

An Age-Dependent Tag Return Model for Estimating Mortality and Selectivity of an Estuarine-Dependent Fish with High Rates of Catch and Release

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Abstract.—Red drum *Sciaenops ocellatus* support commercial and recreational fisheries in North Carolina, but the stock was overfished in the 1980s because fishing was unregulated. Subsequent fishery regulations increased subadult survival into adult age-classes, but overall stock status is difficult to assess because of migration to ocean waters, prohibited harvest of older fish, and relative importance of catch and release. We analyzed 24 years of tagging data from the North Carolina Division of Marine Fisheries to assess the effects of two regulation changes (effected in 1991 and 1998) on fishing mortality rate (F) and selectivity (SEL) patterns of red drum. We used an age-dependent tag return model that accounted for both harvest and catch-and-release fishing. Using external estimates of natural mortality (M) and annual tag retention rate, we obtained precise estimates of annual F ; an overall tag reporting rate (λ); and fate-specific, age-specific, and regulation-period-specific SEL. Estimated F of fully selected red drum was high and variable before 1991 (mean $F = 2.38$) but decreased in magnitude and variability after 1991. A dome-shaped pattern of SEL was observed for harvested fish in all regulation periods; maximum SEL occurred at age 2, when red drum were of harvestable size and found in more-accessible estuarine waters. Selectivity for caught-and-released red drum generally decreased for younger ages and increased for older ages in later regulation periods. The λ was estimated at 18% and was generally insensitive to changes in the inputs of M or tag retention rate. As catch-and-release fishing increases, tag return models may be important tools for studying fish populations, as long as practical issues, such as λ , tag loss, timing of tagging, and hooking and tagging mortality, are addressed.

The recent surge in popularity of catch-and-release fishing is creating new challenges for management of many fish species (Lucy and Studholme 2002). Many fishery models require knowledge of mortality at a given age or size; catch-and-release fishing poses a problem, because the sizes of released fish (i.e., selectivity [SEL] of releases) are often not available.

When considering catch-and-release fishing, traditional tag return models are hindered by the assumption that all captured fish are harvested; this assumption results in overestimation of exploitation rates (Brownie et al. 1985; Pollock et al. 1991; Hearn et al. 1998; Hoenig et al. 1998a, 1998b). Smith et al. (2000) developed models to adjust survival for situations in which (1) tags of caught fish are clipped just before release, (2) rates of natural mortality (M) and tag reporting (λ) are known, and (3) all variables are age independent. More recently, Jiang et al. (2007) developed an age-dependent model that allows for the separation of fish

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that are caught and released and subsequently harvested; in this model, mortality of harvested fish is differentiated from “mortality” of tags removed prior to the live release of fish. However, Jiang et al.’s (2007) model does not allow for the use of separate SEL values for harvested and caught-and-released fish. This separation is most critical when size regulations are suspected to cause differences in SEL.

Red drum *Sciaenops ocellatus* use estuarine and coastal habitats along the southeastern Atlantic and Gulf coasts of the USA (Wenner 1992). Their management is complicated by catch-and-release fishing. Red drum support major recreational fisheries and a limited bycatch commercial fishery in North Carolina (NCDMF 2001) that primarily focuses on subadult age-classes (i.e., ages 1–3; Wenner 1992). In the North Carolina recreational fishery during most years, released red drum outnumber harvested red drum (National Marine Fisheries Service [NMFS], Fisheries Statistics and Economics Division, Silver Spring, Maryland, unpublished data). Red drum are managed through a variety of regulations in North Carolina, including an annual commercial cap, bycatch allowance limits, and minimum and maximum size limits. Most importantly, harvest of red drum now occurs at the subadult stage and the long-lived adults are not harvested. Therefore, it is difficult to assess the status of red drum, because information on larger, older fish of the spawning stock is limited.

The reduction in vulnerability to the fishery, which is observed in older red drum as they migrate from estuarine to coastal waters, is another factor complicating stock assessment. Harvestable red drum in the southeastern USA occur in easily accessible inland waters, but age-3 or age-4 red drum move towards coastal beaches and inlets, where fishing pressure is probably reduced. Thus, age-independent tag return models, such as the Brownie model or instantaneous-rates versions of the Brownie model (Brownie et al. 1985; Pollock et al. 1991; Hearn et al. 1998; Hoening et al. 1998a, 1998b), are not appropriate. Latour et al. (2001) attempted to ameliorate this problem for subadult red drum in South Carolina by removing the upper-right corner of the age-dependent Brownie recovery matrix (i.e., the “chop option”), which corresponded to the oldest fish (i.e., those most likely to have emigrated from the study system). Alternatively, Jiang et al. (2007) extended the instantaneous-rates tag return model to account for age dependence in fishing mortality and SEL; the explicit modeling of SEL allowed for factors such as emigration to be separated from mortality.

Red drum in North Carolina were overfished in the 1980s, but size and bag restrictions that were implemented in the early 1990s significantly increased subadult survival (escapement into adult age-classes;

Vaughan and Carmichael 2000). Estimated escapement levels from 1992 to 1998, however, were still below the level believed necessary for attaining optimum sustainable yield (Vaughan and Carmichael 2000). The objective of our study was to estimate fishing mortality and SEL of North Carolina red drum via tag return data from harvest and catch-and-release fishing. We extended previous tag return modeling by (1) estimating λ internally (i.e., by fixing M), (2) accounting for tag loss for two types of tags, (3) incorporating the first capture for all caught-and-released red drum, (4) incorporating separate SEL values for harvested and caught-and-released fish, and (5) accounting for fish that were not tagged at the beginning of the year. The study results provide an alternative to traditional stock assessment approaches for red drum management and illustrate how tag returns from catch-and-release fishing can be used to make informed management decisions for other species.

Methods

Red drum have been tagged since 1983 by North Carolina Division of Marine Fisheries (NCDMF) personnel as well as by recreational and commercial fishers. The NCDMF has used various methods to collect red drum opportunistically throughout the study, including pound nets, hook and line, a runaround gill net, trammel nets, and electrofishing (see Burdick et al. [2007] for a full description). Recreational fishers have been involved in tagging since 1984 and primarily target adult red drum. On average, 20 volunteer anglers have tagged red drum each year since recreational tagging began in 1984. Commercial fishers assisted in tagging until 1990, primarily tagging subadult red drum caught in pound nets and gill nets. Only healthy fish were tagged and released.

