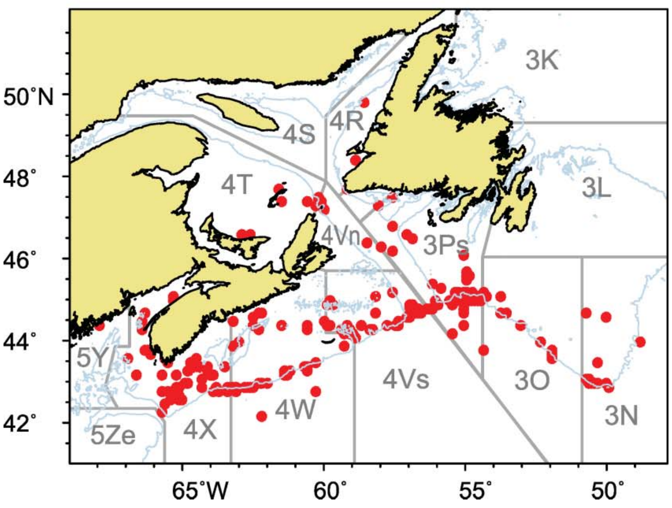


FIGURE 1. Plot of **(a)** release locations of Atlantic Halibut tagged in North Atlantic Fisheries Organization (NAFO) divisions 4VWX and 3NOPs and **(b)** reports of recapture. The locations of Atlantic Halibut recaptured off Iceland ($n = 2$) and Greenland ($n = 1$) are not shown. Gray lines and text indicate the NAFO areas. Light-blue lines represent the 200-m bathymetric contour. [Figure available online in color.]

TABLE 2. List of symbols used in this paper.

| Symbol | Description |
|---|---|
| $M$ | Instantaneous natural mortality |
| $F_i$ | Instantaneous fishing mortality |
| $F_i^*$ | Instantaneous fishing mortality during the first 6 months after release |
| $\%\text{Tags}_i$ | Proportion of tags for each North Atlantic Fisheries Organization (NAFO) division $i$ |
| $\text{Area}_i$ | Area of NAFO division $i$ |
| $\text{CPUE}_i$ | Catch per unit effort for each NAFO division $i$ |
| $\phi$ | Initial tagging survival |
| $\lambda$ | Tag reporting rate |
| $\theta_i^{2t}$ | Probability that a fish released with two tags will be recovered with $t$ tags in the $i$th year after release |
| $R_i$ | Probability that a tag present at the start of the $i$th year after release will be present at the end of the year |
| $\theta$ | Cumulative tag retention |
| $dt$ | Number of fish with two tags |
| $st$ | Number of fish with single tags |
| $L$ | Likelihood function |
| $Y_{ij}^{2t}$ | Observed number of fish released in year $i$ with two tags and recovered in year $j$ with $t$ tags |
| $E_{ij}^{2t}$ | Expected number of fish released in year $i$ with two tags and recovered in year $j$ with $t$ tags |
| $\text{AIC}_c$ | Akaike's information criterion corrected for small sample size |
| $GOF$ | Goodness of fit |
| $\hat{c}$ | Over-dispersion factor |
| $t_{max}$ | Maximum age |
| $t_m$ | Age at sexual maturity |
| $L_\infty$ | Asymptotic maximum length |
| $K$ | Von Bertalanffy growth coefficient |
| $T$ | Temperature, °C |

(km$^2$) of each NAFO division during the halibut survey ($i$):

$$\%\text{Tags} = \frac{\text{Area}_i \cdot \text{CPUE}_i}{\sum_i \text{Area}_i \cdot \text{CPUE}_i}. \quad (1)$$

See Table 2 for definitions of the above symbols and other symbols used throughout the paper. If not enough Atlantic Halibut were caught and tagged in a particular NAFO division, additional fish were tagged during the halibut commercial index sets or during commercial fishing. The commercial index sets are commercial sets that occur during the halibut survey from which detailed data on the Atlantic Halibut catch are collected.

Atlantic 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 (den Heyer et al. 2012). Tagged Atlantic Halibut were returned to the water immediately; only Atlantic Halibut that were believed to have a high probability of survival were tagged. Observers recorded release information, including date, location, tag numbers, TL, and morphology codes that described fish health and hooking injuries. It was not possible to assess the sex of Atlantic Halibut at the time of release. The release data were entered into the DFO–industry surveys database.

*Tag reporting*.—Fishermen were asked to report the tag number(s), date of recapture, location of recapture, length, and sex

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of tagged Atlantic Halibut that were caught during commercial fisheries or industry surveys. The AHC provided a \$100 reward for each fish reported with either one or two tags, and the participant's name was entered into a quarterly lottery for \$1,000. The tags indicated the \$100 reward, and 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 given tag envelopes to encourage collection of information on recapture location, date, and fish morphology. When the information provided was insufficient, fishermen were contacted for clarification of reports. For each tagged Atlantic Halibut that was reported, the participant was sent a thank-you letter, which included a map of the tagging and recapture locations and a description of net movement. A summary of the tagging program was presented to the AHC annually.

*Data management*.—The Atlantic Halibut tagging database was queried on 26 August 2010, and all records for fish released during 2006–2008 were extracted. Atlantic Halibut that were re-released ($n = 4$) were not included in this analysis. A small number of fish that were released with a single tag ($n = 2$) or with archival pop-up tags ($n = 12$) was also excluded.

*Estimating cumulative tag loss*.—Cumulative tag loss as a function of time at large was estimated by using the methods of Seber and Felton (1981). Time at large was divided into intervals (1–100, 101–200, 201–400, 401–600, 601–800, 801–1,200, and 1,201–2,000 d), and the number of fish recovered with one or two tags for each interval was tallied. The tag retention parameters ($R_i$) were estimated based on the ratio of the number of fish recovered with one tag to the number of fish recovered with two tags. Consequently, these estimates were unaffected by assumptions about initial tagging survival ($\phi$), tag reporting rate ($\lambda$), or probability of recapture. For example, if fewer fish survived tagging, then the total number of recoveries would be smaller, but the ratio of fish with one tag to fish with two tags would be the same. Similarly, if tag reporting or catchability changed, then the numbers of fish would change, but the ratio in the numbers would not. Cumulative tag retention ($\theta$) was estimated following Seber and Felton (1981) as

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

where $dt$ is the number of fish with double tags and $st$ is the number of fish with a single tag (i.e., fish that lost one tag). The cumulative tag loss is the complement of this value. The SE was estimated by using the delta method.

