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Estimates of Fishing and Natural Mortality for Subadult Red Drum in South Carolina Waters

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Abstract.—Subadult red drum *Sciaenops ocellatus* were sampled in Charleston, South Carolina, from 1991 to 1999. Tagged individuals were subjected to either live recapture and release by research biologists or harvest and subsequent tag recovery by recreational anglers. Tag recovery data aggregated into 4-month periods were analyzed using Brownie models that were parameterized in terms of fishing effort and instantaneous rates of fishing (F) and natural (M) mortality. Within-year estimates of fishing effort were calculated from the U.S. National Marine Fisheries Service's Marine Recreational Fisheries Statistics Survey and adjusted to reflect a 4-month harvesting period. The level of annual effort appeared stable over all years and was held constant for all analyses; however, the within-year seasonal pattern of fishing effort varied substantially. Estimates of F and M depended heavily on the values used for the tag-reporting rate (λ) and the tag-retention and immediate survival rate (ϕ). For age-1 fish, values of $\phi \cdot \lambda$ ranging from 0.8 to 0.3 produced F values between 0.27 and 0.71 and M values between 0.88 and 0.44, respectively. For age-2 fish, similar values for $\phi \cdot \lambda$ yielded F values of 0.35–0.92 and M values of 1.37–0.83, respectively. The natural mortality estimates for age-2 fish also reflect emigration from the bay and estuarine systems to the coastal ocean.

Red drum *Sciaenops ocellatus* inhabit temperate and subtropical nearshore and estuarine waters along the southern Atlantic coast from Virginia to southern Florida, and throughout the Gulf of Mexico from Florida to northeastern Mexico (Wenner 1992). Historically, red drum have supported several major recreational and commercial fisheries along the eastern coastline. However, increased fishing pressure since 1950 has reduced the abundance of Atlantic red drum and rendered many of those commercial fisheries inoperable. Currently, all commercial fisheries along the Atlantic coast are closed, except in North Carolina where 113,398 kg can be landed annually (NCDMF 1998). Recent stock assessments based on a combined catch data set (Florida, Georgia, North Carolina, and South Carolina) indicated that southern Atlantic populations may be overfished and that subadult mortality (ages 1–4) continues to limit recruitment to the adult population (Vaughan 1992, 1996).

In South Carolina, recreational anglers seek red drum primarily within coastal bays and estuarine waters because in South Carolina adult red drum cannot be retained (SAFMC 1990) and subadult red drum inhabit coastal estuarine environments (adult red drum are generally found offshore). Because fishing pressure occurs primarily on the subadults (Wenner 1992), information on subadult mortality is extremely valuable; that is, recruitment to adulthood will probably fail to maintain a stable population if the subadult population is overexploited.

Despite the importance of red drum as a recreational resource, limited information exists on the population dynamics and life history of red

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drum within South Carolina. In recognition of this deficiency, the South Carolina Wildlife and Marine Resources Department (SCWMRD) began conducting a long-term tagging study on subadult red drum residing within Charleston Harbor and the adjoining Ashley, Wando, and Cooper rivers. The study began in the late 1980s and was designed to generate data that would allow fisheries scientists to infer fishing and natural mortality rates of subadult red drum inhabiting those areas.

In this paper, we analyze the South Carolina red drum tagging study. Recent modifications of the Brownie et al. (1985) models developed by Hoenig et al. (1998a, 1998b) were utilized to analyze red drum tag recovery data from 1991 to 1999. Estimates of total mortality (Z) were calculated and subsequently partitioned into instantaneous rates of fishing (F) and natural (M) mortality. In conjunction with the tagging study three auxiliary studies were conducted to estimate the tag-reporting rate (λ), short-term handling and tag-induced mortality rate (ϕ), and tag-shedding rate. Those results and a sensitivity analysis were examined to characterize their effects on estimates of fishing and natural mortality.

Methods

Tagging protocol.—Monthly tagging of subadult red drum was conducted by SCWMRD scientists from 1991 to 1999. Capture and tagging occurred at designated stations within Charleston Harbor, and each station encompassed several specific sites (Figure 1). Before each tagging event, tagging sites were randomly selected from the sampling stations, but adjacent sites were not sampled unless they were separated by a physical barrier (e.g., creek, dock, etc.). Each month, 12 out of 23 sites were sampled.

At each site, a double-layer monofilament trammel net (180 m long, 2.1 m deep; outer wall, 17.5-cm-square mesh of 0.09-mm monofilament; inner wall, 3.13-cm-square mesh of 0.47-mm monofilament; float line of 1.25-cm polyfoam and 0.95-cm braided polypropylene; lead line, 22.7 kg per 180 m) was set against the shoreline in the form of an arc. We set the net with a rapidly moving (approximately 28 km/h) Florida net boat. Then, the surface of the water in the sealed-off area was violently disturbed with wooden poles to frighten any enclosed fish into the trammel net. The net was retrieved and the catch was placed in onboard oxygenated holding tanks.

Red drum not previously marked and less than 55 cm total length (TL) were tagged with sequentially numbered internal anchor tags and those greater than 55 cm with stainless steel dart tags. The internal anchor tags were inserted into the fish through a small incision in the abdominal cavity. The stainless steel-tipped dart tags were inserted at an angle into the body musculature on the left side of the first dorsal fin (i.e., the ''shoulder'' of the fish). A small sample of scales was removed from each fish greater than 55 cm TL and used to estimate age. Scale samples were also removed from recaptured individuals to examine the repeatability of the age determination in the same individual. Each fish was released at the site of capture immediately after tagging.