Internal anchor, nylon dart, and steel dart tags were employed throughout the study. Subadults were mainly tagged with Floy internal anchor tags (FM-84 and FM-89SL from 1987 to 1998; FM-95W from 1999 to 2006). Internal anchor tags were inserted into a small incision made by a scalpel approximately 10 mm posterior to the pelvic fin and dorsal to the midventral line. Nylon dart tags (Floy FT-1 and FT-2) were also used on a limited number of subadults, primarily during the middle years of the study. These tags were inserted posterior to the trailing edge of the dorsal fin at an acute angle so that the dart would lock behind the pterygiophores. Adults were primarily tagged with Hallprint stainless-steel dart tags (FH-69; monofilament core was used from 1984 to 1998; stainless-steel wire core was used thereafter). The dart tags were inserted firmly into the muscle two or three scale rows behind the middle of the first dorsal fin. All tags were labeled with a unique tag number, a message

TABLE 1.—Primary size limits (total length [TL]), bag limits (number of fish), and annual cap (= maximum) in the North Carolina red drum recreational and commercial fisheries during three harvest regulation periods (window = only fish within the TL range could be harvested).

Regulation period	Recreational regulations	Commercial regulations
Early (1983–1991)	Minimum size = 356 mm TL; only 2 fish >812 mm TL	Minimum size = 356 mm TL
Middle (1992–1998)	Window = 457–686 mm TL; bag = 5 fish, only 1 fish > 686 mm TL	Maximum = 113,636 kg; window = 457–686 mm TL
Late (1999–2006)	Window = 457–686 mm TL; bag = 1 fish	Window = 457–686 mm TL; bag = 7 fish

(“REWARD”), and a mailing address. The reward given for returned tags was US\$2 through 1989 and increased to \$5 in 1990. In addition, three \$100 prizes were given away in annual drawings from each year’s returned tags (Ross and Stevens 1992). Upon receipt of information from a recapture event, NCDMF personnel contacted each fisher about the fate of the fish and tag, gear used, and location of capture. Reporting rate was assumed to be equal for dart and internal anchor tags.

We developed a 6-month (January–June and July–December) age–length key derived from 17 years of North Carolina red drum aging data (Ross et al. 1995) to convert fish total length (TL) at tagging to an estimated age based on a January 1 birth date (Takade and Paramore 2007). The 6-month interval was selected because of rapid summer growth rates of subadult red drum in North Carolina. The key provided very good separation of length-groups for fish younger than age 4. Sexually mature red drum were grouped into a single age-bin (age 4 and older [4+]; Ross et al. 1995). Thus, we used four age-groups (ages 1, 2, 3, and 4+) for all analyses. Previous aging work on adult red drum in North Carolina determined that maximum age was 62 years (Ross et al. 1995; NCDMF 2001), suggesting that age-4+ red drum in our study potentially ranged from age 4 to 62.

We estimated annual fishing mortality rates; an overall λ ; and fate-specific, period-specific, and age-specific SEL values by using a modified version of the Jiang et al. (2007) instantaneous-rates formulation. We assumed that the instantaneous fishing mortality rate (F) for fish at age k in year j was $F_{jk} = SEL_k(F_j)$, where SEL_k is the SEL coefficient for age- k fish and F_j is the F in year j for fully recruited fish ($SEL = 1.0$). We extended previous work by modeling SEL separately for harvested fish and caught-and-released fish. We allowed SEL to vary by age but required it to be constant within an age for each of three regulation periods—early (1983–1991), middle (1992–1998), and late (1999–2006)—that corresponded to major management periods in the red drum fishery of North Carolina (Table 1). Based on several trial runs (e.g., switching $SEL = 1.0$ between different age-groups), SEL for harvested fish was set equal to 1.0 for age-2

fish in all periods. Selectivity for caught-and-released fish was set equal to 1.0 for age-1 fish in the early and middle periods and for age-2 fish in the late period.

Jiang et al. (2007) demonstrated how to model tag returns from harvested fish and from fish that are caught and released with their tags clipped. To do this, Jiang et al. (2007) separated the “death” of a tag from the death of a fish; they ignored fish that were caught and released with their tags intact. A large proportion of reported tags in our study, however, came from fish that were caught and released with their tags intact. If we excluded these reported tags, F would be underestimated because catch-and-release mortality would not be accounted for. Tags reported from fish caught and released with tags intact were treated as though they were cut off; subsequent captures of those fish were then ignored. By treating all released fish the same whether their tags were clipped or intact, we were able to account for catch-and-release mortality more accurately than would have been possible if these recoveries had been ignored. Reporting rate was assumed to be equal for harvested and released fish.

The expected number of tags returned (R) from fish tagged at age k , released in year i , and harvested in year j is

$$E(R_{ijk}) = N_{ik} \times P_{ijk}, \tag{1}$$

where

$$P_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk} \right) (1 - S_{ijk}) \\ \times \frac{F_j SEL_{k+j-i}}{F'_j SEL'_{k+j-i} + F_j SEL_{k+j-i} + M_k} \lambda \phi^{j-i} \\ \text{when } j > i \\ (1 - S_{ijk}) \\ \times \frac{T_{Fk} F_j SEL_k}{T_{Fk} F'_j SEL'_k + T_{Fk} F_j SEL_k + T_{Mk} M_k} \lambda \\ \text{when } j = i, \end{cases} \tag{2}$$

in which $S_{ijk} = \exp[-(T_{Fk}F_j\text{SEL}_{k+j-i} + T_{Fk}F'_j\text{SEL}'_{k+j-i}) - T_{Mk}M_k]$.

Here, S_{ijk} is the annual survival rate, N_{ik} is the number of fish that are tagged at age k and released in year i , P is the probability of recovery, F_j is the F experienced by fish, F'_j is the F for tags of fish that were caught and released in year j , SEL is the SEL of harvested fish, SEL' is the SEL of caught-and-released fish, ϕ is the annual tag retention rate, and T is the proportion of the year remaining after the average tagging date (i.e., a multiplier used to adjust F and M , as explained below). A central assumption of Brownie tag return models is that tagging occurs at the beginning of the year, but in our case most red drum were tagged in the final third of the year. If not accounted for, F and M would be biased low in a fish's first year because fish tagged in the fall would have a much shorter period over which to experience mortality. We accounted for fall tagging by multiplying all F - and M -values of fish in their first tagging year by 0.33 (i.e., both T_{Fk} and $T_{Mk} = 0.33$), because most tagging occurred in the final third of the year. Because age-1 fish first recruit to the fishery in the fall and therefore only experience F during the last 4 months of each year, no adjustment was required for their F -value ($T_{F1.0} = 1.00$).