*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. We chose this model over a model that assumed complete mixing because the incomplete mixing model fit the data better. Following the methods of Hoenig et al. (1998b), the expected number of fish released and recaptured can be expressed as shown in Table 3. Notably, in the incomplete mixing model, it is not possible to estimate instantaneous fishing mortality in year 1 ($F_1$) separately from fishing mortality in the first 6 months after release ($F_1^*$). The multiyear tagging analysis assumes that (1) every fish has the same chance of being caught and thus having its tag reported (homogeneity of catchability), (2) every fish has the same survival rate (homogeneity of survival), and (3) natural mortality is constant across ages and time. The expected number of recoveries is estimated by assuming a constant instantaneous natural mortality ($M$), $F$ for a cohort in the year of release ($F_i^*$), and year-specific $F$ ($F_i$). The $\phi$ and $\lambda$ also are assumed to be constant. We assumed that fishing takes place uniformly over the entire year and that tagged fish are released halfway through the calendar year. This is not true for the Atlantic Halibut fishery, but Hoenig et al. (1998a) showed that estimates are relatively insensitive to this assumption.

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 that are tagged and released in the first year are only subject to half a year of fishing mortality and natural mortality. Second, tag loss is considered in the model. The tag retention parameter ($\theta_i^{2t}$; the probability that a fish released with two tags will be recovered with $t$ tags in the $i$th year after release) is computed by assuming that (1) tag retention rates are only

TABLE 3. Expected number of Atlantic Halibut recoveries given $N_i$ fish tagged and released in year $i$ and recovered in year $j$, assuming constant instantaneous natural mortality ($M$), year-specific instantaneous fishing mortality ($F$) under complete mixing ($F_i$) and under incomplete mixing ($F_i^*$), constant initial tagging survival ($\phi$), constant tag reporting rate ($\lambda$), and the probability $\theta_k^{2t}$ that a fish released with two tags will have $t$ tags retained ($t = 1, 2$) in the $k$th year after release ($k = 1, \ldots$). 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.

| $i$ | Expected recoveries, $j = 1$ | Expected recoveries, $j = 2$ | Expected recoveries, $j = 3$ |
|---|---|---|---|
| 1 | $\frac{N_1\phi\lambda(0.5F_1^*)\theta_1^{2t}}{0.5F_1^*+0.5M}[1-e^{(-0.5F_1^*-0.5M)}]$ | $\frac{N_1\phi\lambda F_2\theta_2^{2t}}{F_2+M}[1-e^{(-F_2-M)}]e^{(-0.5F_1^*-0.5M)}$ | $\frac{N_1\phi\lambda F_3\theta_3^{2t}}{F_3+M}[1-e^{(-F_3-M)}]e^{(-0.5F_1^*-F_2-1.5M)}$ |
| 2 |  | $\frac{N_2\phi\lambda(0.5F_2^*)\theta_1^{2t}}{0.5F_2^*+0.5M}[1-e^{(-0.5F_2^*-0.5M)}]$ | $\frac{N_2\phi\lambda F_3\theta_2^{2t}}{F_3+M}[1-e^{(-F_3-M)}]e^{(-0.5F_2^*-0.5M)}$ |
| 3 |  |  | $\frac{N_3\phi\lambda(0.5F_3^*)\theta_1^{2t}}{0.5F_3^*+0.5M}[1-e^{(-0.5F_3^*-0.5M)}]$ |

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a function of time since release and not of calendar year and (2) the probability of loss for one tag is independent of the probability of loss for the other tag. Further, we assume that the reporting rate for single- and double-tagged fish is the same, as the reward is given for a recaptured fish and not per tag. The tag retention parameters are computed as follows (again allowing for the first half-year after release):

$$
\begin{aligned}
&\theta_1^{22} = \left(\sqrt{R_1}\right)^2 ;\ \theta_2^{22} = \left(\sqrt{R_1}\right)^2 R_2^2 ;\\
&\theta_3^{22} = \left(\sqrt{R_1}\right)^2 R_2^2 R_3^2 ;\ \ldots .\\
&\theta_1^{21} = 2\left(\sqrt{R_1}\right)\left(1-\sqrt{R_1}\right) ;\\
&\theta_2^{21} = 2\left(\sqrt{R_1}\right)\left(1-\sqrt{R_1}\right) R_2^1 + 2\left(\sqrt{R_1}\right)^2 R_2^1\left(1-R_2^1\right) ;\\
&\theta_3^{21} = 2\left(\sqrt{R_1}\right)\left(1-\sqrt{R_1}\right) R_2^1 R_3^1 + 2\left(\sqrt{R_1}\right)^2 R_2^1\left(1-R_2^1\right)\\
&\qquad \times R_3^1 + 2\left(\sqrt{R_1}\right)^2 R_2^2 R_3^1\left(1-R_3^1\right) ;\ \ldots .
\end{aligned}
\tag{3}
$$

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. 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 its tags than a fish harvested near the end of the calendar year. The plot of cumulative tag loss over time (Figure 2) indicates that most of the tag loss occurs in the first year after release. We have also implicitly assumed that tag loss is uniform through the year such that tag retention in the first 6 months is a simple function of yearly tag retention. However, Cadigan and Brattey (2003) showed that the Kirkwood (1981) model may be more appropriate for Atlantic Cod *Gadus morhua*. Our data show a high initial rate of tag loss followed by a decline in the rate over time; consequently, our method will tend to underestimate the true tag loss in the first 6 months, but given the aggregated nature of our data the effect is expected to be small. Further, models with two or three yearly tag retention parameters (e.g., a model with separate parameters for tag retention rates in year 1, year 2, and year 3+ after release) should be sufficient to account for the general shape of the cumulative tag retention curve when the data are aggregated to and modeled on a yearly basis. The expressions for the probability of losing a tag account for the loss of either tag (anterior or posterior tag) on the fish and the potential timings of the loss. For example, a fish that is recaptured with a single tag in the second year after release could have lost the other tag in the first year or in the second year. These expressions can be easily derived for the general case using matrices as shown by Cowen et al. (2009). Although the data from the last column of Table 4 suggest that the tag retention rates may vary among release groups, the counts in 2010 were small and the variation in rates among release cohorts may be an artifact of sampling variation. Furthermore, the data are too sparse to allow estimation of a year effect in the tag loss rate. We did not use the exact times at liberty (e.g., as in Xiao

