Fishing Mortality in North Carolina's Southern Flounder Fishery: Direct Estimates of Instantaneous Fishing Mortality from a Tag Return Experiment

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Abstract.—Estimation of harvest rates is often a critical component of fishery stock assessment and management. These assessments are often based on catch-at-age data sets generated over many years, but estimates of instantaneous fishing mortality (F) can also be obtained from a shorter-term tag return study. We conducted a 2-year tag return experiment to generate direct estimates of F for southern flounder *Paralichthys lethostigma* in a North Carolina estuary. The southern flounder supports lucrative commercial and recreational fisheries within the state and has experienced heavy fishing pressure for more than a decade. During 2005 and 2006, fish were captured and tagged with the assistance of commercial harvesters in the New River estuary. Tag returns were used to generate monthly estimates of F, which demonstrated a clear seasonal pattern that was consistent between years. Several important assumptions of the tag return model were accounted for through the use of double-tagged individuals, the distribution of both high- and standard-reward tags, and the completion of an independent controlled experiment to evaluate mortality related to tagging. Annual estimates of F exceeded the short-term management target in both years. Residual patterns suggest that the estimates may actually have been biased low, possibly due to delayed mixing of tagged fish. Thus, despite recently amended fishery regulations, F in the North Carolina southern flounder gill-net fishery still has the potential to greatly exceed targeted levels, which may delay stock recovery. Tag return studies can provide reliable (and nearly real-time) information about F and natural mortality as long as the experimental design addresses specific assumptions related to tagging-induced mortality, tag shedding, and nonreporting of tags.

The estimation of fishing mortality is a critical component of modern fisheries stock assessment. These rates measure the impact of a fishery on the stock, and most fisheries management agencies currently use target and threshold levels of fishing mortality as reference points. Instantaneous fishing mortality rates (F) often are estimated by using age-structured modeling approaches, such as virtual population analysis (VPA) and catch-at-age analysis. These methods use a catch-at-age matrix to indirectly estimate levels of stock size and F (Gulland 1983; Hilborn and Walters 1992). They are most useful for examining historic fishery trends because of the uncertainty for recent cohorts that have not completed

their lifetime in the fishery (Hilborn and Walters 1992). Other typical sources of uncertainty are assumed rates of natural mortality (M) and the assumption that no net migration occurs. When one or more indices of abundance are available, it is generally assumed that the indices are proportional to stock size (i.e., that catchability is constant; Deriso et al. 1985; Hilborn and Walters 1992). Invalid assumptions about these parameters and relationships can produce biased estimates of stock status (Sinclair et al. 1985; Hutchings and Meyers 1994; Swain et al. 1994; Walters and Maguire 1996).

Tag return programs have been recommended to provide rapid estimates of F that can complement the indirect modeling approaches, which rely on a long time series of catch-at-age data (Martell and Walters 2002; Walters and Martell 2002). Unbiased current estimates of F are valuable for fisheries managers, who must often make time-sensitive management decisions based on recent trends in the fishery. Tag return models provide direct estimates of F while relying on a different set of assumptions than common age-structured approaches. Several of these assumptions

relate to practical issues, such as tag loss, and can be met with adequate study design.

The principal assumptions made by tag return models are broadly related to the fate of tagged fish, the level of mixing of tagged and untagged fish, and the timing of tagging (Ricker 1975; Youngs and Robson 1975). Misspecifications of tag retention, tag reporting rate (λ), and mortality due to the tagging process can generate large biases in tag return model estimates (Pollock et al. 2001). Tag return models, however, avoid assumptions regarding M by allowing this rate to be estimated internally to the model, and no assumptions are made regarding migratory patterns. In fact, the spatial distributions of tag releases and recoveries may be used to assess migration assumptions made within age-structured models. Importantly, tag return programs can be designed to generate fine-scale spatial and temporal mortality estimates, which can be used to explore the regional and seasonal distributions of mortality within a stock.

A recent stock assessment completed by the North Carolina Division of Marine Fisheries (NCDMF) suggests that North Carolina's commercial fishery for southern flounder *Paralichthys lethostigma* has been characterized by elevated harvest rates for more than a decade. Projections from an age-structured model indicated that a target F of 0.95 would achieve the spawning biomass target by 2008 (NCDMF 2004). To reduce annual harvest rates, several management changes were initiated in 2005 that included an increase in the minimum size limit, a 1-month fishery closure, a recreational bag limit, and specific gear restrictions for large-mesh gill nets used to target southern flounder (NCDMF 2004).

The southern flounder fishery in North Carolina has several features that could compromise estimates of F based on age-structured methods, such as VPA. The fishery is characterized by a pulse of elevated landings and high catch per unit effort in the fall, when fishermen target southern flounder as they migrate offshore prior to spawning (Watterson and Monaghan 2001). These seasonally varying catch rates reflect changes in catchability rather than changes in abundance; thus, it would not be possible to use fishery effort or catch rates to "tune" the model. Further, the population is not closed to migration. A previous large-scale tagging study revealed that many southern flounder tagged in North Carolina were recaptured after extensive southerly migrations (Monaghan 1992). Thus, a tag return study may provide a useful complementary tool in this fishery by offering an unbiased, rapid assessment of harvest rate trends after the recent regulatory changes.

Here, we report on the results of a tag return experiment conducted over 2 years in the New River, North Carolina. The primary objective was to generate direct estimates of the F experienced by southern flounder in the estuarine gill-net fishery since 2005 management regulations were enacted. To achieve this objective, we took advantage of recent tag return modeling extensions in which mortality rates and "nuisance" parameters, such as λ and tag retention, are estimated jointly within the tag return model (Polacheck et al. 2006; Burdick et al. 2007; Jiang et al. 2007; Bacheler et al. 2008). Estimating these parameters within the model provides a better indication of model uncertainty than is gained through the more typical approach of external estimation and assignment as fixed values in the tag return model. We also include an examination of alternative approaches for analyzing tag returns of double-tagged fish, and we outline the strengths and weaknesses of each approach as related to estimation of F.

Methods

Study system.—The New River was selected for this study because it has a well-documented history of commercial harvest of southern flounder and because it possesses fishery characteristics that make it well suited to conduct a tag return experiment. The New River is typical of many other North Carolina systems in the execution of the southern flounder fishery, which means that our estimates of F may be broadly applicable within the region. Monofilament gill nets fished in lengths of 100–200 m are currently the predominant gear used. Nets are mainly set parallel to the shoreline at shallow water depths by using small vessels and are generally fished overnight. Historically, pound nets were also utilized by southeastern North Carolina fishermen; however, the use of pound nets has declined in recent years, and currently their use in North Carolina is restricted mainly to larger bays (e.g., Albemarle, Core, and Pamlico sounds) in the central and northern regions of the state (NCDMF 2004).

Tagging methods.—To capture fish for tagging, partnerships were formed with three New River commercial gillnetters. Each fished a different area of the river, which helped to distribute releases of tagged fish throughout the river. Southern flounder were captured in 14-cm stretched mesh gill nets that were soaked for approximately 24 h. Only fish in good condition (behaviorally responsive and without visible wounds) and of legal size ($\geq$356 mm total length) were used in the tagging experiment. After net retrieval, fish were held in insulated coolers for 5–15 min and then were tagged and released at least 200 m from the area of capture, in water at least 2 m deep. Fish were tagged in the dorsal region of the caudal peduncle with bright-

orange cinch-up tags (Floy Tag, Inc.) that were printed with a cash reward amount, a unique identification number, and contact information. Twenty percent of fish were tagged with high-reward (US$50) tags to estimate λ, and the remaining fish were tagged with standard-reward ($5) tags. Among the fish tagged with standard-reward tags, approximately 200 fish were double-tagged each year to estimate tag loss, based on the proportion of double-tagged fish recovered with only one tag intact (Beverton and Holt 1957). Recoveries of tagged southern flounder were made directly from harvesters that contacted us after capturing a tagged fish. Participation in the study by commercial harvesters was promoted through several communication avenues, including posted fliers at gas stations and boat ramps, press releases in local newspapers, and several in-person meetings with harvesters and seafood dealers prior to and throughout the study.