The expected number of tag returns from fish tagged at age k , released in year i , and caught and released in year j is calculated as

$$E(R'_{ijk}) = N_{ik} \times P'_{ijk}, \tag{3}$$

where

$$P'_{ijk} = \begin{cases} \left(\prod_{v=i}^{j-1} S_{ivk} \right) (1 - S_{ijk}) \\ \quad \times \frac{F_j \text{SEL}'_{k+j-i}}{F_j \text{SEL}'_{k+j-i} + F_j \text{SEL}_{k+j-i} + M_k} \lambda \phi^{j-i} \\ \text{when } j > i \\ \\ (1 - S_{ijk}) \\ \quad \times \frac{T_{Fk} F'_j \text{SEL}'_k}{T_{Fk} F'_j \text{SEL}'_k + T_{Fk} F_j \text{SEL}_k + T_{Mk} M_k} \lambda \\ \text{when } j = i, \end{cases} \tag{4}$$

and S_{ijk} is calculated as described for equation (2). Based on the work of Jiang et al. (2007), the tag returns due to harvest (R_{ijk}) and catch and release (R'_{ijk}) from N_{ik} fish follow a multinomial distribution. Therefore,

the likelihood function (L) is

$$L = \prod_{k=1}^K \prod_{i=1}^I \binom{N_{ik}}{R_{iik}, R_{ii+1k}, \dots, R_{iJk}, R'_{iik}, R'_{ii+1k}, \dots, R'_{iJk}, N_{ik} - \sum_{j=i}^J (R_{ijk} + R'_{ijk})} \times \left(\prod_{j=i}^J P_{ijk}^{R_{ijk}} P'_{ijk}^{R'_{ijk}} \right) \times \left[1 - \sum_{v=i}^J (P_{ivk} + P'_{ivk}) \right]^{N_{ik} - \sum_{v=i}^J (R_{ivk} + R'_{ivk})} \tag{5}$$

Maximum likelihood estimates of the model parameters were obtained using SURVIV software (White 1983), which permits coding of the multinomial cell probabilities P_{ijk} .

Our initial estimate of F pertained to harvested fish only and thus did not include any estimate of hooking mortality. To account for effects of hook-and-release mortality on F , the following equation was used to adjust F upward (F_{adjusted}) based on a catch-and-release mortality rate ($\delta = 10\%$) previously estimated for red drum (Jordan 1990) and F' of caught-and-released fish:

$$\hat{F}_{j,\text{adjusted}} = \hat{F}_j + \delta \hat{F}'_j. \tag{6}$$

We fixed tag retention rates of dart and internal anchor tags separately based on previous studies. Burdick et al. (2007) analyzed nylon and steel dart double-tagging data from 2001 to 2004 for adult red drum and found no difference in tag retention between dart tag types. Overall, they estimated an annual retention rate of 0.74 for both dart tag types; this rate was used in our model. To estimate retention of internal anchor tags, we used the arithmetic mean of four studies on red drum and similar species; those studies used double tagging in pond and tank experiments (Sprankle et al. 1996; Wallin et al. 1997; Henderson-Arzapalo et al. 1999; Latour et al. 2001). Each study examined retention rates for Floy internal anchor tags, but we used the FM-84 estimates from Henderson-Arzapalo et al. (1999) because FM-84 was the most commonly used internal anchor tag in our study. Annual retention rates varied between 0.850 and 0.963, and the mean value of 0.91 was used in our baseline model.

To partition F and M using tag return data, λ must be

known. Unfortunately, λ is difficult to estimate for fish in general (Pollock et al. 1991, 2001, 2002; Hearn et al. 2003) and for red drum in particular (Denson et al. 2002). We assumed that we had better knowledge of M than of λ , so we fixed age-dependent M -values for red drum based on a life history estimator that uses body size as a predictor variable (Boudreau and Dickie 1989). This is the same method used to estimate M in the current North Carolina stock assessment. For each age-group, we converted length at tagging to weight based on the equation provided by Ross et al. (1995). The M was thus set at 0.30 for age 1, 0.22 for age 2, 0.16 for age 3, and 0.10 for age 4+. By fixing values of M , we could estimate yearly values of F ; fate-specific, regulation-period-specific, and age-specific SEL; and λ . The age-specific M -values were bracketed by lower (chosen by informed judgment) and higher (Lorenzen 1996) values of M over a range of tag retention rates to examine sensitivity of estimated λ to these two parameters.

An assumption of the Brownie et al. (1985) tag return model is that fish mix thoroughly before harvest. If newly tagged fish are not able to mix with untagged fish before harvest, the tagged individuals may experience a different F than untagged fish and therefore would not be representative of the larger population. Hoenig et al. (1998b) showed that incomplete mixing could be allowed by using a nonmixing model to estimate mortality in the first period separately from mortality in the subsequent periods. Because of the nature of our age-dependent model, use of a nonmixing model would have caused a loss of all information on F and SEL of age-1 fish. Instead, tag returns occurring within 7 d of tagging were excluded from analysis to allow some time for fish to mix with the larger population (e.g., Jiang et al. 2007).

In our full model, F was allowed to vary by year and SEL was allowed to vary by fate, age, and regulation period. Reduced models assumed that F -values were constant within regulation periods or across all years of the study or that SEL was constant across all red drum ages, constant across all years of the study within a particular age-class, or equal for harvested and caught-and-released fish. We compared 14 reduced models with our full model using Akaike's information criterion (AIC), which selects the model with the lowest AIC value based on the best tradeoff between the number of parameters and likelihood of the models (Burnham and Anderson 2002). The AIC values were computed as

$$AIC = -2 \log[l(\hat{\theta}|y)] + 2k, \quad (7)$$

where $\log[l(\hat{\theta}|y)]$ represents the log-likelihood func-

tion evaluated at the maximum likelihood estimates $\hat{\theta}$ given the data y ; k represents the number of parameters.