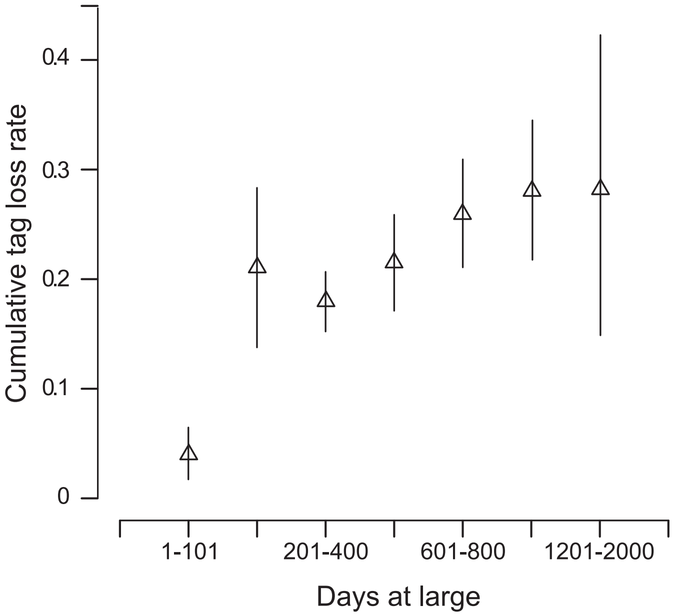

FIGURE 2. Estimated cumulative tag loss rates (triangles; ±SE) calculated for Atlantic Halibut in each time interval at large (1–100, 101–200, 201–400, 401–600, 601–800, 801–1,200, and 1,201–2,000 d).

TABLE 4. Summary of Atlantic Halibut recovery data (each released fish had two tags): the number of fish recovered with a single tag (*st*) and the number of fish recovered with both tags (double-tagged, *dt*). Data are pooled over all lengths at release, all areas of release, all areas of recovery, etc. Year-classes are calendar years.

| | | Year of recovery | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2006 | | 2007 | | 2008 | | 2009 | | 2010 | |
| Year of release | Number released | *st* | *dt* | *st* | *dt* | *st* | *dt* | *st* | *dt* | *st* | *dt* |
| 2006 | 526 | 1 | 15 | 13 | 25 | 9 | 17 | 7 | 12 | 4 | 4 |
| 2007 | 828 | | | 2 | 11 | 27 | 69 | 16 | 27 | 9 | 7 |
| 2008 | 707 | | | | | 3 | 18 | 12 | 43 | 11 | 6 |

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1996) because of the difficulties in integrating an individual-based model for tag retention with the pooled model for release and recapture.

*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 (Table 3). Cormack and Jupp (1991) showed that equivalent inference can be obtained by using a Poisson distribution and the observed recoveries, with the likelihood function constructed as

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

where $Y_{ij}^{2t}$ and $E_{ij}^{2t}$ are the observed and expected numbers of fish that are released in year $i$ with two tags and recovered in year $j$ with $t$ tags. Standard numerical techniques can be used to maximize the likelihood to obtain parameter estimates. The SEs were obtained from the inverse of the Hessian matrix, which was numerically determined after the likelihood was maximized.

Model evaluation was performed in two ways. First, we examined the standardized residuals:

$$\varepsilon_{ij}^{2t} = \frac{Y_{ij}^{2t} - E_{ij}^{2t}}{\sqrt{E_{ij}^{2t}}}. \tag{5}$$

These should have an approximate normal distribution. A plot of the standardized residuals versus the expected counts should not show any trends, and most of the standardized residuals should be between −2 and +2. Second, we calculated a measure of the goodness of fit (*GOF*) as follows:

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

which should have an approximate chi-square distribution with df calculated as

$$\text{df} = (\text{number of } Y\text{-values}) - (\text{number of estimated parameters}), \tag{7}$$

where the $Y$-values are as defined earlier and the parameters to be estimated are shown in Table 3.

The *GOF* statistic should be used with caution when some of the expected counts are small (i.e., this study), as small values tend to inflate the *GOF* statistic. A measure of over-dispersion in the data can be estimated as

$$\hat{c} = \frac{GOF}{\text{df}}, \tag{8}$$

and can be used to adjust the estimated SEs (they need to be multiplied by $\sqrt{\hat{c}}$) to account for a lack of fit in the data. Usually, an acceptable residual plot and values of $\hat{c}$ less than about 4 indicate an acceptable fit (Lebreton et al. 1992).

Hoenig et al. (1998a) showed that although estimation of the product of $\phi$ and $\lambda$ is theoretically possible, most tagging data sets are too sparse to permit estimation of these quantities. These parameters should be fixed based on independent data, such as those from holding tank studies. For example, Neilson et al. (1989) performed a holding tank study to assess survivorship of Atlantic Halibut exposed to typical fishing practices, and Peltonen (1969) conducted a study in which Pacific Halibut *Hippoglossus stenolepis* were held captive for an assessment of tagging mortality. The former study identified a mortality rate of 23%, while the latter study reported 3.8% mortality over a 14-d period under reasonably good conditions for captivity. Based on the results of these studies, we used a range of values (0.7, 0.8, 0.9, and 1.0) for $\phi$ in our model fitting. Although our protocol involved longline sets of 6–12 h, we selected for individuals that did not exhibit serious injury at the time of release, so we consider a $\phi$ of 80% to be a reasonable estimate. We also present models with $\lambda$ values of 0.9 and 1.0. In this study, the fishing industry is a partner, and the $100 reward and lottery entry for each return should be sufficient incentive to produce a high $\lambda$. Several studies use a $100 reward as the high-value reward with an assumed $\lambda$ of 100% as a benchmark for the reporting of other tags (e.g., Cadigan and Brattey 2006; Bacheler et al. 2009; Cowen et al. 2009). However, even with a $\lambda$ of 100%, almost 10% of the reports were received without sufficient information on recovery date and could not be included in the model (den Heyer et al. 2012); thus, we prefer 0.9 as the estimate of $\lambda$.

The influence of fish length at the time of release on estimates of $F$ and $M$ was investigated by refitting the model 50 times. With each iteration, the data set was truncated by increasing the minimum length at release by 2 cm.