Since sufficient numbers of fish could not be captured and tagged before the fishing season began, fish were tagged during each month of the fishing season after the project began in August 2005 (August to November in 2005; May to November in 2006). A monthly time step was incorporated into the tagging model to better meet model assumption 6 listed below. Estimated monthly F-values were summed across months in each year to generate annual rates.

Tag return model.—To estimate F by using a tag return experiment, several specific assumptions must be met (Ricker 1975; Youngs and Robson 1975):

(1) No tags are lost.
(2) The mortality of tagged fish does not differ from the mortality of untagged fish.
(3) All tags are recognized and reported upon recovery.
(4) Tagged fish randomly mix with untagged fish.
(5) Tagged fish are caught at the same rate as untagged fish.
(6) All fish are released instantaneously at the start of each interval.

Each of the assumptions was accounted for in our estimation of F. As described below, the instantaneous rates tag return model developed by Hoenig et al. (1998a) was modified to include immediate and long-term tag loss (assumption 1) and incomplete reporting (assumption 3). Tagging-related mortality (assumption 2) was evaluated independently by using a controlled laboratory experiment in which southern flounder were tagged and held for 128 d. Survival related to the tagging process (s) was estimated based on the proportion of fish surviving the experiment. The variance of s was estimated as a binomial variance ($s[1 - s]/n$, where $n =$ the total number of fish used in the survival experiment). Model sensitivity to s was evaluated by calculating the percent change in annual F-estimates when s was set at its upper and lower 95% confidence limits.

Tag loss, mortality due to tagging, and incomplete reporting can each lead to an underestimate of the return rate and thus can negatively bias F-estimates. Loss of tags and mortality due to tagging reduce the pool of available tags, generating negative bias in the return rate (return rate = number of recoveries/number available for recovery). We tagged some fish with two tags to estimate tag retention parameters. Attaching two tags to a single animal is a well-established means for estimating tag retention rates (Beverton and Holt 1957). In using this approach, we made three assumptions about double-tagged cohorts: (1) tags attached to the same animal were a random sample from all tags; (2) the probability of tag shedding was independent among fish and among multiple tags on the same fish; (3) M, migration, catchability, and λ were independent of the number of tags attached to an animal (Wetherall 1982; Hearn et al. 1991). Postrelease survival may be estimated by subjecting fish to capture and handling processes and observing subsequent survival under controlled laboratory conditions or in replicate field enclosures (Pollock and Pine 2007). To avoid potential biases associated with confinement in small field cages and fluctuating environmental conditions (Pollock and Pine 2007), we elected to monitor tagged fish in several large aquaria (640 L) under controlled conditions. However, both laboratory and field methods for monitoring postrelease fish can still potentially underestimate postrelease mortality and generate negative bias in F-estimates since neither accounts for predation on postrelease fish. Incomplete reporting results in fewer-than-expected recoveries, also generating negative bias in the return rate and model estimates of F (Pollock et al. 2001). To estimate λ, we tagged a subset of fish with high-reward tags. This approach requires the assumption that all high-reward tags that are recovered are subsequently reported ($\lambda = 100\%$).

Low catch per unit effort made it difficult to meet assumption 6 (capture of fish at the beginning of each time interval) during all monthly intervals. Since not all fish were tagged at the beginning of each month, fish tagged later in the month were only subject to a fraction of the total mortality during the month in which they were tagged. To reflect this partial mortality during the first month at large, the F and M during each cohort's initial month of tagging were multiplied by a scalar (m_i) equal to the proportion of each month remaining after the mean day of tagging for each cohort, following Latour et al. (2001b). The sensitivity of the

tagging model F-estimates to this parameter was evaluated by comparison with estimates of F generated under the assumption of full monthly mortality during the month of tagging (i.e., all $m_i = 1$).

We explored two approaches for modeling tag returns: (1) a joint-likelihood model with separate tag retention and tag return components and (2) an integrated tag return model. Both approaches used double-tagged fish to estimate tag retention, but they differed in how double-tagged fish were handled in the tag return analyses. The joint-likelihood approach uses double-tagged fish to estimate both mortality and tag retention parameters, which leads to a lack of independence between the estimates of these parameters. Therefore, we also explored an alternative integrated model approach that achieved complete independence of estimated mortality and tag retention. In the integrated model, fish receiving one tag versus those receiving two tags were handled separately because they had different probabilities of retaining a tag (retaining one versus at least one of two tags).

Joint-likelihood model.—For the tag retention component, we used an exponential decay model to describe the probability of retaining a tag until time t:

$$Q(t) = \rho e^{\phi t}, \qquad (1)$$

where ρ is the probability that a fish retained its tag immediately after tagging and Φ is the instantaneous rate of long-term (chronic) tag loss (Barrowman and Myers 1996; Polacheck et al. 2006). Given the recapture at time t of a fish originally marked with two tags, the probability of observing both tags is $\lambda_{AA} Q(t)^2$, where λ_{AA} is the reporting rate for a double-tagged fish. This expression assumes that the tag loss rate is the same for the two tagging positions and that both tags would be reported if retained. The probability that the recaptured fish retained only one tag and was reported is $\lambda_A 2Q(t)[1 - Q(t)]$. A fish shedding both tags cannot normally be identified, so the likelihood used probabilities that were conditional on retaining at least one tag (Barrowman and Myers 1996; Polacheck et al. 2006). Assuming that λ values were equal for double- and single-tagged fish, the conditional probability of observing a double-tagged fish given its recapture at time t ($p(t)_{AA}$) was

$$p(t)_{AA} = Q(t)^2 / \left\{ Q(t)^2 + 2Q(t)[1 - Q(t)] \right\}, \quad (2)$$

whereas the probability of having only one tag ($p(t)_A$) was

$$p(t)_A = \frac{2Q(t)\left[1 - Q(t_g)\right]}{Q(t_g)^2 + 2Q(t_g)\left[1 - Q(t_g)\right]}. \qquad (3)$$

The tag retention likelihood component (L_1) over all r times at large was then

$$L_1 = \prod_{g=1}^{r} \left[p(t_g)_{AA} \right]^{n_{AA}} \left[p(t_g)_A \right]^{n_A}, \qquad (4)$$

where $n(t)_{AA}$ and $n(t)_A$ are the numbers of tag returns after t_g days at large with two tags and one tag, respectively. We assumed that the likelihood was a function of time at liberty only and was independent of release times. Ninety-seven of 157 returns of double-tagged fish occurred within 30 d of release, so it was possible to estimate immediate tag retention from the field experiment.

For the tag return likelihood component (L_2), we used an instantaneous rates formulation (Hoenig et al. 1998) of the discrete-rates Brownie et al. (1985) model. In the Brownie et al. (1985) model, the expected number of recoveries is based on the number tagged during each time interval (N_i), the return rate (f_j), and the rate of survival (S_j) from one time interval to the next (Table 1). The instantaneous rates formulation splits total mortality into F and M rates that are commonly used in fisheries stock assessments. Instantaneous rates have the advantage of additivity, so seasonal estimates of mortality can be summed to generate annual rates when using an instantaneous rates formulation. The expected number of recoveries, $E(R_{ij})$, of fish tagged in month i and recovered in month j was $N_i P_{ij}$, where N_i = the number tagged and released in month i and P_{ij} = the probability of a tag return in month j from a fish tagged and released in month i. For fish receiving a single standard tag, P_{ij} was defined as

$$P_{ij} = \begin{cases} s\lambda\rho\left(\prod_{v=i}^{j-1} S_{iv}\right)(1 - S_{ij})\left[F_j / (F_j + M_y + \phi)\right] \\ \qquad \text{when } j > i \\ s\lambda\rho(1 - S_{ij})F_j / (F_j + M_y + \phi) \\ \qquad \text{when } j = i, \end{cases}$$

$$(5)$$

where s is the probability of surviving the tagging process, λ is the probability that a recovered standard tag was reported, ρ is the probability of tag retention immediately after tagging, F_j is the instantaneous rate of fishing mortality in month j, M_y is the monthly instantaneous rate of natural mortality for year y, and Φ is the monthly rate of long-term tag loss (tag attrition model: Kleiber et al. 1987; Hampton 1996). Expressions for month-j survival for fish tagged in month i were

$$S_{ij} = \exp\left[-(F_j + M_y + \phi)\right] \qquad \text{for } j > i, \qquad (6)$$

and

TABLE 1.—Expected tag recovery matrix using a discrete-rates formulation (Brownie et al. 1985) and assuming no violation of assumptions (j = month of recovery; N = number tagged during each time interval; f = return rate; S = survival). For the instantaneous rates formulation and the integrated tag retention model, parameters s, λ, ρ, and Φ are added to account for short-term survival of tagging, tag reporting, immediate tag retention, and long-term tag shedding.