If tagged fish are not completely independent, overdispersion can result. Burnham and Anderson (2002) recommended a quasiliikelihood AIC approach (QAIC) for cases in which overdispersion is the reason for lack of model fit. The QAIC values are computed as

$$QAIC = -2 \log[l(\hat{\theta}|y)]/\hat{c} + 2k, \quad (8)$$

where \hat{c} is a variance inflator factor, which can be calculated as

$$\hat{c} = \chi^2/df, \quad (9)$$

where χ^2 corresponds to the chi-square value of the Pearson goodness-of-fit test of the most general model in the considered set of models and df represents the degrees of freedom for the test. We inflated all SEs in this paper by the square root of \hat{c} , as suggested by Burnham and Anderson (2002).

Results

Overall, 45,295 red drum were tagged from 1983 to 2006 and used in our analyses. The fewest fish were tagged in 1983 ($N = 92$ fish), whereas the largest number was tagged in 1994 ($N = 5,054$ fish). Ages 1 and 4+ were tagged much more frequently than ages 2 and 3 (Table 2). The proportion of fish tagged with internal anchor tags (instead of dart tags) declined with age: 0.90 for age 1, 0.74 for age 2, 0.25 for age 3, and 0.01 for age 4+.

Commercial and recreational fishers reported tags from 4,722 red drum (10.4% of the total number tagged), of which 2,439 were harvested, 1,483 were released with tags intact, and 800 were released after the tags had been cut off. The ultimate fate of a fish and tag depended on year and age at recovery (Figure 1). The proportion of fish harvested generally decreased over time for all age-groups and the proportion of fish that were caught and released generally increased over time; these trends were most obvious for ages 1 and 4+. In most years and age-groups, the proportion of fish released with tags intact was greater than the proportion released after the tags had been cut off.

Based on AIC and QAIC values, the best model was our full model, which allowed F to vary by year and SEL to vary by fish fate, regulation period, and age (Table 3). None of the reduced models was considered a viable candidate based on AIC or QAIC. Our estimate of \hat{c} was 5.68 from the full model; therefore, all SEs were inflated by 2.38 (i.e., square root of 5.68).

The F_{adjusted} , which accounted for catch-and-release mortality, was variable over the study period for fully selected fish (Figure 2A). During the early regulation

TABLE 2.—Number of red drum that were tagged and recovered in North Carolina recreational and commercial fisheries, 1983–2006. Fish were assigned to one of four age-groups (1, 2, 3, or 4 and older [4+]) by use of an age-length key.

Year	Age at tagging					Total	Age at recovery				
	1	2	3	4+	1		2	3	4+	Total	
1983	74	2	0	16	92	16	0	0	0	16	
1984	22	52	10	220	304	5	4	0	1	10	
1985	42	15	18	224	299	4	3	1	0	8	
1986	1,517	44	21	137	1,719	76	4	1	2	83	
1987	459	32	9	219	719	95	45	1	5	146	
1988	783	36	13	346	1,178	155	21	3	7	186	
1989	283	107	51	502	943	76	44	11	12	143	
1990	110	149	117	454	830	15	35	10	13	73	
1991	2,214	69	31	531	2,845	267	9	1	10	287	
1992	1,158	311	41	406	1,916	98	86	2	7	193	
1993	1,429	599	152	470	2,650	128	153	29	9	319	
1994	3,768	224	205	857	5,054	816	59	32	12	919	
1995	428	391	50	616	1,485	26	190	8	24	248	
1996	290	132	67	630	1,119	20	20	14	17	71	
1997	1,962	124	34	706	2,826	159	30	10	14	213	
1998	1,326	1,614	47	708	3,695	50	256	6	25	337	
1999	1,011	1,004	186	852	3,053	28	135	38	25	226	
2000	602	563	214	1,052	2,431	41	135	44	35	255	
2001	171	388	260	921	1,740	8	102	78	35	223	
2002	193	112	112	1,003	1,420	7	16	23	45	91	
2003	47	338	145	777	1,307	4	21	8	16	49	
2004	272	30	141	1,035	1,478	13	2	4	0	19	
2005	397	547	129	1,158	2,231	26	75	3	32	136	
2006	551	1,802	348	1,250	3,951	42	318	44	67	471	
Total	19,119	8,685	2,401	15,090	45,295	2,175	1,763	371	413	4,722	

period, F was high and variable (mean = 2.38, minimum = 0.80 [1991], maximum = 3.90 [1989]). In the middle and late regulation periods, however, F was consistently lower, reaching a minimum of 0.27 in 2004 and never exceeding 2.20 in any year. The mean F of fully selected fish was similar between the middle (0.59) and late (0.90) periods.

The F' generally increased throughout the study (Figure 2A). No red drum were caught, released, or reported in 1983 or 1985, so F' in those years was 0. Excluding those years, F' varied between 0.09 and 1.47.

Regulation changes did not affect all age-groups of red drum equally (Figure 2B). The mean F for age-1 red drum was 1.54 in the early regulation period, declined to 0.16 in the middle period (decrease = 1.38, or 90%), and further decreased to 0.06 in the late period (decrease = 0.10, or 63%). For ages 2 and 3, F decreased (by 80% and 83%, respectively) only in the middle regulation period (i.e., there was no additional decrease in the late period). The F of age-4+ fish was low in the early regulation period (0.07), decreased to 0.03 in the middle period, and was 0.00 in the late period.

Selectivity of tagged red drum in North Carolina varied by fate, regulation period, and age (Figure 3). In all periods, a dome-shaped curve was observed for the

SEL of harvested red drum, and maximum SEL was observed for age-2 fish (Figure 3A). The SEL of harvested age-1 fish decreased with each change in regulation. For caught-and-released fish, SEL was highest for age 1 and decreased for older ages in the early and middle periods (Figure 3B); age-2 fish were fully selected in the late period.

We estimated an overall λ of 0.18 (SE = 0.01) from our baseline model and had slightly higher estimates when higher M or lower tag retention rates were used (Table 4).