Mortality estimation.—Following models described by Hoenig (1998a, 1998b), tag return data are generally represented by an upper triangular matrix of tag recoveries. For example, the matrix for a study with I periods of tagging and J periods of recovery would be

$$R = \begin{bmatrix} r_{11} & r_{12} & \cdots & r_{1J} \\ — & r_{22} & \cdots & r_{2J} \\ \vdots & \vdots & \ddots & \vdots \\ — & — & — & r_{IJ} \end{bmatrix}, \qquad (1)$$

where r_{ij} is the number of tags recovered in period j that were released in period i (note, $j \geq i$ and $J \geq I$).

Application of tag-recovery models involves constructing a matrix of expected values and comparing them to observed data. Under a model formulation that specifies time-specific instantaneous fishing mortality rates and a constant instantaneous natural mortality rate, the matrix of expected values corresponding to equation (1) would be

$$E(R) = \begin{bmatrix} N_1\phi\lambda u_1(F_1, M) & N_1\phi\lambda u_2(F_2, M)e^{-(F_1+M)} & \cdots & N_1\phi\lambda u_J(F_J, M)e^{-(\Sigma_{k=1}^{J-1} F_k+(J-1)M)} \\ — & N_2\phi\lambda u_2(F_2, M) & \cdots & N_2\phi\lambda u_J(F_J, M)e^{-(\Sigma_{k=2}^{J-1} F_k+(J-2)M)} \\ \vdots & \vdots & \ddots & \vdots \\ — & — & — & N_I\phi\lambda u_J(F_J, M)e^{-(\Sigma_{k=I}^{J-1} F_k+(J-I)M)} \end{bmatrix}, \qquad (2)$$

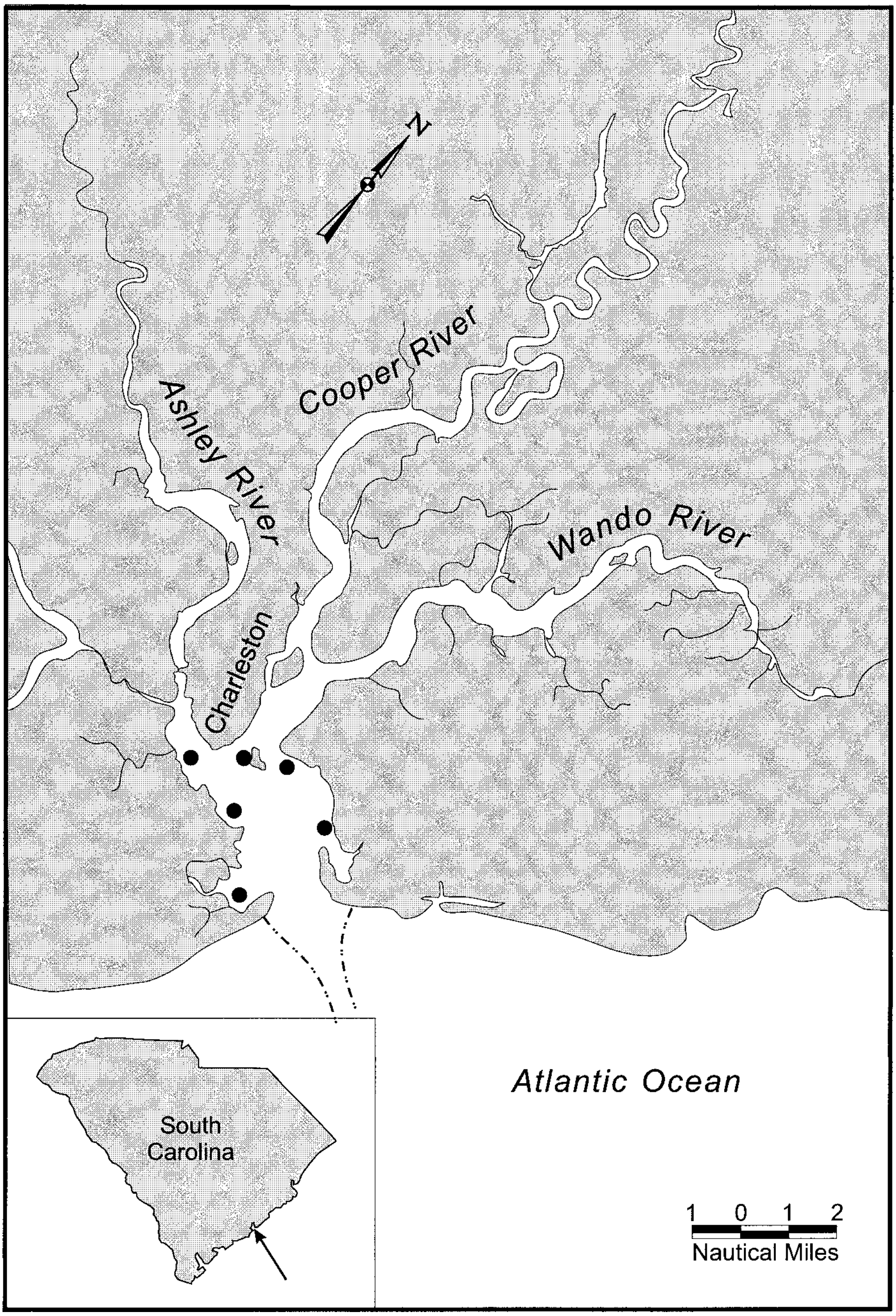

FIGURE 1.—Sampling stations (solid circles) used to study natural and fishing mortality of subadult red drum in South Carolina from 1991 to 1999.

