COASTAL RECREATIONAL FISHING LICENSE
FINAL PERFORMANCE REPORT

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Grant Number: NCDENR Task Order #2226 (NCSU Project ID# 550621-02472)

Grant Title: Movement and Mortality of spotted seatrout in North Carolina: a combined conventional tag and telemetry approach

Grant Award Period: 09/01/09 –12/31/13

Project Costs:

	Budgeted	Expenditures
	$299,563	$299,563
TOTAL	$299,563	$299,563

Final Project Summary: The goals of this project were to estimate seasonal and annual rates of fishing mortality (*F*) for both the recreational and commercial fishing sectors, estimate seasonal natural mortality rates (*M*) and determine the importance of winterkill, and estimate movement rates of spotted seatrout in NC. Data from the first comprehensive tag-return and telemetry study of spotted seatrout in NC were used to meet these goals. Both laboratory and field studies, including high-reward and double tagging, were conducted to obtain estimates of auxiliary parameters (e.g., reporting rate, tag retention, and tagging-induced mortality) necessary for the tag-return modeling. There was no measured mortality associated with tagging but reporting rate and loss of internal anchor tags limited returns in this study. Seasonal and annual estimates of *F* were consistently lower than *M* from 2008 to 2012. Additionally, the timing of high natural mortality events estimated from conventional tagging was confirmed by high estimates of natural mortality in telemetered fish in two out of three winters; telemetry data indicate that overwinter mortality of spotted seatrout in NC is due to acute thermal stress at low temperatures. Overall, half of returned fish were recaptured near the tagging location; however, many recaptured fish also moved greater distances, generally coinciding with spring migrations north and fall migrations south. Less than 10% of spotted seatrout tagged in NC were recaptured outside of the state's jurisdiction, mostly in Chesapeake Bay (9.4%) but also in SC (0.4%), indicating some exchange but also likely spatial structuring of the stock. Effective management of this valuable fishery resource relies on an accurate understanding of stock structure and the relative importance of harvest and winterkill on population dynamics. Future assessments of spotted seatrout in NC would be improved by consideration of more direct estimates of and annual variability in *M*, as well as consideration for the patterns in temperature-driven latitudinal mixing from Chesapeake Bay to NC.

Movement and Mortality of Spotted Seatrout in North Carolina:
A Combined Conventional Tag and Telemetry Approach

FINAL REPORT*
Submitted December 31, 2013

*The contents of this report are the basis of a N.C. State University doctoral dissertation by Timothy A. Ellis

ABSTRACT

Spotted seatrout (*Cynoscion nebulosus*) is one of the most economically important sportfish in the U.S. South Atlantic and Gulf of Mexico, including North Carolina. The state's recent stock assessment concluded the population is overfished; however, the extent to which variability in natural mortality (*M*), particularly during winter, affects annual estimates of fishing mortality (*F*) is unknown. This is potentially important because North Carolina is near the species' northern geographical limit, where spotted seatrout are particularly vulnerable to lethal winter conditions. Data from the first comprehensive tag-return and telemetry study of spotted seatrout in North Carolina, along with fishery-independent gill net survey data collected by the North Carolina Division of Marine Fisheries, were used to estimate *F*, *M*, and total mortality rates ($Z = F + M$). Both laboratory and field studies, including high-reward and double tagging, were conducted to obtain estimates of auxiliary parameters (e.g., reporting rate, tag retention, and tagging-induced mortality) necessary for the tag-return modeling. There was no measured mortality associated with tagging but reporting rate and loss of internal anchor tags limited returns in this study. From 2008 to 2012, tag-return model estimates indicate that bimonthly instantaneous mortality rates ranged from 0.025 to 0.148 for *F*, and from 0.080 to 2.678 for *M*. Estimated annual estimates of *F* were lower and *M* higher than those reported for spotted seatrout in North Carolina's recent age-based stock assessment, where *M* was fixed using general life-history relationships based on weight and longevity. Estimates of bimonthly-*Z* from tag-

return data were similar to bimonthly-*Z* estimates from a separate analysis of survey data. Additionally, the timing of high natural mortality events estimated from conventional tagging was confirmed by both high estimates of natural mortality in telemetered fish and high total loss estimates observed in gill net survey data in two out of three winters; telemetry data indicate that overwinter mortality of spotted seatrout in North Carolina is due to acute thermal stress at temperatures below 5-7 °C. Tag-return data suggest that the movements of spotted seatrout in North Carolina vary by region within the state but that 56% of fish overall were recaptured within 20 km (~11 nautical miles) of the tagging location. Interestingly, 25% of recaptured fish had moved distances in excess of 100 km (~54 nautical miles), with half of these fish recovered more than 180 km (~97 nautical miles) from the original point of release. These long-distance movements generally coincided with spring migrations north and fall migrations south. Overall, 9.8% of spotted seatrout tagged in North Carolina were recaptured outside of the state's jurisdictional boundaries, mostly in Chesapeake Bay (9.4%) but also in South Carolina (0.4%). Populations of spotted seatrout in North Carolina and Virginia were recently assessed as one unit stock; however, tagging data from North Carolina and Virginia do not unequivocally imply homogeneity in stock structure. Effective management of this valuable fishery resource relies on an accurate understanding of stock structure and the relative importance of harvest and winterkill on population dynamics. Future assessments of spotted seatrout in North Carolina would be improved by consideration of more direct estimates of and annual variability in *M*, as well as consideration for the patterns in temperature-driven latitudinal mixing from Chesapeake Bay to North Carolina.

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SECTION 1

TAG-RETURN ESTIMATES OF FISHING AND NATURAL MORTALITY RATES

INTRODUCTION

Successful management of exploited fish populations relies on an accurate understanding of the sources and levels of mortality affecting abundance. Determining the relative importance of the fishing and natural components of mortality on population dynamics is a complex but fundamental objective of fishery stock assessments and is key to identifying optimal levels of harvest and to regulate for fishery sustainability (Hilborn and Walters 1992; Quinn and Deriso 1999). Estimates of fishing mortality rate (*F*), a measure of fishery influence on a stock, are frequently generated from a variety of age-structured modeling techniques that require long-term survey (abundance) and composition (age) data from fishery-dependent and fishery-independent sampling (Gulland 1983; Hilborn and Walters 1992; Haddon 2001). These estimates of *F* establish management guidelines for allowable exploitation rate and invoke statutory directives (e.g., rebuilding criteria) to fisheries managers, particularly when current harvest levels are unsustainable (i.e., overfishing is occurring).