Discussion

Our tag return modeling technique provided an effective and succinct approach to estimate patterns of F and SEL for an estuarine species experiencing high rates of catch-and-release fishing. We accounted for catch-and-release mortality associated with the first capture of released fish, used separate SEL values for fish of different fates, estimated λ internally, and incorporated tag loss for two tag types. We also modified the tag return model to accommodate tagging at times other than the start of the year. By making these modifications with 24 years of tagging and recovery data, we were able to estimate model parameters with high precision and to show that patterns of F and SEL were influenced by regulations

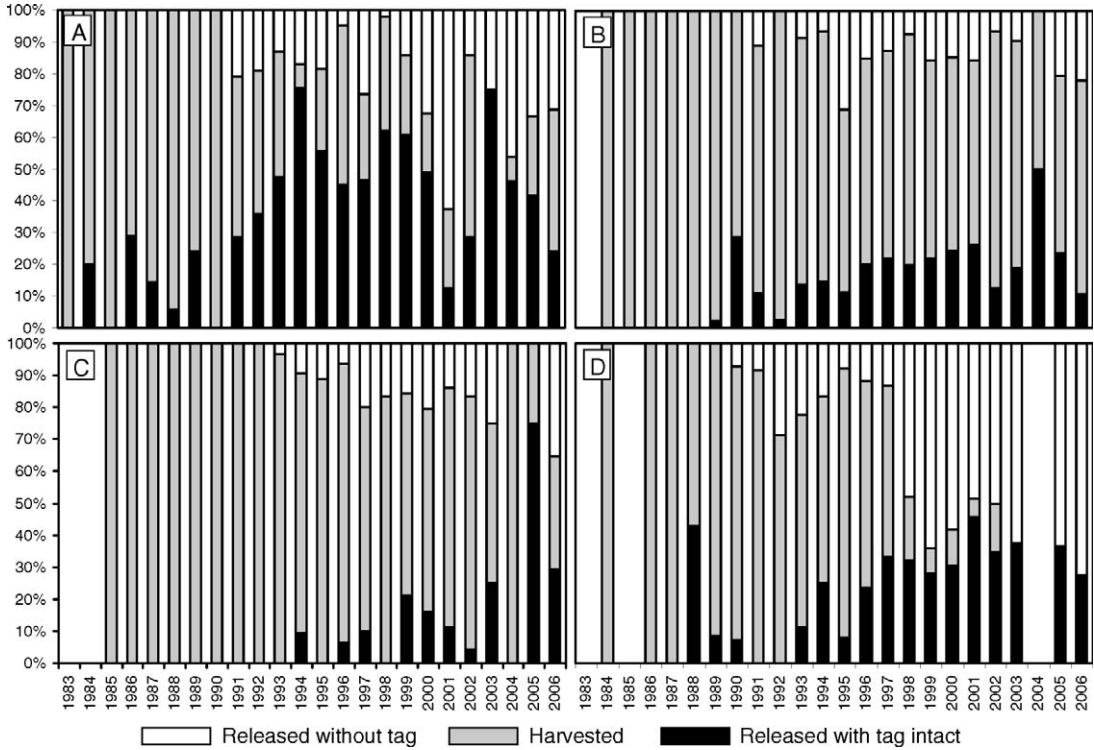


FIGURE 1.—Percentage of yearly (1983–2006) tag returns in North Carolina for four age-groups (age at recovery) of red drum that were caught and released without their tags (white bars); harvested (gray bars); or caught and released with tags intact (black bars): (A) age 1, (B) age 2, (C) age 3, and (D) age 4 and older.

in North Carolina. Our methodology advances the field of fisheries tag return modeling and provides a unique complement to traditional stock assessment techniques (Pine et al. 2003; Walters and Martell 2004).

In Brownie tag return models, the fate of the fish and tag is most critical. Developed originally for waterfowl, Brownie models traditionally assumed that all reported tags were from harvested animals. Recent modifications by Jiang et al. (2007) extended the Brownie framework to include fish that were caught and released with their tags cut off. We refined the Jiang et al. (2007) model to include fish that were caught and released with their tags intact, because a large proportion of our study fish were in this fate category. Failure to include reported tags from fish that were caught and released with their tags intact would have resulted in the underestimation of catch-and-release mortality and, ultimately, F . By treating fish released with intact tags as though the tags had been cut off and by excluding subsequent recoveries of this group of fish, we could more accurately represent the true impact of catch-and-release fishing on red drum. A drawback of this approach is the exclusion of 4% of the recoveries that occurred after the initial recovery and

TABLE 3.—Akaike’s information criterion (AIC) and quasiliikelihood AIC (QAIC) values for 15 models with varying assumptions about fishing mortality (F) and selectivity (SEL) of red drum in North Carolina, 1983–2006 (l = likelihood; subscripts: y = year-specific value, f = fate specific, p = regulation period specific [see Table 1 for description of regulation periods], a = age specific, period = constant value).

Model	Number of parameters estimated	Log l	AIC	QAIC
F_ySEL_{fap}	65	-2,034	4,198.7	1,839.2
F_ySEL_{fa}	53	-2,216	4,537.8	1,968.2
F_pSEL_{fap}	25	-2,424	4,897.6	2,087.0
F_pSEL_{fa}	21	-2,444	4,930.0	2,095.8
F_ySEL_{ap}	56	-2,442	4,995.9	2,164.1
F_ySEL_a	50	-2,489	5,077.7	2,191.6
F_pSEL_{fa}	13	-2,645	5,316.7	2,248.7
F_pSEL_{fa}	9	-2,667	5,351.8	2,259.2
F_pSEL_{ap}	16	-2,807	5,646.4	2,390.8
F_pSEL_{ap}	12	-2,837	5,699.0	2,408.0
F_pSEL_a	10	-2,876	5,772.9	2,436.8
F_pSEL_a	6	-2,999	6,010.4	2,532.2
$F_ySEL.$	47	-4,029	8,151.8	3,479.7
$F_pSEL.$	7	-4,471	8,956.5	3,771.1
$F_pSEL.$	3	-4,556	9,118.8	3,834.6