where ϕ is the short-term probability of surviving the tagging process with the tag intact, λ is the tag-reporting rate (ϕ and λ are considered constant over time), and $u_k(F_k,M)$ is the exploitation rate in period k. Note that the exploitation rate u_k is a function of F_k and M and depends on the seasonal pattern of fishing. Specifically, for a pulse (Type I; Ricker 1975) fishery, the relationship $u_k = (1 -$

e^{-F_k}) holds, whereas for a continuous (Type II) fishery, the exploitation rate takes the form $u_k = [F_k/(F_k + M)]\,(1 - e^{-(F_k+M)})$.

Given the instantaneous rates formulation, Hoenig et al. (1998b) showed that it is possible to allow for incomplete mixing of newly tagged animals. If, upon release, newly tagged animals do not mix throughout the tagged population immediately, it follows that those individuals would experience a different fishing mortality rate than previously tagged animals. The matrix of expected values corresponding to equation (1) for a nonmixing model would be

$$E(R) = \begin{bmatrix} N_1\phi\lambda u_1^*(F_1^*, M) & N_1\phi\lambda u_2(F_2, M)e^{-(F_1^*+M)} & \cdots & N_1\phi\lambda u_J(F_J, M)e^{-(F_1^*+\Sigma_{k=2}^{J-1} F_k+(J-1)M)} \\ \text{—} & N_2\phi\lambda u_2^*(F_2^*, M) & \cdots & N_2\phi\lambda u_J(F_J, M)e^{-(F_2^*+\Sigma_{k=3}^{J-1} F_k+(J-2)M)} \\ \vdots & \vdots & \ddots & \vdots \\ \text{—} & \text{—} & \text{—} & N_I\phi\lambda u_J(F_J, M)e^{-(F_I^*+\Sigma_{k=I+1}^{J-1} F_k+(J-I)M)} \end{bmatrix}, \quad (3)$$

where $u_k^*(F_k^*,M)$ is the exploitation rate in period k for those individuals not fully mixed into the tagged population. If $I = J$, then $u_J(F_J, M)$ is replaced by $u_I^*(F_I^*, M)$.

At minimum, application of the Hoenig et al. (1998a, 1998b) models requires information on the number tagged each period and the tag-recovery matrix. Additional information pertaining to fishing effort, tag-induced mortality and retention, and tag-reporting rate (as well as other types of data) can be incorporated into the models. The recovery data from each cohort of tagged fish follow a multinomial distribution, and the computer program AVOCADO (Hoenig et al. unpublished program), which uses the routine *nlmin* in Splus (Seattle, Washington), can be used to calculate maximum likelihood parameter estimates (note that the parameters being estimated depends directly on the model specification).

Model assumptions.—We analyzed age-specific subadult tag-recovery data (1991 to 1999) for red drum with the models described by equations (2) and (3). To generate most estimates, we used models specifying a 4-month period for tagging and recovery and that assumed fishing occurred continuously throughout each period. We considered 6- and 12-month time scales (see Appendix for those results), but recovery matrices reflecting a finer time scale than 4-months were overly sparse and led to imprecise estimates. The exact model parameterization used for data analysis resulted from imposing the following three assumptions (Table 1).

(1) Individuals do not fully mix into the tagged population until they have been at liberty for 4 months. Because subadult red drum exhibit strong fidelity to particular habitat types and areas within the estuarine system (C.A.W., personal observation), we assumed that newly tagged fish would not be able to disperse and fully mix into the tagged population within 4-months. Consequently, a nonmixing model was considered to account for the different fishing mortality rates experienced by newly and previously tagged red drum.

(2) Period-specific fishing mortality was proportional to period-specific effort. The estimation of 4-month fishing mortality rates and a single natural mortality rate over 9 years of data led to a model that contained 28 parameters (27 Fs and 1 M). To reduce the overall number of parameters and provide better precision for those parameters being estimated, period-specific fishing mortality was assumed to be proportional to period-specific fishing effort. That is, $F_k = qE_k$ for each 4-month period k, where E_k is the fishing effort in period k, and the catchability coefficient q is the fraction of the population caught by one unit of fishing effort when that fraction is small (Ricker 1975). This and assumption (1) led to a 3-parameter model (i.e., the model contained the abnormal catchability coefficient q^*, the normal catchability coefficient q, and the natural mortality parameter M). Data from the National Marine Fisheries Service's Marine Recreational Fisheries Statistics Survey (MRFSS) were used to estimate relative fishing effort for each period of the year. The initial bimonthly estimates of fishing effort were adjusted to reflect a 4-month period. Although the within-year effort pattern varied substantially, the annual level of effort did not appear to vary much between years and was assumed to remain constant. Effort

TABLE 1.—Instantaneous rates formulation for expected number of tag recoveries in a three-period tagging study where newly tagged animals are not fully mixed into the tagged population in the period of tagging, fishing mortality is proportional to fishing effort, and natural mortality is constant over time. The following variables are used: N_k = number tagged in period k; q^* = catchability coefficient for newly tagged animals; q = catchability coefficient for previously tagged animals; E_k fishing effort in period k; M = instantaneous rate of natural mortality, $u_k{}^*(q^*E_k, M)$ = exploitation rate for newly tagged animals in period k; $u_k\ (qE_k, M)$ = exploitation rate for previously tagged animals in period k; ϕ = short-term tag retention and survival rate; λ = tag reporting rate.