Natural mortality rate (*M*) is a principal parameter of most fishery stock assessment models because of its direct relationship with population productivity. However, unlike harvest, natural deaths are largely unobservable and therefore inherently more difficult to quantify (Quinn and Deriso 1999). The general approaches to estimating *M* have been extensively reviewed and include both direct (i.e., species/stock specific) and indirect (i.e., meta-analyses or life-history correlates) methods (see Vetter 1988; Hightower et al. 2001; Hewitt et al. 2007; Brodziak et al. 2011). Indirect estimates of *M*, such as the Hoenig (1983) longevity-based or the Lorenzen (1996) weight-based approximations, are frequently used in stock assessments because often

they are the only estimates available. However, the precision at which these and other life-history correlates predict M is unknown and generally considered to be poor (Vetter 1988; Pascual and Iribarne 1993). Furthermore, these indirect estimates of M are often assumed to remain constant across age and time (Hightower et al. 2001). Any variability or inaccuracy in M can significantly affect the outcome of an assessment and thus the management recommendations (e.g., harvest limits) based on that assessment (Clark 1999; Williams 2002).

The necessity for more accurate estimates of mortality rates in managed fish populations has led to the development and use of alternative methods that provide estimates independent of those generated through traditional age-structured stock assessment approaches, particularly methods for modeling the mortality of marked fish (see review by Pine et al. 2012). Fishery-dependent tag-return studies, in which researchers mark fish with an external tag and rely on fishery participants to report harvested tagged individuals, extend modeling concepts established in analyses of migratory waterfowl band-recovery data (Brownie et al. 1985; Pollock et al. 1991; Hearn et al. 1998; Hoenig et al. 1998*a*, 1998*b*; Smith et al. 2000; Latour et al. 2001*a*; Jiang et al. 2007; Bacheler et al. 2008; Smith et al. 2009; den Heyer et al. 2013). Using auxiliary estimates of the tag-reporting rate (λ) (i.e., the fraction of harvested/caught-and-released tags that are returned by the fishery), tag retention (ϕ), and survival from the tagging procedure (s), tag-return models can partition the instantaneous total mortality rate (Z) into estimates of F and M (i.e., $Z = F + M$) (Hoenig et al. 1998*a*). Inaccuracies in these key auxiliary parameters will bias mortality estimates determined from tag-return data (Pollock 1991; Pollock et al. 2001; Miranda et al. 2002; Brenden et al. 2010).

Spotted seatrout (*Cynoscion nebulosus*) is one of the most economically important recreational marine fish species in the United States. Their estuarine dependency and wide

distribution throughout the U.S. South Atlantic and Gulf of Mexico make spotted seatrout an easily accessible game and food fish for anglers, and as such they are consistently targeted more than any other species (NOAA Fisheries Service). In North Carolina, directed angler effort in this fishery has generally increased in recent years (NCDMF 2012), with an estimated $46.3 million spent on recreational fishing trips targeting spotted seatrout in 2012 (John Hadley, NCDMF economist, pers. comm.). A recent age-structured assessment completed by the North Carolina Division of Marine Fisheries (NCDMF), where *M* was both fixed and indirectly estimated through weight-based parameters and longevity, concluded that the stock in North Carolina and Virginia was below the management objective of 20% for spawning potential ratio (i.e., overfished) and has experienced harvest rates exceeding the $F_{20\%}$ threshold (i.e., overfishing) throughout the entire 18-year time series (1991-2008) (Jensen 2009; ASMFC 2012). However, the extent to which variability in *M*, particularly during winter, affects annual estimates of *F* is unknown. Throughout the species' geographic range, mass mortalities of spotted seatrout have been attributed to periods of low temperature extremes (Wilcox 1887; Smith 1907; Storey and Gudger 1936; Gunter 1941; Gunter and Hildebrand 1951; Simmons 1957; Tabb and Manning 1961; Moore 1976; Green et al. 1990; McEachron et al. 1994; Martin and McEachron 1996; NCDMF 2012). In North Carolina and Virginia specifically, spotted seatrout are at the species' northern latitudinal limit and are therefore regularly exposed to lethal winter conditions; understanding the relative importance of harvest and winterkill on population dynamics is essential for effective management of the spotted seatrout fishery in this region.

Here, we use data from the first comprehensive tag-return study of spotted seatrout in North Carolina to estimate bimonthly *F* and *M* between 2008 and 2012. Both laboratory and field studies were conducted to obtain estimates of auxiliary parameters (e.g., λ, ϕ, and s)

necessary for the tag-return modeling. Using recent advancements in the Hoenig et al. (1998*a*, 1998*b*) instantaneous rates formulation of the Brownie et al. (1985) model, mortality rates and auxiliary parameters were estimated jointly within the tag-return model so that model uncertainty could be more adequately assessed (Polacheck et al. 2006; Jiang et al. 2007; Bacheler et al. 2008, Bacheler et al. 2009*c*; Smith et al. 2009). We also use five years (2008-2012) of fishery-independent survey data collected monthly by the NCDMF to estimate Z for comparison to tag-return estimates and provide discussion of our results relative to the recent NCDMF spotted seatrout stock assessment. The estimates of mortality from this study provide managers with critical information about seasonal and annual variability in F and M.

METHODS

Data from two independent but co-occurring studies were used in separate Bayesian models of spotted seatrout mortality: (1) a multiyear, reward-based external tagging initiative by North Carolina State University (NCSU) and (2) a coastwide fishery-independent gill net survey conducted by the NCDMF. The methodologies used to collect and analyze these data are detailed below. Symbols used throughout this section are listed and defined in Table 1.