Time interval	Number tagged (N_i)	Number of tags retained	Expected recoveries		
			$j = 1$	$j = 2$	$j = 3$
Brownie model formulation[a]					
$i = 1$	N_1	NA	$N_1 f_1$	$N_1 S_1 f_2$	$N_1 S_1 S_2 f_3$
$i = 2$	N_2			$N_2 f_2$	$N_2 S_2 f_3$
$i = 3$	N_3				$N_3 f_3$
Instantaneous rates formulation[b]					
$i = 1$	N_1	NA	$\dfrac{N_1 s \lambda \rho F_1}{(Z_1 + \Phi)}\left[1 - e^{-(Z_1 + \Phi)}\right]$	$\dfrac{N_1 s \lambda \rho F_2}{(Z_2 + \Phi)}\left[1 - e^{-(Z_2 + \Phi)}\right]\left[e^{-(Z_1 + \Phi)}\right]$	$\dfrac{N_1 s \lambda \rho F_3}{(Z_3 + \Phi)}\left[1 - e^{-(Z_3 + \Phi)}\right]\left[e^{-(Z_1 + Z_2 + 2\Phi)}\right]$
$i = 2$	N_2			$\dfrac{N_2 s \lambda \rho F_2}{(Z_2 + \Phi)}\left[1 - e^{-(Z_2 + \Phi)}\right]$	$\dfrac{N_2 s \lambda \rho F_3}{(Z_3 + \Phi)}\left[1 - e^{-(Z_3 + \Phi)}\right]\left[e^{-(Z_2 + \Phi)}\right]$
$i = 3$	N_3				$\dfrac{N_3 s \lambda \rho F_3}{(Z_3 + \Phi)}\left[1 - e^{-(Z_3 + \Phi)}\right]$
Integrated tag retention model formulation[a,c]					
$i = 1$	N_1	1	$2N_1 s \lambda \rho (f_1 - \rho f_1')$	$2N_1 s \lambda \rho (f_2 S_1 - \rho f_2' S_1')$	$2N_1 s \lambda \rho (f_3 S_1 S_2 - \rho f_3' S_1' S_2')$
		2	$N_1 s \lambda \rho^2 f_1'$	$N_1 s \lambda \rho^2 f_2' S_1'$	$N_1 s \lambda \rho^2 f_3' S_1' S_2'$
$i = 2$	N_2	1		$2N_2 s \lambda \rho (f_2 - \rho f_2')$	$2N_2 s \lambda \rho (f_3 S_2 - \rho f_3' S_2')$
		2		$N_2 s \lambda \rho^2 f_2'$	$N_2 s \lambda \rho^2 f_3' S_2'$
$i = 3$	N_3	1			$2N_3 s \lambda \rho (f_3 - \rho f_3')$
		2			$N_3 s \lambda \rho^2 f_3'$

[a] $f_j = \left\{F_j\left[1 - e^{-(Z_j + \Phi)}\right]\right\}/(Z_j + \Phi); f_j' = \left\{F_j\left[1 - e^{-(Z_j + 2\Phi)}\right]\right\}/(Z_j + 2\Phi); S_j = e^{-(Z_j + \Phi)}; S_j' = e^{-(Z_j + 2\Phi)}$.

[b] $Z_j = F_j + M_j$; F_j = instantaneous rate of fishing mortality; M_j = instantaneous rate of natural mortality.

[c] Double-tagged cohorts only.

$$S_{ij} = \exp\left[-m_i(F_j + M_y + \phi)\right]$$
$$\text{in the month of tagging } (j - i). \quad (7)$$

These expressions applied to survival of the tagged cohort because they included mortality experienced by fish and shedding of tags. The scalar m_i equaled the proportion of the month remaining after the mean date of tagging for the ith cohort. Equivalent expressions were used for high-reward tags, except that λ was set equal to 1.0 (i.e., λ of high-reward tags was assumed to be 100%).

Two simple ad-hoc approaches were used to handle tag returns of double-tagged fish. Method 1 used only the tag from the standard tagging location (i.e., excluded returns of double-tagged fish retaining only the extra tag). Method 2 excluded all recoveries of double-tagged fish (i.e., using them only in L_1).

The L_2 was the product of likelihood expressions for standard- and high-reward tags:

$$L_2 = \prod_{i=1}^{I}\left(\prod_{j=1}^{J} P_{ij}^{R_{ij}}\right)(P_{iJ*})^{(N_i - \Sigma_j R_{ij})}, \quad (8)$$

where P_{iJ*} is the probability that a fish from cohort i is not recovered and is calculated as

$$P_{iJ*} = 1 - \sum_{j=i}^{J} P_{ij} \quad (9)$$

(Hoenig et al. 1998a). Parameter estimates were obtained by maximizing the joint likelihood (product of L_1 and L_2).

Integrated tag return model.—In the integrated approach, cohorts of fish tagged with a single standard- or high-reward tag were modeled by using the same equations as in the tag return component of the joint-likelihood model. Double-tagged fish were handled differently: equations derived by Polacheck et al. (2006) were used to represent the probability of a double-tagged fish being returned with either one tag or two tags (Table 1). By specifying the cell probabilities for tag returns with one or two tags, it was possible to simultaneously estimate both tag retention and mortality parameters from these cohorts. Tag returns of double-tagged fish were pooled by month of tagging and month of recovery. This resulted in a loss of information compared with the tag retention component of the joint-likelihood model, which used exact time at liberty for double-tagged fish.

In the integrated model, the probability of recovering a double-tagged fish with only one tag intact was

defined as

$$
P_{ij} = \begin{cases} 2s\lambda\left\{\rho\prod_{v=i}^{j-1}S_{iv}(1-S_{ij})\left[F_j/(F_j+M_y+\phi)\right]\right. \\ \qquad \left. -\rho^2\prod_{v=i}^{j-1}S'_{iv}(1-S'_{ij})\left[F_j/(F_j+M_y+2\phi)\right]\right\} \\ \qquad\qquad \text{when } j > i \\ 2s\lambda[\rho(1-S_{ij})F_j/(F_j+M_y+\phi) \\ \qquad -\rho^2(1-S'_{ij})F_j/(F_j+M_y+2\phi)] \\ \qquad\qquad \text{when } j = i, \end{cases}
$$

(10)

and the probability of recovering a double-tagged fish with both tags intact was defined as

$$
P_{ij} = \begin{cases} s\lambda\rho^2\prod_{v=i}^{j-1}S'_{iv}(1-S'_{ij})\left[F_j/(F_j+M_y+2\phi)\right] \\ \qquad\qquad \text{when } j > i \\ s\lambda\rho^2(1-S'_{ij})\left[F_j/(F_j+M_y+2\phi)\right] \\ \qquad\qquad \text{when } j = i, \end{cases}
$$

(11)

where

$$
S'_{ij} = \exp\left[-(F_j+M_y+2\phi)\right] \quad \text{for } j > i \quad (12)
$$

and

$$
S'_{ij} = \exp\left[-m_i(F_j+M_y+2\phi)\right]
$$
$$
\text{in the month of tagging } (j=i). \quad (13)
$$

Here, S'_{ij} applies to survival with both tags intact. The likelihood component for double-tagged fish in the integrated model (L_3) was

$$
L_3 = \left(\prod_{j=i}^{J}P_{Tij}^{R_{Tij}}\prod_{j=i}^{J}P_{TTij}^{R_{TTij}}\right) \\ \times \left(1 - P_{Tij}\sum_{j=i}^{J}P_{Tij} - \sum_{j=i}^{J}P_{TTij}\right)^{N_i-\Sigma_{j-i}^{J}R_{Tij}-\Sigma_{j-i}^{J}R_{TTij}}
$$

(14)

(Polacheck et al. 2006), where subscripts T and TT denote recoveries of double-tagged fish retaining one or both tags, respectively.