## Indirect Estimates of Natural Mortality

Life history and growth parameters for male and female Atlantic Halibut (Sigourney et al. 2006; Armsworthy and Campana 2010) in the northwest Atlantic were used to estimate $M$ by using indirect methods, such as the Beverton and Holt invariants (Charnov 1993; Jensen 1996) and the growth model of Pauly (1980). These estimates are based on statistical relationships across species, and the life history invariants have been shown to correspond to fundamental ecological relationships among life history parameters (Jensen 1996).

Adult female Atlantic Halibut are larger than males. The maximum reported length of a female in the northwest Atlantic is 232 cm (Armsworthy and Campana 2010) and the maximum reported length of a male is 189 cm (Bowering 1986). In a recent bomb radiocarbon-validated aging study using 2,400 thin-sectioned sagittal otoliths collected from Atlantic Halibut on the Scotian Shelf and southern Grand Banks, the maximum age was 38 years for females and 50 years for males (Armsworthy and Campana 2010). Armsworthy and Campana (2010) also modeled growth rates of males and females from the Scotian Shelf

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and southern Grand Banks. Juvenile males and females grow at the same rate, with the growth rate of males beginning to slow at about 70 cm (~5 years) and the growth rate of females slowing at about 100 cm (~7 years). This corresponds with the age at sexual maturity, estimated as 5.8 years for males and 7.0 years for females in New England (Sigourney et al. 2006). Armsworthy and Campana (2010) concluded that there is no evidence for a change in the growth rate of Atlantic Halibut in the last 40 years, and they discussed the impacts of gear size selectivity and sampling location on the estimates of the growth curve. Here, we use the growth parameter estimates (asymptotic maximum length [$L_\infty$] for males = 134.2 cm; $L_\infty$ for females = 205.1 cm; von Bertalanffy growth coefficient [$K$] for males = 0.18; $K$ for females = 0.10) from the model of all data (all gears and all locations) to calculate the indirect estimates of $M$.

## RESULTS

### Direct Estimates of Fishing Mortality and Natural Mortality from Tagging

Between 2006 and 2008, 2,072 Atlantic Halibut were tagged and released. Data for 159 fish could not be used because either the release data or the recapture data could not be resolved. Consequently, 1,913 tagged Atlantic Halibut were used in this analysis. The number of tags released in each NAFO division was roughly proportional to abundance in that area, with slightly more tags released relative to estimated abundance in Division 4V and fewer tags released relative to abundance in Division 3O (Table 1; Figure 1a). As of 26 August 2010, 368 of these Atlantic Halibut had been reported and the recapture information was entered into the tagging database (Table 4; Figure 1b).

Atlantic Halibut tagging occurred primarily during the halibut survey in May, June, and July (Table 5). Tagged Atlantic Halibut were recaptured in all months (Table 6), with the majority of recaptures obtained in the summer (June, July, and August). At the time of release, Atlantic Halibut ranged in TL from 49 to 207 cm. Fish smaller than 81 cm were not immediately susceptible to the fishery and may have had a lower probability of recapture. As Atlantic Halibut at these sizes grow at a rate of roughly 10 cm per year (Armsworthy and Campana 2010), the undersized Atlantic Halibut would have become susceptible to the fishery within a year or two. The mean length of Atlantic Halibut that were released in NAFO Division 3NOPs (mean TL = 115.3 cm; $n$ = 758) was larger than the mean length of fish released in NAFO Division 4VWX (mean TL = 95.5 cm; $n$ = 1,154; Figure 3); in both areas, the mean length declined during the survey (Table 7). The depth of the sets from which Atlantic Halibut were tagged and released ranged from 51 to 832 m.

Time at large for tagged Atlantic Halibut ranged from less than 1 d to more than 3 years. The net distance traveled ranged from 0 to 3,141 km ($n$ = 339), with a median of 27 km. As of August 2012, only 8 of 485 reports were from foreign fleets; of the 231 recaptures with gear type reported, 90 (82%) were caught by longline, 26 (11%) were caught by otter trawl, and 15 (6%) were captured by gill net.

*Tag loss.*—Except for the estimated tag loss rate for 100–200 d at large, which was based on few recaptured fish, estimates of cumulative tag loss rate (Figure 2) increased over time but plateaued after about 1 year at large. The parameter estimates for the combination of $\phi$ and $\lambda$ are presented in Table 8. Residual plots from the models did not show any evident pattern. The estimated over-dispersion factor ($\hat{c}$) was less than 2, indicating an acceptable fit.

TABLE 5. Number of Atlantic Halibut that were tagged and released during each month from 2006 to 2008 ($n$ = 1,913).

| Month | Release year | | | Total number released |
|---|---|---|---|---|
| | 2006 | 2007 | 2008 | |
| 4 | 0 | 0 | 99 | 99 |
| 5 | 11 | 164 | 71 | 246 |
| 6 | 254 | 0 | 441 | 695 |
| 7 | 218 | 505 | 96 | 819 |
| 8 | 43 | 11 | 0 | 54 |

TABLE 6. Number of Atlantic Halibut (tagged as part of the Halibut All-Sizes Tagging Program) that were recaptured during each month from 2006 to 2010 ($n$ = 368). Blank spaces indicate that no data were available.

| Month | Recovery year | | | | | Total number recovered |
|---|---|---|---|---|---|---|
| | 2006 | 2007 | 2008 | 2009 | 2010 | |
| 1 | | 5 | 13 | 12 | 4 | 34 |
| 2 | | 4 | 12 | 11 | 14 | 41 |
| 3 | | 6 | 4 | 13 | 4 | 27 |
| 4 | | 1 | 5 | 4 | 7 | 17 |
| 5 | | 2 | 4 | 14 | 0 | 20 |
| 6 | 1 | 5 | 35 | 24 | 8 | 73 |
| 7 | 1 | 10 | 34 | 18 | 3 | 66 |
| 8 | 3 | 8 | 16 | 11 | 1 | 39 |
| 9 | 5 | 4 | 9 | 5 | | 23 |
| 10 | 3 | 5 | 2 | 2 | | 12 |
| 11 | 2 | 1 | 6 | 1 | | 10 |
| 12 | 1 | 0 | 3 | 2 | | 6 |

TABLE 7. Mean TL (cm) of Atlantic Halibut at the time of release in North Atlantic Fisheries Organization (NAFO) divisions 3NOPs and 4VWX during each year.