NCSU Multiyear Tag-Return Study

Capture technique

Spotted seatrout were predominantly captured using hook-and-line. Hook-and-release mortality rates for spotted seatrout are generally low across hook and bait types; however, careful consideration regarding hooking location and proper handling is needed (Matlock et al. 1993; Murphy et al. 1995; Duffy 2002; Stunz and McKee 2006; James et al. 2007). Criteria were established to determine if a landed spotted seatrout was a candidate for tagging. First, all

candidates were limited to mouth hook-ups only. Deep-hooked and foul-hooked individuals were immediately released. Additionally, all candidates did not exhibit any physical signs of trauma from the landing process. Any mouth-hooked individuals with excessive bleeding or visible tissue damage were immediately released. Finally, all fish were handled with wet hands and tagged on a wet surface. A limited number of spotted seatrout were also captured for tagging using electrofishing.

Tagging procedure

From September 2008 through October 2012, spotted seatrout (primarily ≥ 305 mm TL) were tagged and released monthly throughout North Carolina and Virginia with the assistance of ten guide-service professionals who were compensated for their participation in the study. Limited temporal and spatial distribution of tagging effort does not allow tagged and untagged fish to fully mix and can severely bias study results (Hoenig et al. 1998*b*; Hightower and Pollock 2013). Therefore, our approach to distribute tagging effort (i.e., coastwide tagging by a select group of taggers) permitted the continual release of tagged spotted seatrout across North Carolina and in Virginia. All taggers were trained and periodically assessed to help ensure consistency in handling and tagging methodology. Individuals were marked with internal anchor tags (Floy Tag, Inc., Washington, USA; Model FM-95W) that had a stainless steel wire core surrounded by plastic tubing attached to a plastic anchor disc. Internal anchor tags were inserted ventrally just posterior of the pelvic fin through a small incision made using a size-12 stainless steel surgical blade. No antiseptic treatment was applied to the incision before or after tag insertion. The tag number(s), date, total length (TL; nearest quarter inch), and geographic coordinates (latitude and longitude) associated with each individual release were recorded.

Internal anchor tag streamers (i.e., external portion) were labeled with a unique identification number, a toll-free phone number, the name of the research organization (i.e., NCSU), and instructions to return the tag for a reward. Due to the general deterioration of external fish tags from prolonged exposure to the aquatic environment (Henderson-Arzapalo et al. 1999), additional measures were taken to ensure that each retained tag was identifiable if recaptured. In the event that one section of the external streamer was damaged more than the other, both sides were printed with the tag number and on opposite ends. Additionally, the anchor disc (i.e., internal portion) was labeled with the tag number and contact phone number. In order to estimate λ, approximately 15% of released individuals received a red, high-reward (US $100) tag, specifically labeled with "CUT TAG $100 REWARD." All other individuals were released with a yellow, standard-reward (US $5, hat, or t-shirt) tag bearing the label "CUT TAG REWARD." Among these standard-reward tag releases, approximately 25% of individuals received two internal anchor tags, one on either side of the body. This double tagging of a subset of fish released with standard-reward tags provided information necessary to estimate tag retention (see details in subsequent section on *Tag-return modeling*). Randomization helped ensure that the desired proportions for high-reward and single- and double-tag standard-reward releases were maintained continually across space and time.

Information on recaptured spotted seatrout with tags was obtained directly from fishery participants. Reporting of tagged fish was promoted throughout the duration of the study by means of flyers posted at boat ramps, fish houses, and tackle shops, as well as through extensive communication through broadcast, print, and digital media. Data consisting of the tag number(s), date and location of capture, fish TL (usually provided in inches), general conditions of the tag and tag insertion point, specific sector of the fishery participant (i.e., commercial or

recreational), and fate of the fish and tag (i.e., kept, released with tag intact, or released with tag cut off) were determined during a follow-up phone interview for each reported recapture of a tagged spotted seatrout. The release- and recovery-TL measurements in inches were converted and rounded to the nearest millimeter for all analyses.

Tag-return modeling

One major advantage of using tag-return studies to estimate mortality rates is that they allow for a known cohort size (i.e., initial number of tag releases). In order to use tag-return data to estimate F and M, numerous assumptions regarding the tagged population relative to the untagged population must be met (Ricker 1975):

1. Tagged individuals mix completely with the untagged population such that it can be assumed that the tagged fish are representative of the entire population. In this study, continual releases of tagged spotted seatrout had a wide spatial coverage to ensure these individuals were well mixed in the population.
2. All tagged individuals considered in the model have the same survival and recovery probabilities. Given that all tagged spotted seatrout were fully recruited to the recreational fishery, the sector attributed with the majority of landings (Jensen 2009; NCDMF 2012), we assumed that all individuals were subjected to the same mortality and selectivity processes.
3. Tagged fish have independent fates. Aggregations of tagged individuals can bias and affect the precision of mortality estimates (Pollock et al. 2004). Spotted seatrout exhibit schooling behavior and can converge in high numbers, especially during winter months; however, these aggregations are independent of whether a fish is tagged or not.

4. Each tag return is assigned to the correct model time-step (e.g., month, year). In this study, the date of tag recovery reported by fishers returning tags was assumed to be accurate enough for correct assignment to a bimonthly time-step for the tag-return model.

Bias in mortality estimates can also be introduced by three auxiliary parameters necessary for tag-return modeling: tagging-induced mortality, tag loss, and non-reporting of recovered tags. Information from the literature is useful but it is preferable to conduct auxiliary studies on these parameters, as published values introduce unknown bias (Hightower and Pollock 2013). Holding experiments can be conducted to examine mortality associated with tagging and tag shedding (Pollock and Pine 2007); see details in later section on *Laboratory Estimates of Tagging-Induced Mortality and Tag Retention* for details of our controlled observational study methods. An alternative and preferable approach to investigate tag retention is to conduct a double-tagging study on released fish (Beverton and Holt 1957; Barrowman and Myers 1996; Fabrizio et al. 1999; Hyun et al. 2012). Following Barrowman and Myers (1996), tag-return data on double-tagged fish were used in an exponential decay model to describe tag retention as a function of days-at-liberty (t):

$$Q_t = \rho e^{-\phi t},$$

where Q_t is the probability of tag retention at time t after release, ρ is the probability of tag retention immediately after tagging, and ϕ is the chronic tag-loss rate. This model was fitted to tag-return data outside of the instantaneous rates mortality model (described below) to estimate ρ. The conditional probabilities of observing the two recovery states from doubled-tagged releases (i.e., *TT* for retention of both tags or *T* for retention of only one tag) were:

$$p_{TT}^{TT}(t) = Q_t^{\,2},$$

$$p_{T}^{TT}(t) = 2Q_t[1 - Q_t].$$

For recoveries where only one of the two tags were retained, an adjustment of $p_T^{TT}(t)$ is made to account for nonsimultaneous release of tags, and was defined by:

$$Adj_p_T^{TT}(t) = p_T^{TT}(t) / (p_T^{TT}(t) + p_{TT}^{TT}(t)).$$

Returns where spotted seatrout retained only one of the original two tags follow a binomial distribution (i.e., categories are days-at-liberty and retention of a single tag). The likelihood function ($L_{tagloss}$) over the total observed k days-at-liberty then was:

$$L_{tagloss} = \prod_{i=1}^{k} \left[Adj_p_T^{TT}(t_i) \right]^{n_T},$$

where n_T is the number of returned tagged spotted seatrout after t_i days-at-liberty that retained only one tag. This approach to estimating tag retention assumed that double-tagged fish were a random subset of all tagged spotted seatrout, that Q_t was unrelated to tag insertion point (i.e., left versus right side of the body) and independent for both tags, and that behavior, M, s, and λ were unbiased by whether a fish was tagged with one versus two tags (Wetherall 1982; Hearn et al. 1991). Additionally, we assumed that all tags retained were reported; this assumption was met through fisher confirmation in the follow-up phone interview if only one of the two original tags were initially reported [e.g., when asked, fishers would then either report the second tag number (if tag was present) or would comment that a sore or scar was visible but no second tag was present].

Following Pollock et al. (2001), a high-reward component was also implemented as part of the tag-return study to estimate a separate λ for both the recreational and commercial fishing sectors (see details in previous section on *Tagging procedure*). An assumption of 100%

reporting of all recovered high-reward tags is necessary for this approach; therefore, λ is an estimate of the sector-specific reporting rates for standard-reward tags recovered in the recreational and commercial fisheries. Since standard rewards were given for associated information about each recaptured fish and its fate (i.e., not per tag), we assumed that λ was equivalent for single- and double-tagged fish.

An integrated tag-return modeling approach was used to simultaneously estimate F, M, λ, and long-term tag-retention from the recoveries of single- and double-tagged standard-reward, and single-tagged high-reward spotted seatrout based on the Hoenig et al. (1998*a*) instantaneous-rates formulation of the discrete-rates Brownie et al. (1985) model (Polacheck et al. 2006; Smith et al. 2009). The effective population size of tagged fish was reduced immediately (i.e., Type I losses) by initial tag-loss, ρ, and survival from the tagging procedure, s (Beverton and Holt 1957). External estimates of ρ and s were fixed in the integrated tag-return model; the model estimated all other parameters internally. Additionally, we accounted for both harvest and catch-and-release (from here forward referred to as discard) mortality by following the approach of Jiang et al. (2007), where we modeled tags-at-risk as opposed to tagged fish (Bacheler et al. 2009*c*; Hightower and Pollock 2013). This approach required that multiple recaptures of individuals released with tags intact, beyond the first recapture, be ignored (Bacheler et al. 2008); this did not limit the number of tag returns as only one tagged spotted seatrout was caught and reported more than once (i.e., twice) in our study. A bimonthly time step was chosen for our tag-return model to examine the seasonal variability in mortality, with bimonthly-release and -recovery periods in a given year defined as January/February, March/April, May/June, July/August, September/October, and November/December.

Observed data were compared to a matrix of expected tag-recoveries (see Figure 1 of Smith et al. 2009). The expected number of tag recoveries, $E(R_{ij})$, from bimonthly-release period i in bimonthly-return period j was $N_i P_{ij}$, where N_i is the number of tagged spotted seatrout released in bimonth i, and P_{ij} is the probability that a tagged spotted seatrout released in bimonth i will be recovered in bimonth j. For single standard-reward tag recoveries from harvested spotted seatrout:

$$P_{x_{ij}} = \begin{cases} s\lambda_x \rho \left(\prod_{v=i}^{j-1} S_{iv} \right) \left(1 - S_{ij}\right) \left[F_{x_j} \Big/ \left(F'_j + F_j + M_j + \phi \right) \right] & when\ j > i \\ s\lambda_x \rho \left(1 - S_{ij}\right) \left[F_{x_j} \Big/ \left(F'_j + F_j + M_j + \phi \right) \right] & when\ j = i, \end{cases}$$

where s is initial survival from tagging procedure (externally estimated and assumed constant), λ is the tag-reporting rate (assumed constant), ρ is immediate tag retention (externally estimated and assumed constant), F_j is the instantaneous fishing mortality rate of harvested tags, F'_j is the instantaneous fishing mortality rate for tags of discards, M_j is the instantaneous natural mortality rate, and ϕ is the bimonthly tag-loss rate (Type II loss, Beverton and Holt 1957: tag-attrition model, Kleiber et al. 1987; Hampton 1996: assumed constant). These probabilities were modeled separately for tags returned from either the recreational ($x = r$) or commercial ($x = c$) fishing sector; therefore, estimates of λ_x and F_{x_j} are sector-specific. For single standard-reward tag recoveries from discarded spotted seatrout $\left[E\left(R'_{ij}\right) = N_i P'_{ij} \right]$:

$$P'_{ij} = \begin{cases} s\lambda_r \rho \left(\prod_{v=i}^{j-1} S_{iv} \right) \left(1 - S_{ij}\right) \left[F'_j \Big/ \left(F'_j + F_j + M_j + \phi \right) \right] & when\ j > i \\ s\lambda_r \rho \left(1 - S_{ij}\right) \left[F'_j \Big/ \left(F'_j + F_j + M_j + \phi \right) \right] & when\ j = i, \end{cases}$$

in which the recreational fisher reporting rate (λ_R) was used due to the few number (n = 5) of tag returns from discarded spotted seatrout in the commercial fishing sector. Bimonth-*j* survival for single-tag releases in bimonth-*i* was:

$$S_{ij} = \exp\left[-\left(F'_j + F_j + M_j + \phi\right)\right],$$

where $F_j = F_{r_j} + F_{c_j}$, and F_{r_j} and F_{c_j} are the instantaneous recreational and commercial fishing mortality rates in bimonth-*j*, respectively. For single high-reward tagged individuals, a constant λ of 1.0 was used in the same probabilities just defined, under the assumption that λ was independent of whether the fish was harvested or discarded (see Bacheler et al. 2009*c*). Recoveries of single-tag releases due to harvest ($R_{x_{ij}}$) and discard (R'_{ij}) follow a multinomial distribution. The likelihood function for single tags (L_{single}) was:

$$L_{single} = \prod_{i=1}^{I}\left(\prod_{j=1}^{J} P_{r_{ij}}^{R_{r_{ij}}} P_{c_{ij}}^{R_{c_{ij}}} P'^{R'_{ij}}_{ij}\right)\left[1 - \sum_{j=i}^{J}\left(P_{r_{ij}} + P_{c_{ij}} + P'_{ij}\right)\right]^{\left[N_i - \sum_{j=i}^{J}\left(R_{r_{ij}} + R_{c_{ij}} + R'_{ij}\right)\right]}.$$