Period	Recovery period 1	2	3
1	$N_1\phi\lambda u_1^*(q^*E_1, M)$	$N_1\phi\lambda u_2(qE_2, M)e^{-(q^*E_1+M)}$	$N_1\phi\lambda u_3(qE_3, M)e^{-(q^*E_1+qE_2+2M)}$
2		$N_2\phi\lambda u_2^*(q^*E_2, M)$	$N_2\phi\lambda u_3(qE_3, M)e^{-(q^*E_2+M)}$
3			$N_3\phi\lambda u_3^*(q^*E_3, M)$

for shore and private boats was defined as a fishing trip in which the angler specified red drum as the target species (species preference) or a fishing trip in which a red drum was caught. The MRFSS estimates of fishing effort used for each 4-month period from 1991 to 1999 were 0.14 for January to April, 0.34 for May to August, and 0.52 for September to December

(3) Tagging in each period of the year occurs at the midpoint of the 4-month period. The Hoenig et al. (1998a, 1998b) models implicitly assume that all individuals are tagged at the start of each period. Aggregation of data into 4-month periods causes a violation of this assumption because the SCWMRD tagging program is conducted on a monthly basis. Red drum tagged in the first of the 4-month period will experience more fishing and natural mortality than individuals tagged in the last month of the period. Hence, we assumed that all individuals tagged in a 4-month period were tagged at the midpoint of that period. This implied that the fishing and natural mortality rates in the first 4-month period had to be reduced by 50% for each tagged cohort.

The chop option.—We developed a new innovation, known as the ''chop option,'' which is simply a variable that specifies how much of the data in the upper right corner of the recovery matrix should be ignored during the data analysis. Eliminating portions of the recovery matrix is sometimes appropriate because older tagged individuals may exhibit different life history characteristics that produce different mortality rates than apply to younger tagged individuals. Because the oldest tagged fish are those that are marked at the beginning of the study and recaptured near the end of the study, treating recoveries in the upper right corner of the recovery matrix as part of the ''never-seen-again'' category would adjust for potential mortality rate differences between the two groups (recall that tag-recovery data follow a multinomial probability distribution and that a reduction in the number of possible fates for a tagged fish will still yield multinomial data). The value of the chop variable represents the number of diagonals in the matrix treated as not applicable.

The maturity schedules of male and female red drum are known to be slightly different. Specifically, males reach sexual maturity by age 2–3 and females by age 3–4 (Wenner 1992; Vaughan 1996). Regardless of the age at first reproduction, South Carolina red drum emigrate from the estuarine environment and inhabit coastal ocean waters upon commencement of the adult phase of the life cycle (Wenner 1992). Given this life history pattern, it follows that most subadult red drum will remain in the estuaries for about 3–4 years. Because the SCWMRD tagging data spans 9 years, subadults captured in the beginning of the study would have reached sexual maturity and emigrated to the coastal ocean well before the last year of the study. To allow for potential differences in apparent mortality caused by offshore migration, several levels of the chop variable were investigated during the analysis (recall that harvest of adult red drum in South Carolina is prohibited, so fishing mortality will vary spatially). Specifically, the chop variable was varied incrementally, and parameter estimates were calculated under conditions where the number of diagonals eliminated ranged from 0 to 22 (removal of more than 22 diagonals led to numerical difficulties during the estimation process).

Auxiliary studies.—To analyze the red drum tagging data with the model displayed in Table 1, additional information on the tag-reporting rate, the short-term handling mortality rate, and the tag-loss rate was needed. Three auxiliary studies were conducted to estimate those parameters.

(1) The tag-reporting rate was estimated from a high-reward tagging study (Henny and Burnham 1976; Conroy and Blandin 1984; Pollock et al.

1991). Scientists from both South Carolina and Georgia designed a high-reward tagging study to estimate the tag-reporting rate for red drum in each state (Smith and Woodward 1999). Fish were tagged with one of two types of tags: a conventional or standard tag (control) or a high-reward tag offering US$100 for its return. Between October 1996 and July 1997 a total of 1,800 hatchery-produced subadult red drum from wild adults were grown to legal size (35.5 cm TL) and released at three sites within each of two estuaries in both South Carolina and Georgia. The fish were divided into 12 groups of 150, and at each site 75 control tags and 75 high-reward tags were released. Assuming that all of the recaptured high reward tags were reported, overall and state-specific tag-reporting rates were estimated by comparing the recovery rate of control tags with that of high-reward tags. Estimates of past tag-reporting rates were based on that relative recovery rate under the assumption that the behavior of the anglers (e.g., willingness to report recovered tags) remained constant when the high-reward study was initiated.