| Release year | NAFO 3NOPs | NAFO 4VWX |
|---|---|---|
| 2006 | 120.9 | 96.7 |
| 2007 | 115.6 | 95.0 |
| 2008 | 111.6 | 94.9 |

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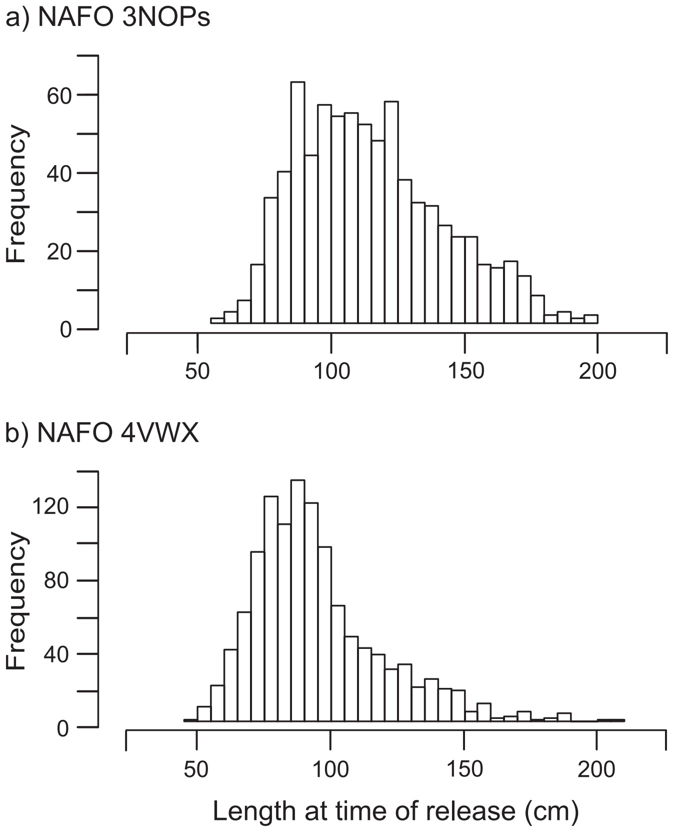

FIGURE 3. Length frequency histograms describing Atlantic Halibut TL at the time of release in **(a)** North Atlantic Fisheries Organization (NAFO) Division 3NOPs ($n = 758$) and **(b)** NAFO Division 4VWX ($n = 1{,}154$).

The estimated initial annual tag retention rate of 87% (Table 8) is comparable to the estimated cumulative tag loss rate of around 17% in fish that were at large for 200–400 d, as reported in Figure 2. A set of models with three tag retention parameters was also fitted, but they produced essentially the same estimates as the models with two tag retention parameters. Thus, the results from models with three tag retention parameters are not shown.

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 ($F_i + M$) remained relatively constant among the models considered (Table 8), even though the portioning of mortality into natural and fishing sources varied. Estimates of annual survival are robust to different assumptions of $\phi$ or $\lambda$ as well, but the partitioning between $M$ and $F$ is sensitive to the assumptions made about $\phi$ and $\lambda$. As seen in Table 8, estimates of $M$ varied considerably among the models, and there was little ability to distinguish among models based on Akaike's information criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002), as the AIC$_c$ values were all essentially the same. Sampling correlations between $M$ and the time-varying $F$-estimates ranged from moderate (around 0.3) for the fishing parameters for the early years to large (around 0.9) for the later years. Sampling correlation with $F$ during the first 6 months after release ($F^*$) was typically small. This is not surprising because larger estimates of $M$ require larger estimates of $F$ in later years to yield the same number of recoveries from smaller numbers of surviving fish.

Using the multiyear model with incomplete mixing and assuming a $\lambda$ of 90% and a $\phi$ of 80%, the average $M$ for Atlantic Halibut was estimated to be 0.22 (SE = 0.08) and the $F$ was

TABLE 8. Summary of parameter estimates from the incomplete mixing model assuming constant natural mortality ($M$) and time-varying fishing mortality ($F$, $F^*$) of Atlantic Halibut and a two-parameter model of tag loss ($R_1$, $R_2$) under several scenarios for initial tagging survival ($\phi$) and tag reporting rate ($\lambda$). Differences in AIC$_c$ values ($\Delta$AIC$_c$) between the best-fitting model (the model with the minimum AIC$_c$ value of −1,494.9) and the remaining alternatives are reported. Annual tag retention rate in the first year of release ($R_1$) was prorated for the first half-year after release and was estimated to be 0.87 (SE = 0.04); $R_2$ was estimated to be 0.90 (SE = 02). Standard errors were computed but are not reported here; after adjusting for $\hat{c}$, SEs were approximately 0.08 for $M$ and 0.03 for $F_i$. See Table 2 for further definition of symbols.

| | | 2006 | | 2007 | | 2008 | | 2009 | | 2010 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model | $M$ | $F^*$ | $F$[a] | $F^*$ | $F$ | $F^*$ | $F$ | $F^*$[b] | $F$ | $F^*$[b] | $F$[c] | $\Delta$AIC$_c$ |
| $\phi = 0.7, \lambda = 0.9$ | 0.188 | 0.110 | NA | 0.061 | 0.172 | 0.105 | 0.266 | NA | 0.197 | NA | 0.101 | 0.5 |
| $\phi = 0.7, \lambda = 1.0$ | 0.210 | 0.098 | NA | 0.055 | 0.155 | 0.094 | 0.242 | NA | 0.179 | NA | 0.093 | 0.4 |
| $\phi = 0.8, \lambda = 0.9$ | 0.216 | 0.096 | NA | 0.054 | 0.151 | 0.092 | 0.236 | NA | 0.175 | NA | 0.091 | 0.3 |
| $\phi = 0.8, \lambda = 1.0$ | 0.235 | 0.086 | NA | 0.079 | 0.136 | 0.082 | 0.214 | NA | 0.158 | NA | 0.083 | 0.2 |
| $\phi = 0.9, \lambda = 0.9$ | 0.237 | 0.085 | NA | 0.048 | 0.135 | 0.081 | 0.212 | NA | 0.156 | NA | 0.082 | 0.2 |
| $\phi = 0.9, \lambda = 1.0$ | 0.255 | 0.076 | NA | 0.044 | 0.121 | 0.073 | 0.192 | NA | 0.142 | NA | 0.075 | 0.1 |
| $\phi = 1.0, \lambda = 0.9$ | 0.255 | 0.076 | NA | 0.044 | 0.121 | 0.073 | 0.192 | NA | 0.142 | NA | 0.075 | 0.1 |
| $\phi = 1.0, \lambda = 1.0$ | 0.271 | 0.068 | NA | 0.040 | 0.109 | 0.066 | 0.174 | NA | 0.128 | NA | 0.068 | 0.0 |

[a] An estimate of $F$ in year 1 for complete mixing is not available (see text).