For cohorts released with double standard-reward tags, different probabilities were also defined for recoveries based on whether the spotted seatrout were harvested or discarded, and if they retained one or both tags when recaptured (see Polacheck et al. 2006). For spotted seatrout retaining both tags (*TT*), $E\left(R_{TT_{ij}}\right) = N_i P_{TT_{ij}}$ and $E\left(R'_{TT_{ij}}\right) = N_i P'_{TT_{ij}}$ for harvested and discarded fish, respectively. The recovery probabilities were:

for harvested fish,

$$P_{TT_{x_{ij}}} = \begin{cases} s\lambda_x \rho^2 \left(\prod_{v=i}^{j-1} S'_{iv}\right)\left(1 - S'_{ij}\right)\left[F_{x_j} \Big/ \left(F'_j + F_j + M_j + 2\phi\right)\right] & when\ j > i \\ s\lambda_x \rho^2 \left(1 - S'_{ij}\right)\left[F_{x_j} \Big/ \left(F'_j + F_j + M_j + 2\phi\right)\right] & when\ j = i, \end{cases}$$

and for discarded fish,

$$P'_{TT_{ij}} = \begin{cases} s\lambda_r \rho^2 \left(\prod_{v=i}^{j-1} S'_{iv} \right) \left(1 - S'_{ij}\right) \left[F'_j \big/ \left(F'_j + F_j + M_j + 2\phi \right) \right] & when\ j > i \\ s\lambda_r \rho^2 \left(1 - S'_{ij}\right) \left[F'_j \big/ \left(F'_j + F_j + M_j + 2\phi \right) \right] & when\ j = i. \end{cases}$$

These probabilities were also modeled separately for tags returned from each fishing sector (x). For spotted seatrout retaining only one of two tags (T), $E\left(R_{T_{ij}}\right) = N_i P_{T_{ij}}$ and $E\left(R'_{T_{ij}}\right) = N_i P'_{T_{ij}}$ for harvested and discarded fish, respectively. The recovery probabilities were:

for harvested fish,

$$P_{T_{x_{ij}}} = \begin{cases} 2s\lambda_x \left\{ \rho \prod_{v=i}^{j-1} S_{iv} \left(1 - S_{ij}\right) \left[F_{x_j} \big/ \left(F'_j + F_j + M_j + \phi \right) \right] \right. \\ \qquad \left. - \rho^2 \prod_{v=i}^{j-1} S'_{iv} \left(1 - S'_{ij}\right) \left[F_{x_j} \big/ \left(F'_j + F_j + M_j + 2\phi \right) \right] \right\} & when\ j > i \\ 2s\lambda_x \left[\rho \left(1 - S_{ij}\right) F_{x_j} \big/ \left(F'_j + F_j + M_j + \phi \right) \right. \\ \qquad \left. - \rho^2 \left(1 - S'_{ij}\right) F_{x_j} \big/ \left(F'_j + F_j + M_j + 2\phi \right) \right] & when\ j = i, \end{cases}$$

and for discarded fish,

$$P'_{T_{ij}} = \begin{cases} 2s\lambda_r \left\{ \rho \prod_{v=i}^{j-1} S_{iv} \left(1 - S_{ij}\right) \left[F'_j \big/ \left(F'_j + F_j + M_j + \phi \right) \right] \right. \\ \qquad \left. - \rho^2 \prod_{v=i}^{j-1} S'_{iv} \left(1 - S'_{ij}\right) \left[F'_j \big/ \left(F'_j + F_j + M_j + 2\phi \right) \right] \right\} & when\ j > i \\ 2s\lambda_r \left[\rho \left(1 - S_{ij}\right) F'_j \big/ \left(F'_j + F_j + M_j + \phi \right) \right. \\ \qquad \left. - \rho^2 \left(1 - S'_{ij}\right) F'_j \big/ \left(F'_j + F_j + M_j + 2\phi \right) \right] & when\ j = i. \end{cases}$$

Bimonth-j survival (with both tags intact) for double-tag releases in bimonth-i was:

$$S'_{ij} = \exp\left[-\left(F'_j + F_j + M_j + 2\phi \right) \right],$$

where $F_j = F_{r_j} + F_{c_j}$, and F_{r_j} and F_{c_j} are again the instantaneous recreational and commercial fishing mortality rates in bimonth *j*, respectively. Recoveries of double-tag releases due to harvest ($R_{TT_{xij}}$, $R_{T_{xij}}$) and discard ($R'_{TT_{ij}}$, $R'_{T_{ij}}$) follow a multinomial distribution. The likelihood function for double tags (L_{double}) was:

$$L_{double} = \prod_{i=1}^{I}\left(\prod_{j=i}^{J} P_{TT_{r_{ij}}}^{R_{TT_{r_{ij}}}} \prod_{j=i}^{J} P_{TT_{c_{ij}}}^{R_{TT_{c_{ij}}}} \prod_{j=i}^{J} P'^{R'_{TT_{ij}}}_{TT_{ij}} \prod_{j=i}^{J} P_{T_{r_{ij}}}^{R_{T_{r_{ij}}}} \prod_{j=i}^{J} P_{T_{c_{ij}}}^{R_{T_{c_{ij}}}} \prod_{j=i}^{J} P'^{R'_{T_{ij}}}_{T_{ij}}\right) \times$$
$$\left[1 - \sum_{j=i}^{J}\left(P_{TT_{r_{ij}}} + P_{TT_{c_{ij}}} + P'_{TT_{ij}} + P_{T_{r_{ij}}} + P_{T_{c_{ij}}} + P'_{T_{ij}}\right)\right]^{\left[N_i - \sum_{j=i}^{J}\left(R_{TT_{r_{ij}}} + R_{TT_{c_{ij}}} + R'_{TT_{ij}} + R_{T_{r_{ij}}} + R_{T_{c_{ij}}} + R'_{T_{ij}}\right)\right]}$$