(2) Short-term tag retention and handling mortality rate was estimated by holding tagged and untagged red drum in six 661-L circular tanks supplied with continuous flowing seawater from Charleston Harbor. Three trials were conducted during each season to examine effects of three disparate ranges of water temperature: warm (spring and autumn: about 15–22°C), hot (summer: about 25–29°C), and cold (winter: about 8–15°C). The temperature, salinity, and level of dissolved oxygen were monitored in each tank during the trials. Red drum used in this study (253 fish summed over all trials and replicates) were captured with standard trammel nets and transported in onboard holding tanks. In the laboratory, fish were randomly designated to be tagged or untagged (control). Fish less than 55 cm TL received internal anchor tags or were anchor tag controls (untagged); fish greater than 55 cm TL received stainless steel dart tags or were dart tag controls (untagged). We handled all fish (tagged or untagged) in the same fashion and used a random procedure to assign fish to the six tanks. Each tank received a mixture of controls and tagged fish. We tried to keep the number of fish in each tank the same, as well as the number of controls and tagged fish of each size category (>55 cm and <55 cm). Capturing enough fish proved difficult for some trials, so to increase the sample size we included previously tagged fish as controls because they had survived at large for at least 1 month and presumably were free of adverse effects caused the by tagging and handling process. After 96 h, all fish were removed from the tanks, examined for tags, condition, and health and then released.

(3) A double-tagging experiment (Beverton and Holt 1957; Seber 1982; Barrowman and Myers 1996) was conducted to estimate the tag-shedding rate in red drum. Models that use recapture information to estimate survival rates rely on the assumption that individuals do not shed their tags. If tag-loss is chronic, then the observed number of recaptures will be less than the actual number of recaptures during any particular sampling event, and survival rates will be underestimated (Fabrizio et al. 1996). From September 1996 to April 1998, a total of 3,954 subadult red drum from the Charleston Harbor area were tagged with either an internal anchor tag (tag type A; 1,884 fish <55 cm) or a stainless steel dart tag (tag type B; 2,080 fish >55 cm). In addition, each fish received a second tag, a nylon dart tag (tag type C), which was inserted into the body musculature near the first dorsal fin; the tip of the tag was locked in the pterygiophores. Monthly recaptures of double-tagged fish provided information on the shedding rates of both the internal anchor tag and the stainless steel shoulder tag.

Results

Reporting Rate, Handling Mortality, and Tag-Shedding

A series of analyses were conducted to estimate the tag-reporting rate for South Carolina and Georgia. A reporting rate of 0.8 was estimated for South Carolina, based on data that were pooled by reward message (Smith and Woodward 1999). However, when ancillary verbal survey information was used to partition the data and adjust for potential biases, the reporting rate estimate for South Carolina was 0.6 (Smith and Woodward 1999).

For the three water temperature ranges, no mortality of subadult red drum less than 55 cm TL was observed (Table 2). For individuals greater than 55 cm TL, capture and handling mortality was apparent only when the water temperature was 25°C or greater. Under these conditions, the mortality rate ranged from 10.0% to 33.3% and averaged 19.1% (note that the 33.3% mortality rate was based on a trial in which only 9 individuals were held).

Tag-shedding models of the form $Q_x = \rho_x e^{-\phi_x t}$, where x = tag type (A, B), ρ_x is the probability of retention immediately after tagging,

TABLE 2.—Handling mortality of subadult red drum after 96 h by size (total length [TL]) and seasonal classification (water temperature).

Trial number	Temperature (°C)		Number tagged (dead)	
	Capture	Tank	>55 cm TL	<55 cm TL
		Cold water (winter)		
1	12.0–14.0	8.0–11.5	20 (0)	20 (0)
2	12.0–13.0	11.2–12.0	20 (0)	33 (0)
3	14.5–19.5	14.8–16.9	12 (0)	13 (0)
		Hot water (summer)		
1	27.0–28.0	27.9–29.1	21 (3)	3 (0)
2	29.0–30.0	26.0–31.5	9 (3)	13 (0)
3	29.0–30.0	25.0–29.0	20 (2)	10 (0)
		Warm water (spring, fall)		
1	20.0–20.4	20.6–22.7	10 (0)	20 (0)
2	18.5–19.0	18.2–19.7	4 (0)	6 (0)
3	15.0–17.5	18.3–19.0	13 (0)	6 (0)

ϕ_x is the instantaneous rate of tag-shedding, and t is time since tagging in months were used to estimate rates of tag loss for the internal anchor tag and the stainless steel dart tag (Barrowman and Myers 1996). The data from each cohort of double-tagged fish follow a multinomial distribution (the categories are months at liberty and tag combination) and the computer program SURVIV (White 1983) was used to calculate maximum-likelihood estimates from the data displayed in Tables 3 and 4.

Estimates from the tag-shedding models indicated that rates of immediate and chronic tag-shedding were small for both tag types (Table 5). Because loss of the shoulder dart tag was not detected until 9 months at liberty and the numbers of fish examined for tag-loss at more immediate times were sufficiently large, the instantaneous rate of tag-shedding for the shoulder dart tag was ignored and the parameter ρ_B was set equal to 1.0 and not estimated.

To obtain a more accurate estimate of chronic tag-loss for the shoulder dart tag, ϕ_B was set equal to 1.0 for the first 8 months fish were at liberty. Hence, the estimate of 0.0043 for ϕ_B was based on double-tagged individuals that were at large for 9 months or more. No adjustments were made to the internal anchor tag-shedding model because there were no obvious patterns in the data set.