The total integrated model likelihood was the product of L_2 and L_3. For both the joint-likelihood and integrated models, the program SURVIV (White 1992) was used to generate maximum likelihood estimators of model parameters F_j, M_y, ρ, Φ, and λ given the above model structures and observed

recoveries of standard- and high-reward tags, as well as standard tags from double-tagged fish.

There were some months in 2005 (May to July) during which commercial effort data indicated that the fishery was operating extensively (Figure 1), but little or no tagging took place. Since an annual estimate of F was desired for both years, monthly estimates of F had to be generated for months with insufficient tagging data in order to calculate an annual F for 2005. To estimate F during May to July 2005, linear regression analysis was performed by using New River monthly commercial effort (trips; NCDMF commercial harvest statistics) as an explanatory variable and tag return model estimates of monthly F from August to November 2005 as a response variable. If monthly estimates of F generated by the tagging model were strongly related to monthly fishery effort trends, then the regression model could be used to predict F-estimates and variances for the months (May to July) that lacked tagging data.

The annual estimate of F for 2005 was then estimated as the sum of monthly F-estimates generated by the tag return model for August to November and the monthly F-estimates predicted by the regression model for May to July. Because tagging occurred during all months in 2006 for which high commercial effort was documented, regression estimates were not needed, and the annual estimate of F for 2006 was simply estimated as the sum of monthly F-estimates generated by the tag return model for May to November. We constructed a 95% confidence interval (CI) for each annual F-estimate, a z-distribution, and then determined whether the interval contained the target F (0.95).

Model selection.—A full model and four reduced models with different assumptions regarding M were tested in SURVIV. In the full model, F was allowed to vary by month, and M was allowed to vary by year while being held constant over all months within a year. While it was not feasible to estimate both a separate F and M for each interval (Hoenig et al. 1998a), we chose to generate monthly estimates of F in order to more accurately represent the highly seasonal nature of the fishery. The following four reduced models were tested: (1) a single M was estimated for both years 2005 and 2006; (2) M was fixed across both years at the rate assumed in the most recent southern flounder stock assessment ($M = 0.404$; NCDMF 2004); (3) M was fixed across both years at the lowest rate calculated through common life history methods; and (4) M was fixed across both years at the highest rate calculated through common life history methods. Models were ranked based on the quasilikelihood Akaike's information criterion (QAIC; Burnham and
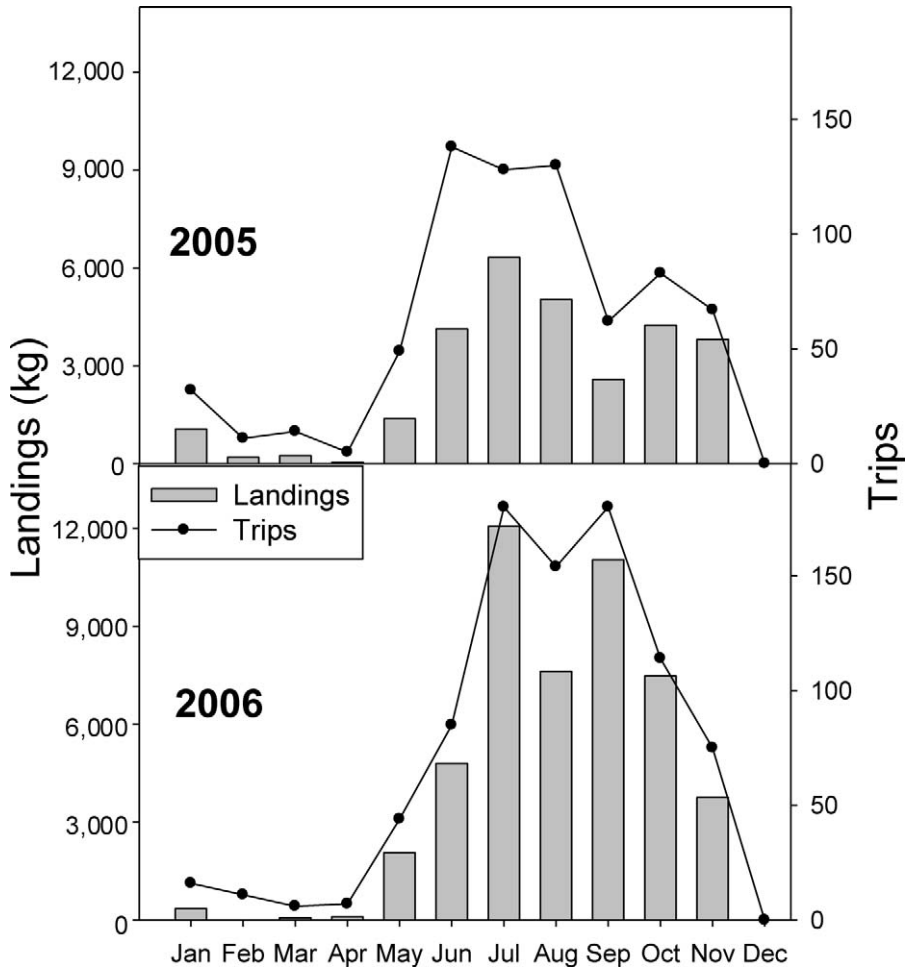
FIGURE 1.—New River, North Carolina, commercial landings of southern flounder and trips in the years 2005 and 2006. Note that in both years, lower landings and fewer trips were documented in January to April compared with all other months during the fishing season.

Anderson 1998), with the lowest QAIC indicating the model with the most support. This version of the criterion adjusts for overdispersion in tag return data that may result from the tendency of some fish species to aggregate, thus violating tagging assumption 4 presented above. In general, overdispersion is unlikely to result in biased estimates, but model precision may be overestimated. We multiplied the variance of each tagging model parameter estimate by a variance inflation factor ($\hat{c}$) to reflect this uncertainty (Burnham and Anderson 1998). To reflect uncertainty in model selection, parameter estimates were averaged over all candidate models by using a normalized weight (Burnham and Anderson 1998).

For tagging models in which M was fixed, several estimates of M were calculated by using common life

history methods. The Hoenig (1983) method estimates M based on the maximum observed age by using a regression equation relating maximum age and total mortality rate for lightly exploited and unexploited stocks. The oldest southern flounder aged in North Carolina was 8 years old (NCDMF 2004). Lorenzen (1996) also developed a regression model relating M to body weight. Eighty-eight percent of all fish recovered during this study were age 1 (W. E. Smith and F. S. Scharf, unpublished data), and average weights for age-1 southern flounder collected from a combination of fisheries-independent and fisheries-dependent sources in North Carolina are listed in the most recent fishery management plan (NCDMF 2004). The Pauly (1980) method estimates M by using the asymptotic maximum length (L_∞), the Brody growth coefficient (K), and

average ambient water temperature as predictors. Bottom temperatures from seven stations throughout the New River were averaged across months during which tagging occurred to estimate the average ambient water temperature to which tagged fish may have been exposed. The L_∞ and K parameters from von Bertalanffy growth models were compiled from several sources that describe southern flounder growth in Texas (Matlock 1991a, 1991b; Stunz et al. 2000), Louisiana (Fischer and Thompson 2004), South Carolina (Wenner et al. 1990), and North Carolina (NCDMF 2004). Eight estimates of M were calculated, and the highest and lowest M-estimates were used to fix this rate across a likely range of M in the tagging models described above.