The total integrated model likelihood function was the product of L_{single} and L_{double}. We used Bayesian analyses in OpenBUGS software (http://www.openbugs.info/w/; Lunn et al. 2009) to estimate parameters in our separate models of tag retention and mortality given the observed tag-return data. In the exponential decay model of tag retention, an uninformative prior distribution was used for ρ [uniform (0, 2)] and ϕ [beta (0.5, 0.5)]. In the instantaneous rates model with integrated tag retention, uniform prior distributions were used for all estimated parameters and were uninformative: F_{r_j} (0, 2), F_{c_j} (0, 2), F'_j (0, 2), M_j (0, 5), ϕ (0, 2), λ_r (0, 1), and λ_c (0, 1). In both OpenBUGS modeling analyses and for all estimated parameters, the first 1,000 samples of the posterior distribution from three Markov chains were excluded in order to meet convergence criteria and to remove bias associated with initial parameter values; a minimum of 10,000 samples per chain were used to estimate all parameter posterior distributions. Convergence of the three Markov chains was assessed visually and confirmed based on the Brooks-Gelman-Rubin statistic ($R < 1.05$; McCarthy 2007). All parameter estimates are presented as posterior means with a 95% credible interval (CrI).

The bimonthly (j) sector-specific fishing mortality estimates, F_{r_j}, F_{c_j}, and F'_j, and natural mortality estimates, M_j, are based on the fates of tags. Those estimates were used to determine the bimonthly fishing ($\hat{F}_{fish_j}$) and total ($\hat{Z}_{fish_j}$) mortality rates for fish: $\hat{F}_{fish_j} = \hat{F}_{r_j} + \hat{F}_{c_j} + \delta \hat{F}'_j$ and $\hat{Z}_{fish_j} = \hat{F}_{fish_j} + \hat{M}_j$, where δ is a previously estimated discard mortality rate for spotted seatrout (10%: Matlock et al. 1993; Murphy et al. 1995; Duffy 2002; Stunz and McKee 2006; James et al. 2007). The recent NCDMF spotted seatrout stock assessment also used this mortality rate for recreational discards (Jensen 2009) and a slightly lower rate of 8% was used in Florida (Murphy et al. 2011). Our use of this rate ignores the potentially higher discard mortality associated with commercial fishing gears (e.g., gill nets; Murphy et al. 1995) predominantly used to target spotted seatrout in North Carolina and Virginia, which could significantly bias our estimates of $\hat{Z}_{fish_j}$ if discards of tagged spotted seatrout from these other gears were high. However, given that very few (n = 5) bimonth-j tag recoveries in our study were reported by commercial fishers as discards, this potential bias is low.

Laboratory Estimates of Tagging-Induced Mortality and Tag Retention

Long-term observational studies were conducted to examine spotted seatrout mortality resulting from implantation of an internal anchor tag and implantation of an acoustic transmitter (see Section 2 for telemetry study), and to also examine the retention of those two tag types in a controlled setting. Observations were made during two separate experiments spanning November 2008 to May 2009 and November to December 2010. In both experiments, hook-and-line-captured spotted seatrout from nearby polyhaline waters surrounding CMAST (34°43' N, 76°45' W) were transported to, and randomly distributed among, four 1,500-l outdoor flow-through holding tanks. Each tank received approximately 20-micron filtered polyhaline seawater

from Bogue Sound at an approximate flow rate of 8 l min.$^{-1}$ and continuous aeration; flow was sufficient to fully exchange tank water approximately 7.5 times day^{-1}. Structure in the form of marl blocks was added to the center of each tank, and a half opaque and half light-penetrable plastic screen provided full cover. Fish were fed a combination of locally collected live and freshly dead prey (*Fundulus* spp., penaeid shrimp spp.) three times a week. Tanks were siphoned at least once a week to remove waste. Data loggers (StowAway TidbiT, Onset Computer Corp., Bourne, MA, USA; ± 0.4 °C accuracy) recorded tank water temperature (°C) every 15 minutes. Additionally, water temperature, salinity, and dissolved oxygen measurements were taken daily for each tank using a temperature-conductivity meter (YSI® Model 85, YSI, Inc., Yellow Springs, OH, USA). Upon termination of each experiment, all surviving fish were euthanized with a lethal dosage of MS-222 and necropsies were performed under the guidance of onsite NCSU College of Veterinary Medicine (CVM) staff to further examine overall health in relation to the presence of an internal anchor tag or acoustic transmitter.

In the first experiment, a total of 44 spotted seatrout were randomly assigned to one of four replicate tanks and to one of three treatments per tank: control (n = 16, 4 tank^{-1}), one internal anchor tag (n = 16, 4 tank^{-1}), or one transmitter (n = 12, 3 tank^{-1}). The twelve acoustically-tagged spotted seatrout were implanted with dummy (i.e., no electronics) transmitters (VEMCO, Bedford, Nova Scotia, Canada; V13, n = 8, 2 tank^{-1}; V16, n = 4, 1 tank^{-1}), identical in dimensions and mass to those used in the telemetry study and following the procedure fully described in Section 2, except that a simple continuous (versus interrupted) suture technique was used to close the incision following transmitter implantation. These fish were added to the experimental tanks 11 days after the control and conventionally-tagged fish; therefore, daily observations of

tag loss, overall health (e.g., normal swimming and feeding behavior), and mortality were made over a period of 236 and 225 d for conventionally- and telemetry-tagged spotted seatrout, respectively.

A total of 63 spotted seatrout were randomly assigned in the second experiment to one of three replicate tanks and to one of three treatments per tank: control (n = 21, 7 tank^{-1}), one internal anchor tag (n = 21, 7 tank^{-1}), or two internal anchor tags (n = 21, 7 tank^{-1}). Tag loss, overall health, and mortality were observed daily for 40 d.