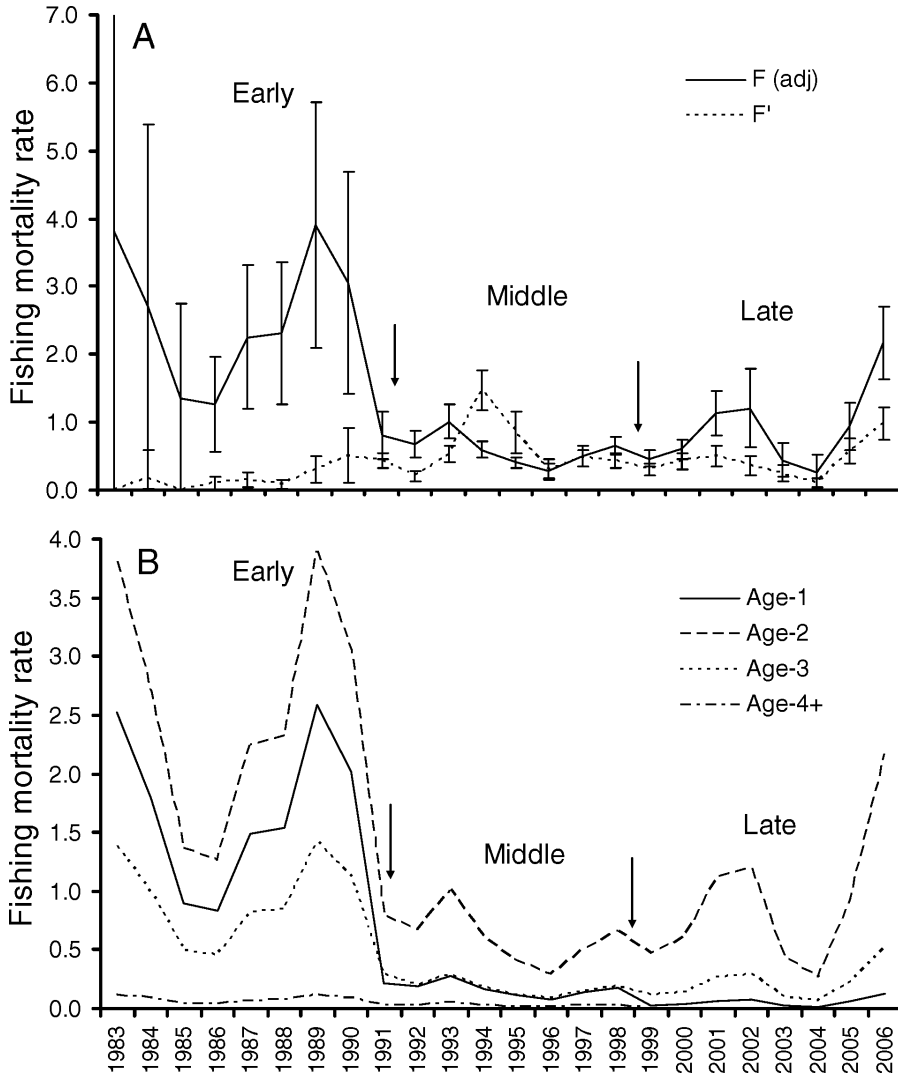


FIGURE 2.—Red drum mean (\pm SE) fishing mortality rate (F) during early (1983–1991), middle (1992–1998), and late (1999–2006) regulation periods (arrows define periods, which are further defined in Table 1) in North Carolina: (A) adjusted F ($F[\text{adj}]$; solid line) and “mortality” of tags (F' ; dotted line) for fully selected fish and (B) age-specific F for ages 1, 2, 3, and 4 and older (4+). Note the difference in y-axis scale between the two panels.

report by a fisher. However, this loss of information was much lower than the loss that would have been incurred due to exclusion of all fish caught and released with tags (35% of recoveries). The advantage of including multiple recaptures is slightly better precision; the disadvantage is a much more complex likelihood computation. The complexity results from recapture events occurring at random times; each fish that is caught and released with an intact tag would have to be modeled separately to account for the unique fraction of the year during which the fish was at large after the first catch-and-release event.

By estimating patterns of SEL explicitly in the tag return model, we avoided the need to discard data on older fish (e.g., Latour et al. 2001). We refined the Jiang et al. (2007) approach and were able to quantify the complex patterns of SEL for North Carolina red drum; these patterns were influenced by fish age, regulation period, and fate of the fish at recovery. It was not surprising that SEL depended on age of red drum, given the presence of a slot limit centered on one or two age-classes and perceived age-dependent emigration rates (Ross et al. 1995). Our tagging approach also showed that regulations not only

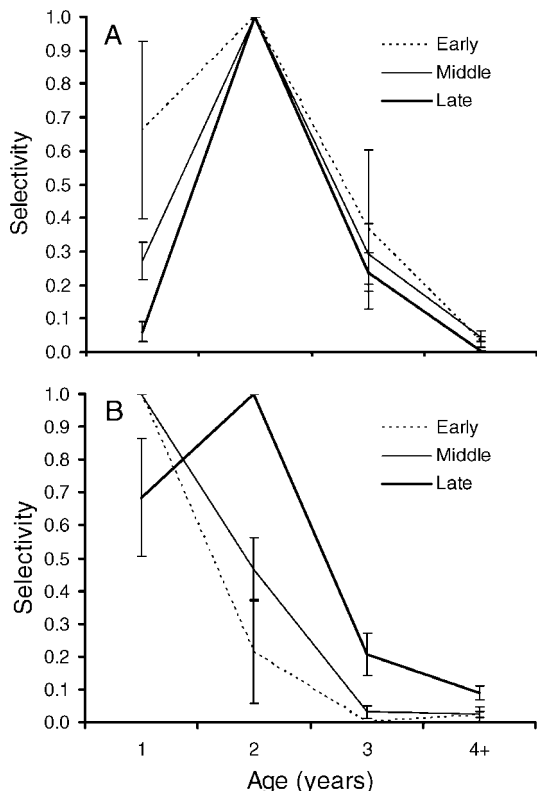


FIGURE 3.—Mean (\pm SE) selectivity rate (SEL; as determined by tagging) during early (1983–1991), middle (1992–1998), and late (1999–2006) regulation periods (further defined in Table 1) in North Carolina for red drum (ages 1, 2, 3, and 4 and older [4+]) that were (A) harvested or (B) caught and released. Error was not estimated when SEL was set equal to 1.

influenced red drum F but clearly affected patterns of SEL as well. For instance, during the middle regulation period, when harvest of red drum less than 457 mm TL was prohibited, SEL for harvested age-1 fish dropped by 90%. Furthermore, the fate of the fish at recovery, whether released or harvested, influenced the patterns of SEL. For example, SEL of all age-groups of caught-and-released red drum (except age 1) has increased in recent regulation periods, suggesting increases in catch-and-release fishing of red drum in North Carolina.