Mortality Estimates

Estimates of Z for red drum tagged at age-1 or age-2 under a nonmixing, delayed-tagging, constant-catchability model ranged from 1.29 to 0.97 and from 1.85 to 1.52, respectively, when the severity of the chop option ranged from 0 to 22 diagonals (Table 6). Because the estimates of fishing effort were intentionally scaled so that the sum of the three within-year estimates would total 1.0, the estimates of q are essentially annual estimates of F (note that the scaling procedure rendered the effort estimates unitless). As the chop increased

TABLE 3.—Observed tag loss, as determined from the numbers of fish with two versus one tag at recapture, for subadult red drum at large for 0–14 months and tag(s) at the time of recapture (e.g., tag combination AC denotes recaptured with tag types A and C, whereas C denotes only one recaptured with only a fish type C). Tag type A is the internal anchor tag placed in fish less than 55 cm TL; tag type B is the stainless steel shoulder dart tag placed in fish greater than 55 cm TL; and tag type C is a nylon shoulder dart tag.

Tag(s) at recapture	Number of months at large														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
								AC-tagged fish							
AC	14	36	24	17	22	20	16	15	19	12	11	24	16	11	11
C	0	1	1	0	1	0	0	0	0	0	0	0	1	2	0
								BC-tagged fish							
BC	20	95	46	44	40	49	26	12	18	21	14	12	9	21	6
C	0	0	0	0	0	0	0	0	0	1	0	2	0	1	1

TABLE 4.—Observed tag loss, as determined from the numbers of fish with two versus one tag of recapture, for subadult red drum at large for 15–29 months and tag(s) at the time of recapture (e.g. tag combination AC denotes a fish type C) recaptured with tag types A and C, whereas C denotes only one recaptured with only tag. Tag type A is the internal anchor tag placed in fish less than 55 cm TL; tag type B is the stainless steel shoulder dart tag placed in fish greater than 55 cm TL; and tag type C is a nylon shoulder dart tag.

Tag(s) at recapture	Number of months at large														
	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
AC-tagged fish															
AC	8	16	8	7	12	9	3	1	6	2	7	3	2	0	0
C	0	2	0	1	1	2	1	0	0	0	1	0	0	0	0
BC-tagged fish															
BC	10	13	6	10	3	1	3	2	4	4	6	5	3	0	3
C	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0

from 0 to 22 diagonals, fishing mortality rates for age-1 red drum ranged between 0.39 and 0.32 and natural mortality rates between 0.90 and 0.65. For chop values between 0 and 22, estimates of F for age-2 red drum varied from 0.49 to 0.42 and for M varied from 1.36 to 1.10.

Sensitivity of model results to the parameter $\phi \cdot \lambda$ was investigated for both age classes (Table 7). Estimates of Z remained constant over the range of $\phi \cdot \lambda$ values considered. Small variations in $\phi \cdot \lambda$ produced substantial changes in the estimates of F and M, indicating that partitioning of Z into its natural and fishing components has a strong dependence on the estimate of $\phi \cdot \lambda$. For the age-1 data, estimates of F increased (0.27 to 0.71) and M decreased (0.88 to 0.44) as $\phi \cdot \lambda$ decreased from 0.8 to 0.3; likewise, for the age-2 data, F increased (from 0.35 to 0.92) and M decreased (from 1.37 to 0.83). All of the mortality estimates generated for the sensitivity analysis were based on a model that specified a value of 20 for the chop variable.

Estimates of mortality, when tag loss was incorporated into the data matrices at the rates given by the double-tagging results, were very similar to those calculated in the absence of tag loss (Table 8). Under a model that specified a chop of 20 and a $\phi \cdot \lambda$ value of 0.6, the age-1 estimate of F increased (from 0.35 to 0.36) and the estimate of M decreased (from 0.79 to 0.75). Analysis of the adjusted age-2 data matrix yielded estimates of 0.47 for F and 1.21 for M, which were only slightly different than the values obtained from analysis of the unadjusted recovery matrix (F = 0.46, M = 1.26).

TABLE 5.—Tag-shedding parameter estimates and standard errors for both the internal anchor tag (tag type A) and the stainless steel dart tag (tag type B).

Parameter	Estimate (SE)
Immediate retention of anchor tag, ρ_A	0.9898 (0.012)
Instantaneous rate of anchor tag loss, ϕ_A	0.0031 (0.002)
Immediate retention of shoulder tag, ρ_B	1.0000 (fixed)
Instantaneous rate of shoulder tag loss after 9 or more months at large, ϕ_B	0.0043 (0.001)

Discussion

Reporting Rate

An accurate estimate of λ is needed if the total mortality rate is to be successfully partitioned into its fishing and natural components. The high-reward study designed by South Carolina and Georgia (Smith and Woodward 1999) is a valid method for estimating the tag-reporting rate. However, the results of that study characterize the tag-reporting rate under the conditions existing when the study

TABLE 6.—Total (Z), fishing (F), and natural (M) mortality estimates for age-1 and age-2 red drum from a nonmixing, delayed-tagging, constant-catchability model with $\phi\lambda = 0.6$ and a varied chop option. See text for additional details.