NCDMF Fishery-Independent Gill Net Survey

The fishery-independent gill net survey (IGNS) conducted by the NCDMF primarily supplies data necessary for annual indices of abundance of economically important finfish species in North Carolina. Additionally, the IGNS provides supplemental data on age, growth, reproduction, distribution, and habitat use. IGNS data extend back to 2001 for Pamlico Sound and to 2003 for the Pamlico, Pungo, and Neuse rivers; however, coastwide survey coverage, including the New and Cape Fear rivers began in 2008. We used data collected from May 2008 through December 2012. Through a stratified random sampling design based on region and water depth (i.e., shallow < 1.83 m and deep ≥ 1.83 m), 19 strata (Pamlico Sound = 8, Pamlico River = 3, Pungo River = 1, Neuse River = 4, New River = 2, and Cape Fear River = 1) were sampled at least monthly from February 15 to December 15 each year; strata were sampled only once in February and December months but twice monthly in all other months, with some deviations from this schedule due to adverse weather, budgetary, or federal regulatory constraints. A sampling event consisted of two experimental gill nets [one shallow (<1.83 m); one deep (≥1.83 m)] set typically within 1 h of sunset and retrieved the following morning (approximately 12-h soak times). Modifications to this design for strata in the southern portions

of the state include: (1) no deep-water sets in the Cape Fear River (with the exception of the navigation channel, this strata is predominantly shallow water habitat) and (2) 4-h soak times beginning within 1 h of sunrise in the New and Cape Fear rivers from April 1 to September 31, intended to minimize interactions with federally protected species. An experimental gill net comprised eight 27.4 m segments of 7.6, 8.9, 10.2, 11.4, 12.7, 14.0, 15.2, and 16.5 cm stretched mesh webbing, totaling 219.5 m in length. Collected spotted seatrout were enumerated, measured for fork length (FL; mm), and a subsample was retained for later analyses of age, sex, and maturity. Occasionally, damaged individuals (i.e., partially eaten or decayed) were counted but not measured.

Analysis of survey data

A subset of all spotted seatrout (n = 837) collected through the IGNS (January 2002-March 2013) was also measured for TL (mm; range: 267-728), which allowed for the conversion of all lengths from fork to total (TL = 1.0409FL-8.5635; R^2 = 0.998). For the period of interest (i.e., May 2008-December 2012), IGNS-catch data were combined across regions but separated into 1 of 23 25-mm TL categories (range: 175-725 mm) and grouped into 1 of 6 bimonthly periods (i.e., January/February, March/April, May/June, July/August, September/October, and November/December) for each year.

We used five years (May 2008 to December 2012) of North Carolina spotted seatrout (n = 2,771) aging data collected by the NCDMF to convert IGNS-catch data in TL to an estimated age. NCDMF aging data were gathered from examining the otoliths of spotted seatrout collected through fishery-dependent and fishery-independent surveys, and were adjusted to a January 1 birth date based on peak annulus formation (i.e., January 1-April 31, May 1 – December 31; Jensen 2009). Spotted seatrout exhibit rapid, sexually dimorphic growth and early maturation,

which results in considerable overlap in sizes-at-age; therefore, the age of IGNS catches could not be accurately assigned according to a standard age-length key. Instead, we used the aging dataset to determine the age composition of spotted seatrout relative to TL when the aged samples were collected. First, NCDMF aging data for each year were separated into length categories and bimonthly periods, identical to those just described. For each bimonthly period (n=28), we then determined the proportions of spotted seatrout in each length category that were assigned a given age. These proportions were applied to the corresponding bimonthly IGNS data to yield fractional catches-at-age for each length category. In the small number of cases where age-composition data were unavailable for a given bimonthly period (i.e., no spotted seatrout were aged in a particular length category for which there are positive catch data in the IGNS), proportions for the nearest 25-mm TL category (usually the immediately adjacent cell) were used. Catches-at-age were then summed across all length categories for each bimonthly period and standardized across all bimonthly periods. Standardization was achieved by first calculating age-dependent catch-per-unit-effort (CPUE), the number of spotted seatrout caught per age group per hour of gill net set in each bimonthly period, and then scaling CPUE upwards by the average number of gill net soak hours in a bimonthly period (single average across all 28 periods).

We conducted an analysis of survey data based on initial cohort size and declining abundance over time due to time-specific *Z*. The model was generalized to account for age- and season-specific vulnerability of spotted seatrout to the IGNS (Hilborn and Walters 1992; Quinn and Deriso 1999). The expected standardized catch-per-unit-effort (CPUE) for cohort *i* in bimonth *j*, $E(C_{ij})$, was:

$$E(C_{ij}) = N_i \alpha_p \gamma_a \left[\exp\left(-\sum_{v=i}^{j-1} Z_{iv} \right) \right],$$

where N_i is the initial abundance of cohort i, α_p is the multiplier for seasonal (p) availability of spotted seatrout to the survey, and γ_a is the survey selectivity for age a. In North Carolina, the majority of spotted seatrout reside in the many tributary creeks of the larger river and sound estuaries for up to six months each year (i.e., overwintering period from October to March). As such, we accounted for the seasonal variation in availability of spotted seatrout to the IGNS, which by design does not survey these overwintering areas. The availability multiplier was assumed constant across ages and years but allowed to vary across six bimonthly periods within each year: January/February, March/April, May/June, July/August, September/October, November/December. We defined age-based selectivity of the experimental gill net as asymptotic (i.e., fully selected above a given age) with a single (increasing) logistic function (Quinn and Deriso 1999):

$$\gamma_a = 1 \Big/ \left\{ 1 + \exp\left[-\left(\beta_1 + \beta_2 a_{ij} \right) \right] \right\},$$

where β_1 and β_2 are the slope and intercept parameters, respectively, and a_{ij} is the fractional age for cohort i in bimonth j. We assumed that γ_a was constant across all bimonthly periods.