[b] Estimates of initial $F$ for incomplete mixing in this year are not available because releases terminated in 2008.

[c] $F$ in 2010 is based on tags recovered up to the end of August and so does not represent a full fishing year.

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estimated to be 0.15 (SE = 0.03) in 2007, 0.24 (SE = 0.03) in 2008, and 0.18 (SE = 0.03) in 2009. Only the product of ϕ and λ appears in the expected counts for Table 3. Consequently, models with a ϕ of 0.9 and a λ of 1.0 give the same estimates (and fit) for the *M* and *F* parameters as a model with a ϕ of 1.0 and a λ of 0.9 (Table 8). If only λ is changed (e.g., increased from 0.9 to 1.0), estimates of *M* increase and estimates of *F* decrease. For the same data set, reducing the λ "increases" the "actual" number of tags captured (e.g., if λ was 0.9 and 10 tags were reported, then the actual number of tags captured was 11 = 10/0.9, but if λ was 1.0, then the number of tags reported equals the actual number of tags captured). If the real number of tags captured increases (all else being equal), this implies that *F* must increase and *M* must decrease. If only ϕ is changed (e.g., increased from 0.8 to 0.9), then estimates of *M* increase and estimates of *F* decrease. An increase in ϕ implies that more tagged fish are available for capture. Consequently, to get the same number of tags back, the *F* must decline, and because total mortality is again based on the subsequent ratio of recoveries, the estimated *M* must increase.

To examine how the minimum length at the time of release affects our estimates of *M* and *F*, the minimum length included in the data set was increased from 50 cm to 200 cm in 2-cm increments. As the minimum length increased, the numbers of fish released and recaptured were both reduced in the data set and the estimates of *F* and *M* increased (Figure 4).

### Indirect Estimates of Mortality

Indirect estimates of *M* ranged from 0.02 to 0.34 for male Atlantic Halibut and from 0.09 to 0.29 for females (Table 9). Brodziak et al. (2011) suggested using a measure of central tendency for estimates of *M* when there is no strong argument for any one estimate. Average estimated *M*-values of 0.19 for males and 0.16 for females were obtained from the constants derived from life history theory for the first two methods (equations 2 and 4 in Table 9); the Pauly method at 5°C, which is the predominant temperature from pop-up satellite tags (Shelley Armsworthy, DFO, personal communication); and the other three methods (equations 6, 7, and 10 in Table 9).

## DISCUSSION

We present the first direct estimates of *F* and *M* of Atlantic Halibut on the Scotian Shelf and southern Grand Banks using a multiyear tagging analysis that allows for incomplete mixing of tagged fish in the first 6 months. As in earlier tagging studies of Atlantic Halibut in this area (Stobo et al. 1988), we observed a greater number of tags reported in the second year postrelease than in the first year postrelease. There are several explanations for this result. It is possible that Atlantic Halibut behavior changes immediately after tagging such that the fish are less likely to be caught. For a number of large pelagic fish, a third or more of individuals tagged with pop-up satellite archival tags exhibited irregular behavior for a few days or months postrelease (Hoolihan et al. 2011). Such irregular behavior could be associated with a reduction in foraging and reduced catchability. Another possibility is that within a fishing season, fishing effort is more mobile than the fish such that the effort is not in the immediate vicinity of the newly tagged Atlantic Halibut. Further, our analysis directly estimated tag loss from double-tagged fish. Unaccounted-for tag loss can lead to underestimation of *F* (Seber and Felton 1981). The combination of high tag retention, double tagging, and low total mortality allows for multiyear tagging analysis.

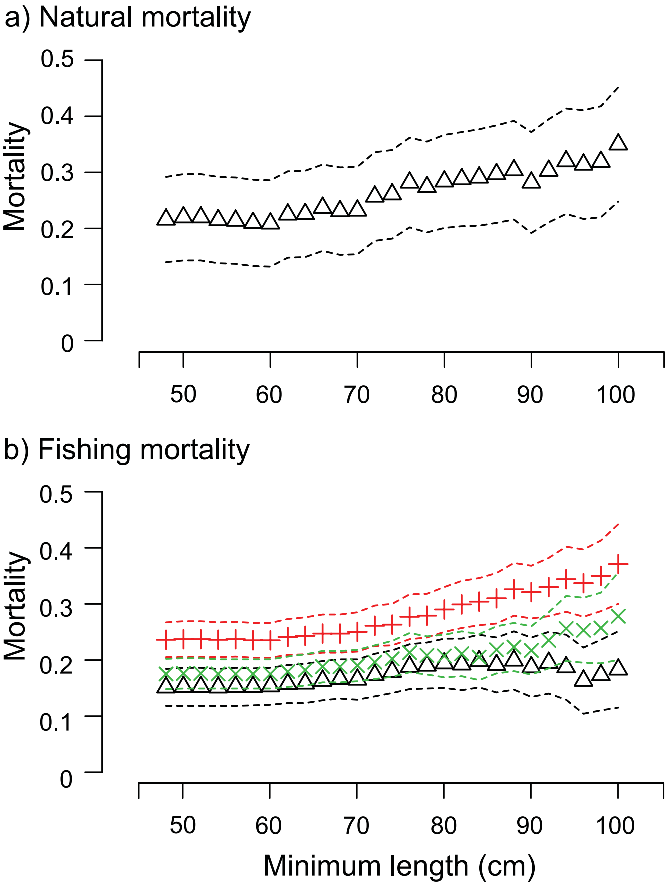

FIGURE 4. Plots of (**a**) natural mortality (black triangles; dashed line = SE) and (**b**) fishing mortality (black triangles = 2007; green ×-symbols = 2008; red plus-symbols = 2009; dashed lines = SEs) from the incomplete mixing model in relation to data sets with increasing minimum TL at release. [Figure available online in color.]