Assessing potential for violation of assumptions.— Our tag return model design allowed us to adjust for various violations, such as tag loss and nonreporting, while incorporating uncertainty associated with tag retention and reporting parameters in our estimates of F. Estimating the variance for s allowed us to assess the sensitivity of our conclusions to possible inaccuracy in this parameter. In addition, we examined the model residual matrix to assess the potential for violations of other tag return model assumptions outlined above. Latour et al. (2001a) demonstrated that nonmixing of tagged and untagged fish (Hoenig et al. 1998b), chronic emigration of tagged animals from the study area, tagging-related mortality or tag loss, and variability in M can result in assumption violations that produce observable patterns in the model residual matrix (observed minus predicted recoveries). The model residual matrix is organized similarly to the Brownie et al. (1985) model outlined in Table 1, with monthly tagging cohorts arranged in rows and month of recovery arranged in columns. Nonmixing occurs when tagged fish are not immediately mixed with the untagged population and can generate specific patterns within the model residual matrix. If tagged fish are released and remain in an area with lower-than-average harvest pressure, a pattern of negative residuals along the main diagonal combined with positive residuals along the super diagonal may be produced. This pattern results from a lower-than-expected rate of recovery during the initial time interval of release, resulting in higher-than-expected survival in the initial time interval and thus higher-than-expected recoveries in the subsequent time interval. If tagged fish are released and remain in an area having a higher-than-average fishing pressure, the opposite pattern may be found, with positive residuals along the main diagonal and negative residuals along the super diagonal. Extensive emigration from the study area can generate a cluster of negative residuals in the upper right corner of the model residual matrix, since fish move out of the study area and are never seen again. Changes in M can create patterns of positive or negative residuals in the columns of the matrix because either fewer (negative residual) or more (positive residual) individuals than expected survive from one time interval to the next, regardless of the time interval of release.

Results

In total, 1,921 southern flounder were tagged during the 2005 ($n = 975$) and 2006 ($n = 946$) fishing seasons. Recoveries of 2005 tags numbered 194 during the 2005 fishing season plus an additional 47 fish that were recovered during the 2006 season (Table 2). Recoveries of 2006 tags numbered 489 during the 2006 fishing season plus an additional 5 fish (not shown) that were recovered during the 2007 season (Table 2). To estimate tagging-related mortality (s), 20 southern flounder were tagged and held in laboratory tanks for 128 d. Three mortalities occurred; one each at 5, 17, and 25 d after tagging. Therefore, short-term tagging mortality was estimated as a discrete rate occurring within the initial month of tagging, and s was then fixed at 0.85 (standard error [SE] = 0.080) in the tag return model. No fish held in the laboratory tanks experienced tag loss.

Tag Return Models

Of the 383 double-tagged fish released, 157 fish were recovered, with times at large ranging from 1 to 387 d (Table 3). Seven fish had only one tag intact, while 150 fish had both tags intact. Using exact times at large and joint-likelihood method 1, we estimated that ρ was 0.983 (SE = 0.012) and the daily instantaneous rate of tag loss (Φ) was 1.56×10^{-4} (SE = 2.1×10^{-4}). Tag retention parameter estimates were very similar using joint-likelihood method 2 ($\rho = 0.984$, SE = 0.011; $\Phi = 1.68 \times 10^{-4}$, SE = 2.0×10^{-4}). Using double-tagged cohorts pooled by month and the integrated tag return model, ρ was estimated to be 0.977 (SE = 0.024) and monthly φ was estimated to be 1.44×10^{-16} (SE = 0.018).

The relatively few returns of tagged fish after the overwinter period (recoveries of 2005 tags in 2006 and recoveries of 2006 tags in 2007) were not included in the tag return models. Many recoveries in the second year after tagging occurred at substantial distances south of the New River. For instance, one fish tagged in 2005 was recovered near Hilton Head Island, South Carolina, in 2007, so it is likely that fish emigrated to areas with different λ, F, and M after the year of their tagging, resulting in a violation of the assumptions of homogeneous reporting and mortality for these fish (assumptions 2 and 3 above).

TABLE 2.—Observed recoveries matrix of all southern flounder tagged with standard tags, high-reward tags, and double tags in the New River, North Carolina, and recovered during 2005 and 2006. Only asterisked data were used in the tagging models. For tag retention method 1, all double-tagged fish were added to the standard tag matrix, with the exception of three recoveries (1 fish each from the August 2005 cohort in September and October 2005 and 1 fish from the May 2006 cohort in July 2006). For tag retention method 2, no double-tagged fish were added to the standard tag matrix.

Month of tagging (i)	Number tagged (N_i)	Number of tags intact	Month of recovery (j)										
			1	2	3	4	5	6	7	8	9	10	11
Standard tags													
Aug 2005 (1)	166*	NA	12*	6*	14*	3*	0	0	0	0	0	0	0
Sep 2005 (2)	184*			7*	23*	10*	0	0	1	0	1	0	2
Oct 2005 (3)	178*				15*	13*	1	0	0	0	2	1	2
Nov 2005 (4)	256*					17*	0	0	1	5	2	2	5
May 2006 (5)	78*						1*	24*	11*	5*	1*	1*	0*
Jun 2006 (6)	207*							26*	47*	18*	3*	0*	0*
Jul 2006 (7)	374*								57*	42*	25*	4*	1*
Aug 2006 (8)	31*									3*	1*	0*	0*
Sep 2006 (9)	36*										5*	5*	1*
Oct 2006 (10)	24*											2*	0*
Nov 2006 (11)	8*												0*
High-reward tags													
Aug 2005 (1)	42*	NA	5*	2*	6*	1*	0	0	0	0	0	1	0
Sep 2005 (2)	45*			2*	10*	0*	0	0	0	0	0	0	0
Oct 2005 (3)	37*				7*	5*	0	0	0	0	1	0	0
Nov 2005 (4)	67*					3*	0	0	1	1	1	2	1
May 2006 (5)	20*						1*	5*	3*	0*	1*	0*	0*
Jun 2006 (6)	47*							6*	15*	9*	3*	0*	0*
Jul 2006 (7)	99*								17*	19*	9*	1*	0*
Aug 2006 (8)	7*									1*	0*	2*	0*
Sep 2006 (9)	8*										1*	2*	0*
Oct 2006 (10)	5*											0*	2*
Nov 2006 (11)	2*												0*
Double tags													
Aug 2005 (1)	42*	1	0*	1*	1*	0*	0	0	0	0	0	0	0
		2	7*	2*	2*	0*	0	0	0	0	0	0	0
Sep 2005 (2)	44*	1		1*	0*	0*	0	0	0	0	0	0	0
		2		1*	9*	1*	0	0	0	0	0	1	0
Oct 2005 (3)	36*	1			0*	0*	0	0	0	0	0	0	0
		2			4*	1*	0	0	2	0	0	0	0
Nov 2005 (4)	75*	1				0*	0	0	0	0	0	0	0
		2				5*	2	1	1	0	1	1	1
May 2006 (5)	18*	1					1*	0*	1*	0*	0*	0*	0*
		2					5*	8*	2*	0*	0*	0*	0*
Jun 2006 (6)	46*	1						0*	0*	0*	0*	0*	0*
		2						11*	16*	4*	1*	1*	0*
Jul 2006 (7)	102*	1							0*	0*	0*	0*	0*
		2							23*	11*	12*	4*	0*
Aug 2006 (8)	7*	1								0*	0*	0*	0*
		2								1*	1*	0*	0*
Sep 2006 (9)	8*	1									0*	0*	0*
		2									2*	1*	1*
Oct 2006 (10)	6*	1										0*	
		2										1*	2*
Nov 2006 (11)	2*	1											0*
		2											0*

The tag return component for joint-likelihood method 1 used almost all of the available data by only excluding three double-tagged fish (those having lost the standard tag). These three fish were recovered from the August 2005 cohort in September (1 fish) and October 2005 (1 fish) and from the May 2006 cohort in July 2006 (1 fish). All double-tagged fish were eliminated from the tag return component of joint-likelihood method 2. Despite the difference in sample size, parameter estimates from the two joint-likelihood methods were very similar (Table 4). The integrated model also produced similar estimates, although precision was lower. Therefore, we considered joint-likelihood method 1 to be our best model for subsequent analyses of mortality estimates.

For joint-likelihood method 1, differences in QAIC scores were never greater than 2, indicating that all models evaluated were plausible candidates given the

TABLE 3.—Times at large and totals for all double-tagged southern flounder that were recovered in the New River, North Carolina, commercial gill-net fishery (TT = double-tagged fish that were recovered with both tags intact; T = double-tagged fish that were recovered with only one tag intact).