Chop	Z (SE)	$F = qE_k$ (SE)	M (SE)
Age-1 red drum			
0	1.29 (0.08)	0.39 (0.03)	0.90 (0.05)
4	1.29 (0.08)	0.39 (0.03)	0.90 (0.05)
8	1.29 (0.08)	0.39 (0.03)	0.90 (0.05)
12	1.28 (0.08)	0.39 (0.03)	0.89 (0.05)
16	1.23 (0.08)	0.37 (0.03)	0.86 (0.05)
20	1.14 (0.10)	0.35 (0.03)	0.79 (0.07)
22	0.97 (0.17)	0.32 (0.04)	0.65 (0.13)
Age-2 red drum			
0	1.85 (0.13)	0.49 (0.04)	1.36 (0.09)
4	1.85 (0.12)	0.49 (0.04)	1.36 (0.08)
8	1.85 (0.13)	0.49 (0.04)	1.36 (0.09)
12	1.85 (0.13)	0.49 (0.04)	1.36 (0.09)
16	1.85 (0.15)	0.49 (0.05)	1.36 (0.10)
20	1.72 (0.15)	0.46 (0.05)	1.26 (0.10)
22	1.52 (0.20)	0.42 (0.05)	1.10 (0.15)

TABLE 7.—Total (Z), fishing (F), and natural (M) mortality estimates for age-1 and age-2 red drum from a nonmixing, delayed-tagging, constant-catchability model with varied $\phi\lambda$ and a chop of 20 diagonals.

$\phi\lambda$	Z (SE)	$F = qE_k$ (SE)	M (SE)
		Age-1 red drum	
0.80	1.15 (0.11)	0.27 (0.03)	0.88 (0.08)
0.70	1.14 (0.11)	0.30 (0.03)	0.84 (0.08)
0.60	1.14 (0.10)	0.35 (0.03)	0.79 (0.07)
0.50	1.14 (0.11)	0.42 (0.04)	0.72 (0.07)
0.40	1.14 (0.10)	0.53 (0.04)	0.61 (0.06)
0.30	1.15 (0.11)	0.71 (0.05)	0.44 (0.06)
		Age-2 red drum	
0.80	1.72 (0.14)	0.35 (0.04)	1.37 (0.10)
0.70	1.73 (0.15)	0.40 (0.04)	1.33 (0.11)
0.60	1.72 (0.15)	0.46 (0.05)	1.26 (0.10)
0.50	1.72 (0.15)	0.55 (0.05)	1.17 (0.10)
0.40	1.73 (0.16)	0.69 (0.07)	1.04 (0.09)
0.30	1.75 (0.16)	0.92 (0.08)	0.83 (0.08)

was conducted and may not resemble the value of λ before the high-reward program was implemented. Because that program did not begin until the fall of 1996, use of that estimate of λ in the analysis of the tag-recovery matrix encompassing 1991–1996 implicitly assumes that the reporting rate in that period was the same as the estimated λ for the later period.

A key assumption to a high-reward tagging program is that all recaptured high reward tags are reported. To satisfy this assumption, all anglers must be aware of the high reward program and be able to recognize high reward tags instantly. If the high reward study is not advertised, anglers that capture tagged fish may ignore the tag because they do not understand its value. The Smith and Woodward (1999) study was not publicized and efforts were not made to determine if anglers knew of the high-reward program. This makes it impossible to characterize the probability of assumption violation and to determine the accuracy of the South Carolina reporting rate estimate. Nonreporting of high-reward tags can be indirectly tested by conducting an interview survey that determines if anglers are aware of the high reward program. Knowledge that anglers are aware of the high-reward program would minimize assumption violation and reduce the likelihood of overestimating the reporting rate.

Handling Mortality and Tag-Shedding

Immediate tag-shedding and tag-induced mortality do not bias total mortality rate estimates provided the fraction of fish that die or exhibit short-term tag loss is constant over all tagging episodes. However, chronic tag-shedding biases total mortality estimates upward because with each sampling event the observed number of recaptures is less than actual number of recaptures. The results of the double-tagging experiment and the holding trials indicated that $\phi \approx 1$ because immediate tag-shedding was small for both tag types and handling mortality was evident only at low levels and for a select proportion of the subadult population. Although chronic tag loss was observed at low levels with both tag types, analyses that incorporated tag loss into the data matrices did not produce significantly different mortality estimates. For both age

TABLE 8.—Total (Z), fishing (F), and natural (M) mortality estimates when the recovery matrices for age-1 and age-2 red drum were adjusted for chronic tag loss. Tag-recovery adjustments were made in accordance with the results of the double-tagging study. Estimates are based on a nonmixing, delayed-tagging, constant-catchability model with $\phi\lambda$ = 0.6 and a varied chop option.

Chop	Z (SE)	$F = qE_k$ (SE)	M (SE)
		Age-1 red drum	
20	1.11 (0.10)	0.36 (0.03)	0.75 (0.07)
22	0.94 (0.17)	0.33 (0.04)	0.61 (0.13)
		Age-2 red drum	
20	1.68 (0.15)	0.47 (0.05)	1.21 (0.10)
22	1.48 (0.20)	0.43 (0.05)	1.05 (0.15)

groups, estimates of fishing mortality remained relatively constant, but estimates of natural mortality decreased slightly when corrections were made for chronic tag loss.

Mortality Estimates

Red drum tagged at age-1 were expected to remain in the estuarine system for 2–3 additional years (6–9 periods). A model that considered fish older than age 3 or 4 would not be realistic because tagged individuals in that age-group generally are not available for capture. To adjust for offshore emigration, various levels of the chop variable were considered. A recovery matrix with a chop variable between 18 and 21 diagonals appears to be most realistic, based on the emigration schedule of age-1 red drum. The model results corresponding to a chop value of 20 reflect an adequate adjustment for emigration of age-1 fish.