Pollock and Raveling (1982) discussed the impacts of heterogeneity in catchability and survival on estimates from the Brownie et al. (1985) model. Those authors suggested that estimates of survival can be biased downward in certain cases of heterogeneity in catchability but that such heterogeneity results in relatively unbiased estimates of annual survival as long as the heterogeneity in catchability is not related to heterogeneity in survival. Heterogeneity in survival rates among animals results in relatively unbiased estimates of annual average survival rate but tends to cause over-dispersion in the number of animals recovered, and therefore the estimated SE should be

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TABLE 9. Indirect estimates of Atlantic Halibut natural mortality ($M$) from life history invariants and growth relationships ($t_m = 5.8$ years for males, 7.0 years for females; $t_{max} = 50$ years for males, 38 years for females; $L_\infty = 134.2$ cm for males, 205.1 cm for females; $K = 0.18$ for males, 0.10 for females). See Table 2 for further definition of symbols.

| Equation number | Equation, constants | Source | $M$ | |
|---|---|---|---|---|
| | | | Males | Females |
| 1 | $C1 = M \cdot t_m$, where $C1 = 1.54$ (for flatfish) | Beverton 1963 | 0.27 | 0.21 |
| 2 | $C1 = M \cdot t_m$, where $C1 = 1.65$ | Jensen 1996 | 0.28 | 0.23 |
| 3 | $C1 = M \cdot t_m$, where $C1 = 2$ | Charnov and Berrigan 1990 | 0.34 | 0.27 |
| 4 | $C2 = M \cdot K^{-1}$, where $C2 = 1.5$ | Jensen 1996 | 0.27 | 0.15 |
| 5 | $C2 = M \cdot K^{-1}$, where $C2 = 1.6$ | Pauly 1980 | 0.29 | 0.16 |
| 6 | $M = 3 \cdot K \cdot [e^{(0.38 \cdot K \cdot t_{max})} - 1]^{-1}$ | Alverson and Carney 1975 | 0.02 | 0.09 |
| 7 | $M = e^{[1.44 - 0.982 \cdot \log_e(t_{max})]}$ | Hoenig 1983 | 0.09 | 0.12 |
| 8 | $\log(M) = -0.0066 - 0.279 \cdot \log(L_\infty) + 0.6543 \cdot \log(K) + 0.4634 \cdot \log(T)$, where $T = 5°\text{C}$ | Pauly 1980 | 0.17 | 0.10 |
| 9 | $\log(M) = -0.0066 - 0.279 \cdot \log(L_\infty) + 0.6543 \cdot \log(K) + 0.4634 \cdot \log(T)$, where $T = 10°\text{C}$ | Pauly 1980 | 0.24 | 0.14 |
| 10 | $M = 3 \cdot K \cdot [e^{(K \cdot t_m)} - 1]^{-1}$ | Roff 1984 | 0.29 | 0.29 |

adjusted (i.e., by using $\hat{c}$). However, the impact of heterogeneity in catchability on our estimates of $M$ and $F$ is unclear given that heterogeneity in survival may occur for both natural mortality and fishing mortality.

Heterogeneity in catchability associated with spatial variability may result from heterogeneity in the distribution of fish and fishing effort. Tags were applied more or less in proportion to abundance across broad NAFO divisions (Table 1) so that the proportion of fish in the population that were tagged would be approximately equal throughout the study area. Effort is also likely to be distributed approximately in proportion to abundance, but this has not been assessed. Spatial heterogeneity in fishing effort could also be confounded with the size composition of the stock and by observers (taggers). For example, the fish tagged in NAFO Division 3NOPs were on average larger than those tagged in NAFO Division 4VWX (Figure 3), and the observers and fishing vessels that work in these divisions tend to be different.

Model runs with increasing minimum size suggested heterogeneity in survival at length, with higher estimates of both $F$ and $M$ as the minimum size of fish in the data set increased (Figure 4). An increase in catchability (and hence $F$) with size is seen in many fisheries, but an increase in $M$ with size is unexpected. Empirical evidence and theory suggest that $M$ is negatively related to size within the size range of fish examined in this tagging study. Lorenzen (1996) described an L- or U-shaped mortality model, with high mortality in the early life history stages, a rapid decrease at younger ages, a plateau for adults, and an increase at the oldest ages in cases where there is survival senescence. If this general model applies to Atlantic Halibut, then we would expect little variability in $M$ as most of the tagged fish were within 2–3 years of reaching sexual maturity.

Emigration of Atlantic Halibut from the study area may have contributed to inflated estimates of $M$. However, the effect of emigration on the estimates depends on the type of emigration. Permanent emigration (i.e., the case in which fish leave but never return) is completely confounded with mortality. Estimates of total mortality will be biased upwards, with the majority of the bias occurring in the estimates of $M$. Under random temporary emigration (i.e., when the presence of fish on the harvest areas follows a random process that is independent from year to year and does not depend on movement in previous years), estimates of mortality are unaffected, but harvest estimates will be biased downward. The impact of temporary emigration, wherein a fish may leave for several years, also leads to an increase in the model's lack of fit. To account for these types of migration, Lindberg et al. (2001) developed methods, but those methods rely on both live and dead recoveries, whereas live recoveries (and releases) did not occur in this experiment.

Given the large size of the Scotian Shelf and southern Grand Banks management unit relative to the median movement distance of 27 km, we believe that emigration of Atlantic Halibut out of the management unit is low. Results of recent tagging in the Gulf of Maine (GOM) suggest that the Atlantic Halibut stock is transboundary, as 33% of the recaptures of Atlantic Halibut tagged in the GOM were obtained in Canada (Kanwit 2007; Col and Legault 2009); however, as of 27 February 2012, only 3 (<1%) of 444 recaptures of Atlantic Halibut tagged on the Scotian Shelf and southern Grand Banks as part of this project occurred in U.S. waters (den Heyer et al. 2012). This striking disparity in these recapture rates is at least partially a function of fishing effort. Other than an experimental longline fishery in the GOM, there is no directed fishery for Atlantic Halibut in U.S. waters. Between 2006 and 2010, landings of Atlantic

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Halibut in U.S. waters were between 18 and 45 metric tons/year, while landings on the Scotian Shelf and southern Grand Banks were between 1,368 and 2,067 metric tons/year. Further, a review of recaptures reported as of 27 February 2012 (den Heyer et al. 2012) found that (1) of the 193 Atlantic Halibut tagged in NAFO Division 3NOPs and recaptured, only 16 (8%) were recaptured in 4VWX; and (2) of the 251 Atlantic Halibut tagged in 4VWX and recaptured, only 22 (9%) were recaptured in 3NOPs. Arguably, movement across the boundary between subareas 4 and 5 in the GOM could be greater than movement across the boundary between subareas 3 and 4 in the much deeper Laurentian Channel. Kanwit (2007) suggested that results of tagging in the GOM supported the Stobo et al. (1988) hypothesis of compensatory movement of juveniles from the west to the east (i.e., into rather than out of our management unit), which would be counter to the drift of early life history stages, as is the established model for Pacific Halibut (Skud 1977; Trumble et al. 1993). However, there are no data on the distribution of early life history stages of Atlantic Halibut on the Scotian Shelf (Stobo et al. 1988), and the distribution of juvenile and adult Atlantic Halibut has not been linked to compensatory movement along the Scotian Shelf.