Days at large	Count	
	T	TT
1	1	13
2		5
3		3
4		5
5		4
6		1
7	1	3
8		3
9		3
10		3
11		4
12		3
14		4
15		6
16		3
17		2
18		2
19		2
20		3
21		4
22		2
23		4
24		2
25		3
27		1
28		3
29		1
30	1	2
32	1	1
33		3
36		2
37		1
38		3
39		1
41		2
43		1
45		1
47		1
48		2
49		1
51		1
52		1
53		1
55	1	1
56		1
57		1
61		2
63		1
65		1
67		2
71		2
73		1
75		2
80		1
81		1
83		1
89		2
93		1
104		2
106		1
112		1
148		1
180		1

TABLE 3.—Continued.

Days at large	Count	
	T	TT
209		1
226		1
259		1
261		1
279		1
283		1
342	1	
363	1	
364		1
387		1

data (Table 5). Estimates of F were very similar among models, which demonstrated that the F-estimates were robust regardless of how M was estimated. Natural mortality estimates used in tagging models with a fixed M ranged from 0.22 to 0.58. The lowest M-estimate was generated by using the Pauly (1980) method and growth parameters for North Carolina southern flounder (NCDMF 2004). The highest M-estimate was generated by using the Hoenig (1983) regression approach. The lack of separation among the models supported the use of model averaging to obtain annual estimates of F and M. The model-averaged estimates of monthly M were 0.033 and 0.027 during 2005 and 2006, respectively. Variance estimation was not possible for the averaged monthly M-estimates because M was fixed at predetermined rates in some models. Annual estimates of M, obtained by summing the monthly estimates, were 0.397 and 0.328 for 2005 and 2006, respectively, resulting in a mean annual M-estimate of 0.362. Return rates were similar for standard- and high-reward tags, and λ was estimated as 0.904 (SE = 0.057).

Regression analysis indicated that 96% of the variation in F-estimates during August to November 2005 could be explained by the trend in monthly commercial effort in the New River southern flounder fishery (Figure 2). The sum of the regression model predictions of F for months during which inadequate numbers of fish were tagged and released, May to July 2005, was 1.06 (SE = 0.073). This sum was added to the tagging model estimate of F for August to November 2005, 0.87 (95% CI = 0.62–1.13; SE = 0.128), yielding a total annual F-estimate of 2.04 (95% CI = 1.76–2.33; SE = 0.147) for 2005. The tagging model generated an F-estimate for 2006 (May to November) of 2.35 (95% CI = 1.91–2.78; SE = 0.221; Figure 3). The target F of 0.95 was substantially below both 95% CIs, so it is unlikely that the management goal was achieved. During both fishing seasons, F peaked in June to July at monthly values of 0.47–0.59, slowly drawing down

TABLE 4.—All estimated southern flounder model parameters generated by using three different tag retention and tag return models and averaging over the five candidate models listed in Table 5 (ρ = short-term tag retention probability; ϕ = instantaneous rate of tag loss; λ = tag reporting rate; M = instantaneous rate of natural mortality; CI = confidence interval, given in parentheses). Estimates of instantaneous fishing mortality (F) are based on tag return models for August to November 2005 and May to November 2006 and regression analysis for May to July 2005. Parameter ϕ in the joint-likelihood models was converted to a monthly rate for comparisons with ϕ in the integrated model.

Tag retention model	ρ (95% CI)	ϕ (monthly; 95% CI)	λ (95% CI)	$F_{\text{Aug–Nov 2005}}$ (95% CI)	$F_{\text{May–Nov 2006}}$ (95% CI)	M_{2005}	M_{2006}
Joint likelihood method 1	0.98 (0.96–1.00)	0.0047 (0.0024–0.016)	0.90 (0.79–1.00)	2.04 (1.76–2.33)	2.35 (1.91–2.78)	0.40	0.33
Joint likelihood method 2	0.98 (0.96–1.00)	0.0050 (0.0029–0.016)	0.89 (0.78–1.00)	1.92 (1.62–2.22)	1.96 (1.63–2.29)	0.44	0.34
Integrated	0.98 (0.93–1.00)	1.44×10^{-16} (0–0.036)	0.92 (0.76–1.00)	1.95 (1.54–2.36)	2.30 (1.69–2.91)	0.34	0.32

to a minimum in November at monthly values of 0.0281–0.110 (Figure 3). Seasonal variation in F was consistent between the two study years.

Sensitivity analysis revealed that the model estimates of F were sensitive to the parameter s and the time when each monthly cohort was tagged. Setting s at its upper 95% confidence limit (95% CI for $s = 0.69$–1.00) resulted in an 18–22% decrease in the annual F-estimates ($F_{2005} = 1.67$, $F_{2006} = 1.83$). Alternatively, setting s at its lower 95% confidence limit resulted in a 26–36% increase in the F-estimates ($F_{2005} = 2.58$, $F_{2006} = 3.19$). We attempted to correct for the average time of each cohort's release with the scalar m_i, which for the default case ranged from 0.25 to 0.93 (Table 6). When m_i was fixed at 1, which assumed that all fish were tagged at the beginning of each time interval and thus were exposed to the full monthly mortality during the initial month of tagging, the model estimates of annual F were 36–52% lower.

Examination of the model residual matrix revealed the potential for nonmixing of tagged and untagged southern flounder during the study. A consistent pattern of negative residuals along the main diagonal and positive residuals along the super diagonal was apparent (Table 7). The estimate of ĉ for the full model (ĉ = 1.35) suggested some overdispersion in the tag return data, which also may have been an artifact of nonmixing if southern flounder tended to aggregate after tagging. Chronic emigration during each fishing season was not apparent, since a pattern of negative residuals in the upper right corner of the residual matrix was not observed. The lack of column or row patterns in the model residuals indicated that variability in M or in the short-term rates of s and tag retention was minimal and did not generate a detectable bias in our estimates of F.

Discussion
Estimates of Fishing Mortality

In the most recent stock assessment completed by the NCDMF, annual F-estimates from VPA ranged between 1.77 and 3.43 over a 12-year period (NCDMF 2004). Although no management target existed prior to the 2004 stock assessment, the values of F exceeded the current target in every year included in the assessment (1991–2002). The NCDMF currently lists the southern flounder stock as overfished (stock biomass below target) and indicates that overfishing (F above target) is still occurring. Uncertainty regarding the estimated values of F would be greatest at the end of the catch time series because those estimates are based on cohorts that have not completed

TABLE 5.—Southern flounder tagging model results based on joint-likelihood method 1, listed from lowest to highest value of the quasilikelihood Akaike's information criterion (QAIC; M = instantaneous rate of natural mortality; w_r = model weight; F = instantaneous rate of fishing mortality; CI = confidence interval; FMP rate = M given in the southern flounder fishery management plan [NCDMF 2004]). Values of F include only tagging model estimates (August to November 2005 and May to November 2006).

Model	QAIC	w_r	$F_{\text{Aug–Nov 2005}}$ (95% CI)	$F_{\text{May–Nov 2006}}$ (95% CI)	M_{2005}	M_{2006}
Low fixed M	297.3	0.309	0.98 (0.73–1.22)	2.32 (1.90–2.75)	Fixed at 0.22	Fixed at 0.22
M fixed at FMP rate	297.6	0.254	0.99 (0.74–1.24)	2.36 (1.93–2.79)	Fixed at 0.404	Fixed at 0.404
High fixed M	298.2	0.168	1.00 (0.75–1.25)	2.40 (1.96–2.83)	Fixed at 0.58	Fixed at 0.58
Full	299.3	0.155	1.00 (0.74–1.25)	2.30 (1.84–2.76)	0.71 (SE = 0.19)	1.16×10^{-15} (SE = 0.37)
Constant M estimated across 2005 and 2006	299.3	0.114	0.98 (0.73–1.22)	2.32 (1.89–2.75)	0.21 (SE = 0.096)	0.21 (SE = 0.096)