Similarly, red drum tagged at age-2 are likely to be at liberty in the estuarine system for only 1–2 years. This emigration schedule would require chopping 21–24 diagonals. Attempts that considered chop values greater than 20 presented numerical difficulties and led to mortality estimates with large standard errors. The inability to adequately adjust for emigration implies the estimates of M for age-2 red drum represent a combined emigration and natural mortality rate.

Estimates of total mortality for both age classes were invariant to the value of $\phi \cdot \lambda$. Intuitively, this follows because estimation of total survival ($S = e^{-Z}$) does not require information on short-term tagging and handling mortality or tag-reporting rate (Brownie et al. 1985). Comparisons of our total mortality estimates with those reported by Ross et al. (1995) for North Carolina red drum and Vaughan (1992, 1996) for combined southern Atlantic populations yielded many similarities. However, there was significant disagreement when the partition of the overall mortality rate was compared. Ross et al. (1995) used relationships among life history metrics, as proposed by Pauly (1980) and Boudreau and Dickie (1989), to estimate M and obtained significantly lower estimates than ours. However, those methods lack the underlying statistical theory captured in the Hoenig et al. (1998a, 1998b) models. More definitive information on emigration and the tag-reporting rate would be very valuable.

Because red drum have a very long life cycle and the spawning population contains approximately 45 year-classes (assuming a maximum age of about 50 years), the effects of overexploiting the subadult population are not likely to be readily expressed or reversed. This characteristic implies that careful consideration must be exercised in developing management plans for red drum. Although fishing mortality estimates in the range of 0.3–0.7 do not seem excessively high, estimates of total mortality greater than 1.0 for the subadult population raise the question of whether or not recruitment to adulthood has been reduced below the threshold level required to maintain a stable population. Unfortunately, the data needed to effectively study the subadult–adult transition is unavailable because of the closure of the offshore red drum fishery and the lack of sampling outside of the bay and estuarine system.

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Appendix

Estimates of Fishing and Natural Mortality from Models with 6- and 12-Month Tagging and Recovery Periods

Analysis of the model that specified a 6-month tagging and recovery period yielded parameter estimates that were very close to those obtained from the 4-month model for both age-1 and age-2 red drum. (Table A.1). The estimates of *F* and *M* for age-1 individuals ranged from 0.38 to 0.34 and 0.91 to 0.80, respectively, as the chop severity increased from 4 to 12 diagonals. A chop option of 12 diagonals under a 6-month time scale is approximately the same as a chop of 20 diagonals under a 4-month time scale. Thus, a comparison of the adjusted models revealed that both models yielded an estimate of approximately 0.80 for *M* and 0.35 for *F*. The parameter estimates for age-2 red drum from the 6-month model followed a similar qualitative pattern when compared with those of the 4-month model. Estimates of *F* for age-2 individuals were both approximately 0.47, but the estimate of 1.32 for *M* from the 6-month model was slightly higher than the value of 1.26 yielded by the 4-month model.

The age-1 estimate of *F* obtained from the pooled 12-month model was larger than those from the 4- and 6-month models (0.45 compared with 0.35 and 0.34), whereas the age-2 estimates were very similar (0.46 compared to 0.46 and 0.47; Table 9). The age-1 estimates of *M* from the 12-month model were consistently higher than those provided by the 4- and 6-month models (0.91 compared with 0.79 and 0.80). In contrast though, the 12-month age-2 estimates of *M* were slightly lower than those obtained from the 4- and 6-month models (1.17 compared with 1.26 and 1.32). For age-2 red drum, however, the effects of emigration from the study system are very significant. The 4- and 6-month estimates of *M* for this age group should be interpreted as a combination of natural mortality and emigration, and it is possible that the 12-month pooling reduced the overall effect of emigration in the model.

TABLE A.1.—Total (Z), fishing (F), and natural (M) mortality estimates for age-1 and age-2 red drum from a non-mixing, delayed-tagging, constant-catchability model with $\phi\lambda = 0.6$ and a varied chop option. Estimates reflect a 6- or 12-month tagging and recovery period.

Chop	Z (SE)	$F = qE_k$ (SE)	M (SE)
		Age-1 red drum, 6-month recovery	
4	1.29 (0.08)	0.38 (0.03)	0.91 (0.05)
8	1.26 (0.08)	0.37 (0.03)	0.89 (0.05)
12	1.14 (0.09)	0.34 (0.03)	0.80 (0.06)
		Age-2 red drum, 6-month recovery	
4	1.82 (0.14)	0.48 (0.05)	1.34 (0.09)
8	1.82 (0.14)	0.48 (0.05)	1.34 (0.09)
12	1.79 (0.15)	0.47 (0.05)	1.32 (0.10)
		Age-1 red drum, 12-month recovery	
3	1.42 (0.10)	0.49 (0.05)	0.93 (0.05)
6	1.36 (0.17)	0.45 (0.08)	0.91 (0.09)
		Age-2 red drum, 12-month recovery	
3	1.82 (0.20)	0.56 (0.10)	1.26 (0.10)
6	1.66 (0.27)	0.49 (0.12)	1.17 (0.15)