We estimated a λ (18%) that was lower than those reported in previous work on red drum. Green et al. (1983) estimated a λ of 36% for red drum that were tagged surreptitiously during creel surveys in Texas. Denson et al. (2002) estimated that λ of recreational fishers was 56.7% in South Carolina and 63.4% in Georgia, where high-reward tagging methods were used. There are three possible explanations for the

TABLE 4.—Estimated tag reporting rates for red drum in North Carolina recreational and commercial fisheries under differing internal anchor tag retention rates and under three scenarios of differing natural mortality rates (M) for four age-groups (1, 2, 3, and 4 and older [4+], respectively): (1) 0.25, 0.20, 0.15, and 0.10 (low values chosen based on informed judgment); (2) 0.30, 0.22, 0.16, and 0.10 (Boudreau and Dickie 1996); and (3) 0.47, 0.35, 0.26, and 0.18 (Lorenzen 1996). Bold value is the reporting rate estimated in a baseline model.

Tag retention rate	M scenario		
	1	2	3
0.95	0.16	0.16	0.19
0.91	0.17	0.18	0.20
0.85	0.19	0.19	0.22
0.80	0.20	0.20	0.23

difference in λ between our study and that of Denson et al. (2002). First, South Carolina and Georgia lack the significant commercial fisheries that exist in North Carolina (NMFS Fisheries Statistics and Economics Division, unpublished data). Because the commercial sector is speculated to report fewer tags than their recreational counterparts, future studies should quantify differences in λ by fishing sector. Second, to avoid influencing the behavior of anglers, high-reward tagging was not advertised in the Denson et al. (2002) study; however, an unintended consequence of no advertising is that fishers may not recognize high-reward tags easily and thus may not report them (Pollock et al. 2001). Serious positive bias in λ occurs when fishers do not report high-reward tags (Conroy and Williams 1981). Lastly, we assumed no tagging mortality, and this assumption, if false, could have led to a downward bias in λ (see below).

It is possible that λ of NCDMF tags increased beginning in 2005. Since early 2005, high-reward tagging of red drum has been used in a complementary study in North Carolina and has been advertised widely in the state; this probably resulted in an increase in λ of NCDMF tags. If λ increased, then F in 2005 and 2006 was probably overestimated and should be viewed cautiously. Because the presence of high-reward tagging can influence the λ of low-reward tags, high-reward tagging should be used either during the entire tagging study or not at all (Pollock et al. 2001).

Our analysis would have been improved if external information about λ had been available, which might have allowed us to estimate red drum M . High-reward tagging, surreptitiously planted tags, angler or port surveys, and catch data from multiple fishery components with a λ of 100% from one component have all been used to estimate λ (Pollock et al. 2002). Perhaps

the best approach is to build into the tagging program an annual experiment to estimate λ (Pollock et al. 2001). For a situation (like ours) in which annual experiments are not conducted, a reasonable alternative is to use information about life history to obtain an assumed M and to produce a robust estimate of λ that is conditional on the assumed M . Ultimately, multiple methodologies to estimate λ will allow more-accurate quantification of F and M .

We had to make assumptions in our tag return model. First, by excluding fish that were recaptured within 7 d, we assumed that we could limit problems associated with nonmixing. If a nonmixing model (Hoenig et al. 1998b) had been used, our estimated F for age-1 fish would have applied only to fish with tags and not to the population as a whole. Longer exclusionary periods would have led to biased estimates, because the numbers of nonreported tags not accounted for when excluding tags would have increased. Second, we assumed that no mortality occurred from the tagging process. A large proportion of fish tagged early in the study were captured out of pound nets, and most of the younger fish were collected more recently with electrofishing; these methods of capture probably result in very low posttagging mortality. Hook-and-line methods were used to collect some of the younger fish and most of the age-4+ red drum in this study; only the healthiest fish were tagged, and the tagging was performed by trained professionals. Latour et al. (2001) employed tank studies in South Carolina to demonstrate that mortality of red drum tagged in water less than 25°C was zero, but mortality of large red drum (>55 cm TL) tagged at temperatures warmer than 25°C was 19.1%. The majority of fish in our study were tagged during fall months, when water temperatures were below 25°C. If posttagging mortality did occur, then λ may have been underestimated. Third, we assumed that λ was equal across all ages and between harvested and released fish. We do not know whether these assumptions are reasonable; however, there is no evidence in the literature to the contrary. Last, parameter estimates could be biased if tagged fish were assigned ages that were incorrect because of the use of an age-length key. We view this as an unlikely source of bias because of the rapid growth and clear separation of length modes through age 3.

Tag return studies can also be improved by using telemetry to obtain detailed information about M (Hightower et al. 2001; Heupel and Simpfendorfer 2002). Combining telemetry and tag return methods allows for reliable estimation of λ and improves the precision of M and F estimates (Pollock et al. 2004). We also suggest that double-tagging experiments be

used to estimate tag retention rates (Seber 1982). Tagging should also be done at the beginning of the year, ideally before the fishery opens; if this is not possible, then the adjustment provided in this paper can be used. Last, high-reward tagging should accompany tag return studies to obtain λ (Pollock et al. 2001), and λ should be estimated separately for each fishing sector, fish age, and fate. With the inclusion of auxiliary studies to estimate tag retention, M , λ , and tagging mortality, tag return models will go even further to provide robust estimates of critical population parameters that could greatly benefit the management of diverse marine and freshwater fisheries.