$$F(t) = 0.0055 \, (\text{trips}) - 0.22$$
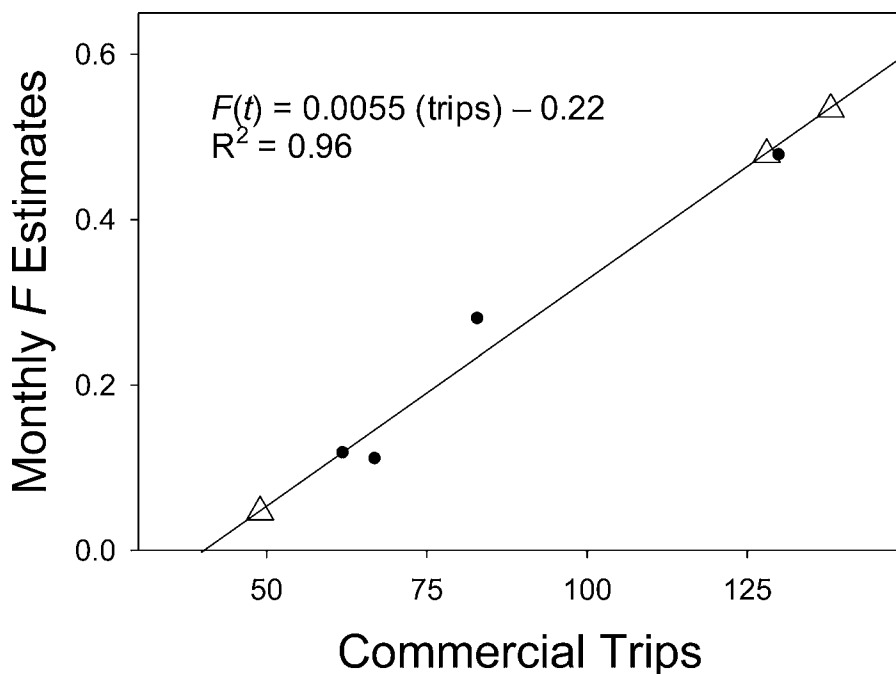$$R^2 = 0.96$$

FIGURE 2.—Linear relationship between New River, North Carolina, commercial trips and monthly estimates of the southern flounder instantaneous fishing mortality rate (F) generated by the tagging model using joint-likelihood method 1 (see Methods) for August to November 2005. The line is the estimate of the fitted regression model. Black circles denote tagging model F-estimates versus trips; open triangles illustrate the predictions of F for May to July 2005.

their lifetimes in the fishery. Walters and Martell (2004) suggested that harvest rate estimates from age-structured models may be unreliable for the last (maximum age/2) years included in a time series. If seven to eight age-classes are represented in the North Carolina southern flounder catch-at-age data (NCDMF 2004), then F-estimates for the final 3–4 years should be interpreted cautiously.

This tagging study provides direct and nearly real-time estimates of F that are a valuable complement to the VPA. The results show the highly seasonal pattern of fishing and establish that the F-estimates remain well above the target level despite regulation changes after adoption of the 2004 fishery management plan. Our results further demonstrate the highly seasonal nature of fishing mortality in this fishery, with a peak in F during summer months. If our findings are broadly representative of other gill-net fisheries for southern flounder throughout the state, they imply that it may take longer than 2008 before the spawning biomass goals outlined in the management plan are achieved.

Data Limitations and Interpretation

Tag return estimates of F are sensitive to violations of assumptions regarding mixing of tagged and untagged fish (assumption 6) and the fate of tagged fish (assumptions 1–3). The potential for nonmixing was revealed by an examination of model residuals (Table 7). We released tagged fish in water of at least 2-m depth and away from the shoreline to allow sufficient time for recovery before they were vulnerable to the fishery, which operates extensively in shallow water (<2 m). Our tagging model assumed that all tagged fish were thoroughly mixed with untagged fish immediately after tagging. However, release in deeper water and extended recovery from the tagging process may have resulted in spatial nonmixing (Hoenig et al. 1998b), a lower-than-expected recovery rate during the initial month of release, and thus a negatively biased F-estimate. Alternatively, spatial nonmixing due to aggregation behavior may have generated the model residual patterns that we observed. We inflated variance estimates to account for over-dispersion in the tag return data, but if the return rate was underestimated due to nonmixing effects, then the model estimates of F would also be negatively biased.

Sensitivity analysis revealed that the model was sensitive to variation in s. We addressed this uncertainty by fixing s at the upper and lower bounds of the 95% CI. Model solutions at those extremes did
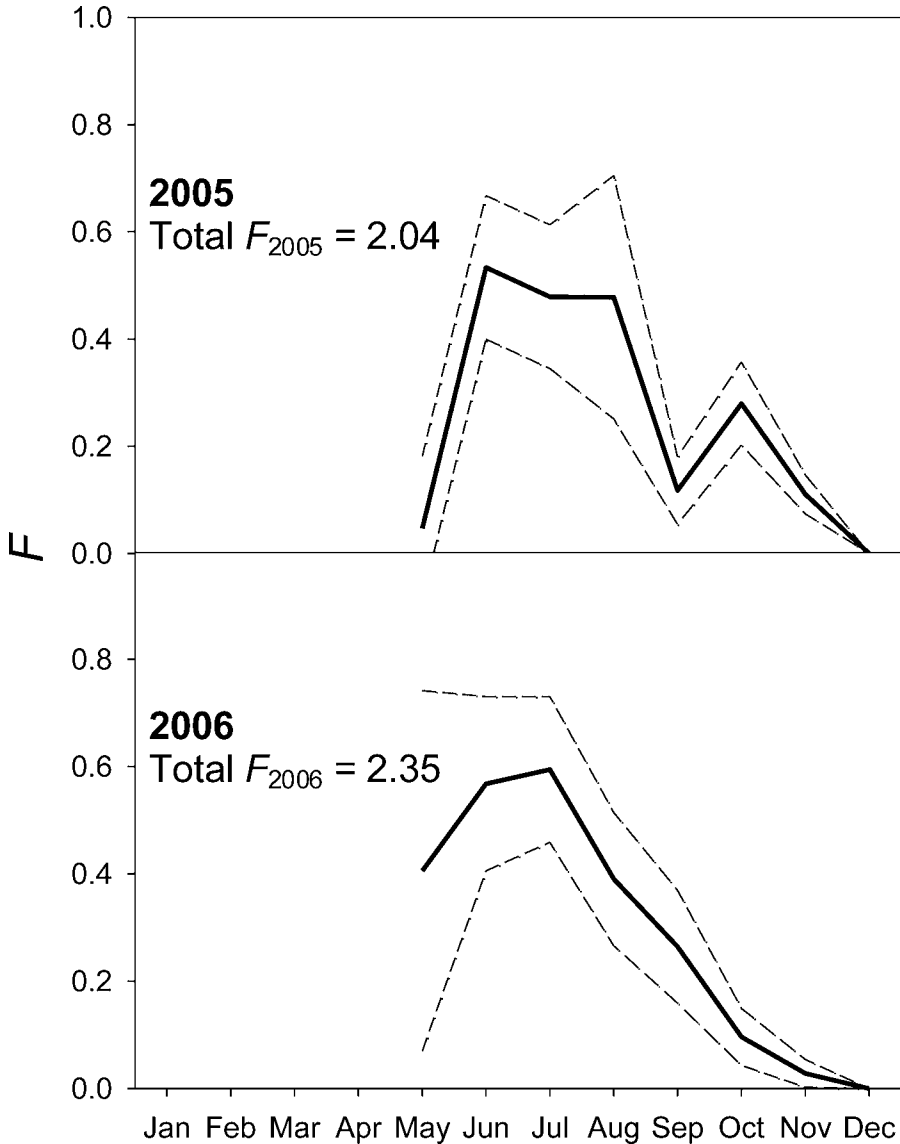
FIGURE 3.—Monthly estimates of the southern flounder instantaneous fishing mortality rate (F; solid lines) and 95% confidence intervals (dashed lines) for 2005 and 2006 generated by using joint-likelihood method 1 (see Methods). The F_{2005} was estimated using both the tagging and regression models, and F_{2006} was estimated using the tagging model.

TABLE 6.—Values of the scalar, m_i, used to adjust southern flounder mortality during the initial month of each cohort's release in the New River, North Carolina.

Month	2005	2006
May		0.267
Jun		0.534
Jul		0.635
Aug	0.359	0.308
Sep	0.247	0.430
Oct	0.426	0.930
Nov	0.863	0.900

not alter the conclusion that F likely exceeded the target during the study period. We also believe that the parameter s could have varied across months as environmental conditions changed, but we lack the data at present to address this possibility.