Atlantic Halibut emigration outside of fishing grounds within the management unit could cause some bias. Large Atlantic Halibut are more common in deeper waters (McCracken 1958; Zwanenberg et al. 1997; Sigourney et al. 2006). Sigourney et al. (2006) also reported seasonal differences in the depth distribution of Atlantic Halibut in the GOM and suggested that larger individuals moved to deeper waters in the autumn to spawn. Satellite-transmitting archival tags have provided evidence of seasonal return movements of individual mature Pacific Halibut, which are believed to spawn in deeper water and return to more-shallow summer feeding grounds (Loher and Seitz 2006; Loher 2008). As discussed earlier, temporary seasonal emigration should not bias estimates of $M$, but the shift in distribution of larger Atlantic Halibut to deeper waters may reduce catchability, hence increasing estimates of $M$. Further, more of the large Atlantic Halibut were tagged on the southern Grand Banks (NAFO Division 3NOPs), where halibut fishing is geographically restricted to avoid bycatch and to avoid conflict with other fisheries. Because of the restricted distribution of the Atlantic Halibut fishery in 3NOPs and thus the restricted distribution of both tag releases and tag returns (Figure 1), emigration from the study area may be more likely, resulting in elevated estimates of $M$ for larger Atlantic Halibut.

Estimates of $F$ increased as the size of the Atlantic Halibut used to estimate $F$ increased (Figure 4), indicating that harvest size selectivity may have affected our results. Different length-dependent patterns in gear selectivity (trawl versus longline) have been shown for Atlantic Halibut (Sigourney et al. 2006; Armsworthy and Campana 2010; Trzcinski et al. 2011) and Pacific Halibut (Trumble et al. 1993; Kaimmer 1999). Although roughly 80% of the tag reports were from the longline fishery, which is expected to have size selectivity similar to that of the halibut survey in which the tags were applied, a combination of fish growth between release and recapture and size selectivity of the fishery could result in increased heterogeneity in both mortality and catchability. Ideally, one would address this issue by estimating selectivity at length within our tagging model, but our data are too sparse to support such an approach.

The incomplete mixing model estimated a constant $M$ of 0.19–0.27 depending on assumptions about $\phi$ and $\lambda$. These $M$-values are substantially higher than that used in the assessment model ($M = 0.1$; Trzcinski et al. 2011) but are bracketed by the indirect estimates of Atlantic Halibut mortality from Beverton and Holt invariants (Charnov 1993; Jensen 1996) and growth models (Pauly 1980; Roff 1984), which ranged from 0.02 to 0.34 for males and from 0.09 to 0.29 for females (Table 9). The mean of the indirect estimates of $M$ for males (0.19) is higher than that for females (0.16). Maunder and Wong (2011) also noted a higher $M$ for males than for females in a review of $M$-estimates for Summer Flounder *Paralichthys dentatus* and other flatfishes. In this review of $M$-estimates from Beverton and Holt (1957), Pauly (1980), Gunderson (1997), and FishBase (Froese and Pauly 2010, cited by Maunder and Wong 2011), $M$ ranged from 0.1 to 0.6.

Atlantic Halibut are similar in size, life history, and ecological role to Pacific Halibut (Trumble et al. 1993). Throughout the 1980s and 1990s, the Pacific Halibut Commission assumed $M$ to be 0.2, although more recent models have assumed an $M$ of 0.15 (Clark and Hare 2006). Clark and Hare (2006) recently estimated $M$ for females at 0.163 and 0.165 from two life history models based on optimal reproductive investment (Lester et al. 2004), providing confidence to their current assessment model assumptions.

Maunder and Wong (2011) argued that well-designed tagging studies provide the most reliable estimates of $M$. Here, we used a multiyear tagging model that directly estimated tag loss and that benefited from a high $\lambda$ associated with a high reward for reported tags. Nonetheless, the precision of the estimates of $F$ and $M$ was relatively poor (CV for $M \sim 100\%$; CV for $F \sim 50\%$), and future studies should consider releasing more tags. Generally, precision can be improved by increasing the number of tags applied, conducting tagging operations in every year, or increasing the recovery rate; however, the latter strategy would be difficult without a corresponding increase in fishing effort given that the $\lambda$ is already high. Pollock and Raveling (1982) found that unless the tagging study was very large, the size of the biases associated with heterogeneity in survival and catchability was modest relative to the SEs of the estimates. In the present study, uncertainty in the estimate of $\phi$ may overwhelm these biases. An improved estimate of initial tagging mortality could be obtained from holding tank studies or alternative tagging programs, such as those employing pop-up satellite archival tags (e.g., Campana et al. 2009).

In all of the models, $F$ was slightly lower in 2009 than in 2008 (Table 8). Although the TAC increased by 225 metric tons between 2008 and 2009, a lower $F$ is reasonable given the

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increase in recruitment to the fishery (Trzcinski et al. 2011). Our estimates from this multiyear tagging analysis assuming a $\lambda$ of 0.9 and a $\phi$ of 0.8 ($F = 0.15$, 0.24, and 0.18 for 2007, 2008, and 2009) corresponded well with the values estimated from a length-based assessment model ($F = 0.20$, 0.29, and 0.21 for 2007, 2008, and 2009; Trzcinski et al. 2011). Although there could be many reasons for correspondence or a lack thereof, the similarity in $F$-values lends confidence to our estimate of the fishery's impact on the recovering Atlantic Halibut stock of the Scotian Shelf and southern Grand Banks.

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