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References

- Boudreau, P. R., and L. M. Dickie. 1989. Biological model of fisheries production based on physiological and ecological scalings of body size. *Canadian Journal of Fisheries and Aquatic Sciences* 46:614–623.
- Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. *Statistical inference from band-recovery data—a handbook*, 2nd edition. U.S. Fish and Wildlife Service Resource Publication 156.
- Burdick, S. M., J. E. Hightower, J. A. Buckel, K. H. Pollock, and L. M. Paramore. 2007. Movement and selectivity of red drum and survival of adult red drum: an analysis of 20 years of tagging data. North Carolina Division of Marine Fisheries, Final Report, Morehead City.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and inference: a practical information-theoretic approach*, 2nd edition. Springer-Verlag, New York.
- Conroy, M. J., and B. K. Williams. 1981. Sensitivity of band reporting-rate estimates to violations of assumptions. *Journal of Wildlife Management* 45:789–792.
- Denson, M. R., W. E. Jenkins, A. G. Woodward, and T. I. J. Smith. 2002. Tag-reporting levels for red drum (*Sciaenops ocellatus*) caught by anglers in South Carolina and Georgia estuaries. U.S. National Marine Fisheries Service Fishery Bulletin 100:35–41.
- Green, A. W., G. C. Matlock, and J. E. Weaver. 1983. A method for directly estimating the tag-reporting rate of anglers. *Transactions of the American Fisheries Society* 112:412–415.
- Hearn, W. S., J. M. Hoenig, K. H. Pollock, and D. A.

- Hepworth. 2003. Tag reporting rate estimation: 3. Use of planted tags in one component of a multiple-component fishery. *North American Journal of Fisheries Management* 23:66–77.
- Hearn, W. S., K. H. Pollock, and E. N. Brooks. 1998. Pre- and postseason tagging models: estimation of reporting rate and fishing and natural mortality. *Canadian Journal of Fisheries and Aquatic Sciences* 55:199–205.
- Henderson-Arzapalo, A., P. Rago, J. Skjveland, M. Mangold, P. Washington, J. Howe, and T. King. 1999. An evaluation of six internal anchor tags for tagging juvenile striped bass. *North American Journal of Fisheries Management* 19:482–493.
- Heupel, M. R., and C. A. Simpfendorfer. 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences* 59:624–632.
- Hightower, J. E., J. R. Jackson, and K. H. Pollock. 2001. Use of telemetry methods to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society* 130:557–567.
- Hoenig, J., N. Barrowman, W. Hearn, and K. Pollock. 1998a. Multiyear tagging studies incorporating fishing effort data. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1466–1476.
- Hoenig, J., N. Barrowman, K. Pollock, E. Brooks, W. Hearn, and T. Polacheck. 1998b. Models for tagging data that allow for incomplete mixing of newly tagged animals. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1477–1483.
- Jiang, H., K. H. Pollock, C. Brownie, J. M. Hoenig, R. J. Latour, B. K. Wells, and J. E. Hightower. 2007. Tag return models allowing for harvest and catch and release: evidence of environmental and management impacts on striped bass fishing and natural mortality rates. *North American Journal of Fisheries Management* 27:387–396.
- Jordan, S. R. 1990. Mortality of hook-caught red drum and spotted seatrout in Georgia. Georgia Department of Natural Resources, Brunswick.
- Latour, R. J., K. H. Pollock, C. A. Wenner, and J. M. Hoenig. 2001. Estimates of fishing and natural mortality for subadult red drum in South Carolina waters. *North American Journal of Fisheries Management* 21:733–744.
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology* 49:627–647.
- Lucy, J. A., and A. L. Studholme, editors. 2002. Catch and release in marine recreational fisheries. American Fisheries Society, Symposium 30, Bethesda, Maryland.
- NCDMF (North Carolina Division of Marine Fisheries). 2001. Red drum fishery management plan. North Carolina Department of Natural and Environmental Resources, Morehead City.
- Pine, W. E., III, K. H. Pollock, J. E. Hightower, T. J. Kwak, and J. A. Rice. 2003. A review of tagging methods for estimating fish population size and components of mortality. *Fisheries* 28(10):10–23.
- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* 21:521–532.
- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2002. Tag reporting rate estimation: 2. Use of high-reward tagging and observers in multiple-component fisheries. *North American Journal of Fisheries Management* 22:727–736.
- Pollock, K. H., J. M. Hoenig, and C. M. Jones. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Pages 423–434 in D. Guthrie, J. M. Hoenig, M. Holliday, C. M. Jones, M. J. Mills, S. A. Moberly, K. H. Pollock, and D. R. Talhelm, Eds. Creel and angler surveys in fisheries management. American Fisheries Society, Symposium 12, Bethesda, Maryland.
- Pollock, K. H., H. Jiang, and J. E. Hightower. 2004. Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Transactions of the American Fisheries Society* 133:639–648.
- Ross, J. L., and T. M. Stevens. 1992. Life history and population dynamics of red drum (*Sciaenops ocellatus*) in North Carolina waters. North Carolina Division of Marine Fisheries, Marine Fisheries Research Completion Report Project F-29, Morehead City.
- Ross, J. L., T. M. Stevens, and D. S. Vaughan. 1995. Age, growth, mortality, and reproductive biology of red drums in North Carolina waters. *Transactions of the American Fisheries Society* 124:37–54.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd edition. Charles W. Griffin, London.
- Smith, D. R., K. P. Burnham, D. M. Kahn, X. He, C. J. Goshorn, K. A. Hattala, and A. W. Kahnle. 2000. Bias in survival estimates from tag-recovery models where catch-and-release is common, with an example from Atlantic striped bass (*Morone saxatilis*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:886–897.
- Sprankle, K., J. Boreman, and J. B. Hestbeck. 1996. Loss rates for dorsal loop and internal anchor tags applied to striped bass. *North American Journal of Fisheries Management* 16:461–464.
- Takade, H. M., and L. M. Paramore. 2007. Stock status of the northern red drum stock. North Carolina Division of Marine Fisheries, Morehead City.
- Vaughan, D. S., and J. T. Carmichael. 2000. Assessment of Atlantic red drum for 1999: northern and southern regions. NOAA Technical Memorandum NMFS-SEFSC-447.
- Wallin, J. E., J. M. Ransier, S. Fox, and R. H. McMichael, Jr. 1997. Short-term retention of coded wire and internal anchor tags in juvenile common snook, *Centropomus undecimalis*. U.S. National Marine Fisheries Service Fishery Bulletin 95:873–878.
- Walters, C. J., and S. J. D. Martell. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.
- Wenner, C. 1992. Red drum: natural history and fishing techniques in South Carolina. South Carolina Department of Natural Resources, Technical Report 17, Charleston.
- White, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. *Journal of Wildlife Management* 47:716–728.