Since estimates of ρ, chronic tag retention ($e^{-\Phi}$), and λ were relatively high for this study, these parameters were more likely to have been overestimated than underestimated. In all three cases, overestimation would have negatively biased our estimates of F. The

TABLE 7.—Model matrix residuals of the averaged southern flounder tagging model for standard tags and high- reward tags. Note the pattern of negative residuals along the main diagonal (single asterisk) and positive residuals along the super diagonal (double asterisks).

Recovery month in 2005					Recovery month in 2006							
Aug	Sep	Oct	Nov	Not seen again	May	Jun	Jul	Aug	Sep	Oct	Nov	Not seen again
Standard tags[a]												
−35.7*	2.5**	14.3	2.8	−46.0	−15.6*	23.1**	8.8	3.6	0.7	1.0	0.0	−59.0
	−9.0*	27.3**	10.5	12.0		−39.0*	31.8**	11.5	1.4	0.7	0.0	−89.5
		−16.2*	10.3**	−11.8			−58.6*	11.1**	26.6	6.9	1.0	−58.4
			2.0*	16.9**				−4.6*	0.2**	−0.2	0.0	186.0
									0.3*	5.4**	2.0	−4.4
										1.4*	1.9**	2.4
											−0.2*	1.7**
High-reward tags[b]												
−9.1*	0.6**	5.6	1.0	1.9	−4.9*	2.7**	1.9	−0.4	0.9	0.0	0.0	−0.3
	−2.0*	8.8**	−0.1	5.4		−11.6*	7.8**	6.6	2.4	−0.1	0.0	−5.3
		−0.4*	4.2**	−3.8			−20.3*	7.8**	6.3	0.7	0.0	5.6
			−2.3*	−6.7**				−1.0*	−0.4**	2.0	0.0	−0.6
									−0.5*	1.9**	0.0	−1.3
										−0.3*	2.0**	−1.6
											0.0*	0.0**

[a] Main diagonal mean = −15.9; super diagonal mean = 12.0.
[b] Main diagonal mean = −4.8; super diagonal mean = 2.6.

potential for bias is greatest for the chronic tag retention rate, which was estimated with very low precision (proportional SEs > 1.0). Estimates of immediate tag retention and λ were precise (proportional SEs < 0.10), so consistent bias due to those parameters appears unlikely. One potential source of bias is the assumption of 100% reporting of the $50 high-reward tags. Although other studies have suggested that amounts up to $100 may be necessary to ensure 100% reporting of high-reward tags (Nichols et al. 1991), we believed that a $50 reward was sufficient in the New River fishery based on the socioeconomic landscape of the community. Reporting rate would have been overestimated in this study if the high-reward amount was inadequate to produce complete reporting of these tags. If this was the case, the actual F would have been higher than we estimated. Thus, considering the evidence for nonmixing and the potential for bias due to tag loss or nonreporting, we conclude that our F estimates could actually be low and that the true values of F may have been greater during both years.

Natural mortality of fishes may fluctuate with seasonal changes in water temperature, and bottom temperature did range between 16.2°C and 28.7°C during this study. Model averaging over candidate models in which M was fixed at different values allowed us to incorporate uncertainty in M when calculating variances for F. Although F was the parameter of interest during this study, better estimates of M would likely have improved the precision and accuracy of our F-estimates. One approach might be tagging in multiple areas to examine spatial differences in F, M, and reporting and to sort out permanent emigration from M. Tag returns from a single fishing season contain limited information about M, so a design is needed that would allow us to analyze returns from the second year after tagging. The low tag returns we obtained from the second year and the return of many tags from South Carolina suggest that emigration from North Carolina waters may have biased estimates of F obtained by using VPA (NCDMF 2004).

Some bias may have been introduced into our annual F-estimates by our use of regression estimates of F for the first 3 months (May to July) during 2005. However, we believe that any bias was probably minor. The seasonal trend in F during 2005 followed a pattern similar to that observed during 2006, the year when we had tag return estimates of F for all months of extensive commercial fishing activity in the river. In addition, although a large portion of the total annual F-estimate for 2005 (52%) was allocated to the 3 months (May to July) when F was estimated from the regression model, those same months contributed a similar, and actually larger, fraction (67%) to the total annual F estimate for 2006. Some additional bias in our annual F-estimates may also have been caused by not including the months January to April during either year. However, we believe this bias would have been small given the lack of returns during January to April and the extremely low commercial landings and effort during these months (Figure 1).

Design of Tag Return Studies

Future tag return studies could improve estimates of F by tagging and releasing fish throughout the distributional range of the stock in order to better understand large-scale migration patterns and estimate regional variation in harvest rate and λ. More substantial (e.g., $\geq$\$100) rewards for high-reward tags might also improve confidence that λ is 100%. Future tag return studies could also estimate seasonal variability in tagging-related mortality by using approaches that minimize or account for the effects of confinement and environmental variability when fish are held in field enclosures (Pollock and Pine 2007). Lastly, better estimates of M may be obtained by using a combination of telemetry and conventional tag return methods (Pollock et al. 2004). Telemetry methods alone have produced reliable seasonal estimates of F and M in large recreational fisheries (Hightower et al. 2001; Thompson et al. 2007), and the combined approach was recently used successfully to separate sources of mortality in a coastal fishery for red drum *Sciaenops ocellatus* that included commercial and recreational sectors (Bacheler 2008).

We used two approaches for analyzing tag returns from single- and double-tagged fish: a joint-likelihood model and an integrated model (Polacheck et al. 2006). Our application of these methods demonstrated the strengths and weaknesses of each. In the joint-likelihood approach, the tag retention component uses exact times at liberty (d) for double-tagged fish. Some fish were returned after only a few days at large, so this method provided a precise estimate of immediate tag retention (compared with the integrated model, for which returns were pooled by month). There were also returns in 2006 of double-tagged fish that had been released in 2005. Those tag returns were not used in the joint-likelihood tag return component or in the integrated model, but in the joint-likelihood tag retention component they produced a reliable estimate of long-term tag retention. The joint-likelihood approach, however, was unable to take full advantage of all available information related to mortality. To satisfy the statistical assumption of independence between likelihood components, we evaluated one approach (method 2) in which double-tagged fish were used for the tag loss component, while fish receiving one standard- or high-reward tag were used in the tag return component. This resulted in a considerable loss of information since 383 fish were double-tagged and 144 of these were returned during the months analyzed in the tag return models. Parameter estimates were, however, similar to those obtained from joint-likelihood method 1, in which we used double-tagged fish in

both the tag retention and tag return components. We ignored the second tag on double-tagged fish (for tag return modeling purposes) in order to use the standard tag return equations derived for fish with only one tag. The two likelihood components were not strictly independent, but L_1 only uses information on double-tagged fish recaptured with one tag versus two tags. That information should not have an effect on mortality rate estimates obtained from the tag return likelihood (Polacheck et al. 2006). Few fish were eliminated from the tag return component by using this method because tag retention was high over the short duration of this study. For a longer study, greater tag loss would probably be observed, so excluding double-tagged fish that had shed the standard tag could result in a potentially large loss of information regarding mortality. The integrated model, on the other hand, was able to simultaneously estimate both mortality and tag retention parameters from recoveries of double-tagged cohorts. The only real disadvantage of this approach was the loss of information about tag retention due to monthly pooling of tagging cohorts (compared with exact times at large used in the joint-likelihood models).

This tag return study provided reliable new information about F for southern flounder because of a careful consideration of model assumptions and the use of a combination of laboratory and field methods to address each assumption. Estimating the various nuisance parameters internally allowed for an assessment of uncertainty in mortality estimates that is not possible when parameters such as tag retention or λ are estimated externally. We have further demonstrated model sensitivity to the exact timing of tagging within each interval and corrected for partial mortality during the initial month of tagging. Tagging southern flounder throughout the year allowed us to characterize the highly seasonal nature of this fishery. Follow-up studies should include tagging throughout the range occupied by the stock in order to sort out mortality and emigration. Those spatially discrete results should be valuable in assessing the regional and overall impacts of future management actions.

Acknowledgments

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