Catches of cohort i in bimonth j, C_{ij}, were assumed to follow a poisson distribution. We used Bayesian analysis in OpenBUGS software to estimate parameters given the observed catch-at-age data. An uninformative prior distribution was used for N_i [normal on *ln*-scale; (0, $1.0e^{-6}$)], $\alpha_{1:2,4:6}$ [uniform (0.01, 1)], β_1 [uniform (-100, 1)], β_2 [uniform (1, 100)], and Z_j [uniform (0, 5)]. Preliminary model runs suggested that the seasonal availability of spotted seatrout to the IGNS was highest during the May/June period; therefore, the prior distribution of α_3 was fixed at 1.0 so that all other α_p were estimated relative to α_3. Final estimates of all parameter posterior distributions were obtained from three Markov chains of 250,000 samples each but excluding the

initial 50,000 samples. The convergence of the three Markov chains was assessed as previously described and all parameter estimates are presented as posterior means with a 95% CrI.

RESULTS

From September 2008 through October 2012, a total of 6,582 spotted seatrout were tagged in North Carolina and Virginia waters (Figure 1), consisting of 3,917 (59.5%) releases with a single standard-reward tag, 1,667 (25.3%) releases with double standard-reward tags, and 998 (15.2%) releases with a single high-reward tag (Table 2). At release, tagged spotted seatrout ranged in TL from 254 to 711 mm, with an overall mean (±SE) TL of 354 (±0.7) mm (Figure 2). A total of 553 (8.4% return rate) tagged spotted seatrout were recovered and reported over five years (through October 31, 2013), including 284 (7.3% return rate), 162 (9.7% return rate), and 107 (10.7% return rate) fish originally released with a single standard-reward tag, double standard-reward tags, and a single high-reward tag, respectively. Tagged spotted seatrout were recovered primarily throughout North Carolina estuarine and coastal waters and in Chesapeake Bay (Figure 3). Information on the date of recapture reported by fishers was sufficient to determine the exact days-at-liberty for 518 of the 553 recoveries of tagged spotted seatrout; however, all tag recoveries were assigned to the correct bimonthly period for our tag-return model of mortality. Days-at-liberty ranged from 1 to 848 with half (53.9%) of all tag recoveries reported within four months of release and few (7.5%) reported beyond one year after release (Figure 4). Only 5.0% of reported tags were recovered within one week of release.

The recreational fishing sector recovered and reported 410 tags in total, including 341 standard-reward tags and 69 high-reward tags, and of which 139 (34%) were reported as discards. The commercial fishing sector recovered and reported 139 tags, including 102

standard-reward tags and 37 high-reward tags, and of which five (4%) were reported as discards. For all reported discards combined, 99 of out 144 (69%) included fisher measurements of fish total length at recapture, which ranged from 292 to 559 mm (mean ± SE: 375.0 ± 6.0 mm). The four remaining tagged spotted seatrout were either recovered dead during scientific sampling (n = 1; high-reward tag) or during extreme cold conditions (n = 3; single standard-reward tags). In order to not bias mortality and reporting rate estimates, these recoveries were not included in the tag-return matrices for our model. Specifically, the initial release and subsequent recovery of the single fish with a high-reward tag that did not survive capture by an electrofishing survey were ignored, and the recoveries of the three fish with a standard-reward tag that were known to have died naturally were ignored.

Tagging-Induced Mortality, Tag Retention, and Tag-Reporting Rate

Laboratory studies

Spotted seatrout mortality from the implantation of either one or two internal anchor tags was not observed in either of our two laboratory experiments: Experiment 1 [Table 3; mean TL ± SE; control (330.8 ± 18.1 mm), one internal anchor tag (319.3 ± 14.1 mm)]; Experiment 2 [Table 4; mean TL ± SE; control (306.4 ± 5.8 mm), one internal anchor tag (307.3 ± 3.1 mm), two internal anchor tags (320.9 ± 3.3 mm)]. One fish with an internal anchor tag died during the first experiment, 122 d post-tagging; however, this mortality was due to the fish escaping the confines of the tank. Mean water temperature during this 236-d experiment was 13.2 °C (range 4.7 – 28.5) and mean salinity was 30.5 ppt (range 27.8 – 33.7). A parasitic outbreak of the dinoflagellate, *Amyloodinium ocellatum*, began on day 251 and resulted in mass mortality of both control and treatment fish, forcing termination of the experiment. The second experiment was also terminated prematurely due to extreme cold weather in early December 2010 that

rapidly reduced water temperatures in the outdoor experimental tanks and resulted in mass mortality. Mean water temperature during this 40-d experiment was 11.7 °C (range 1.7 – 17.8) and mean salinity was 28.7 ppt (range 27.9 – 30.0).

Necropsies of all fish performed at the termination of each experiment, revealed that both control and tagged spotted seatrout were slightly emaciated. However, there was minimal evidence of deleterious effects (e.g., infection or necrosis) from the presence of either one or two internal anchor tags; overall (n = 58 tagged fish in total), only one spotted seatrout was judged by NCSU CVM staff to exhibit signs of infection and necrotic tissue around the insertion point of the internal anchor tag. Based on these long-term observations of mortality due the handling and tagging of spotted seatrout with an internal anchor tag, we fixed s in our integrated tag-return model to 1.0. In addition to survival from the tagging procedure, we also observed no acute or chronic loss of internal anchor tags in either preliminary observational study. The results of mortality and tag expulsion associated with the implantation of a transmitter are presented in Section 2.

NCSU multiyear tag-return study

Of the 162 double-tagged spotted seatrout that were recovered and reported, we were able to determine the exact days-at-liberty for 155 fish, which ranged from 1 to 685 d (Table 5). Thirty-five spotted seatrout retained only one tag at recapture, while the other 120 were recaptured with both tags intact. Using the exact days-at-liberty, our exponential decay model of tag retention converged on a posterior mean estimate of 0.975 (CrI: 0.907, 1.020) for ρ and 9.419 $\times 10^{-4}$ (CrI: 3.568×10^{-4}, 0.002) for daily ϕ. In our integrated tag-return model where double-tagged cohorts were pooled into bimonthly tag-release and -recovery periods, we included this estimate of ρ (based on exact days-at-liberty) as a constant parameter but jointly estimated

chronic tag loss, reporting rates, and mortality. Bimonthly ϕ, the chronic tag-loss rate, was estimated to be 0.044 (CrI: 0.028, 0.063). On an annual scale (i.e., 365 d or 6 bimonthly periods), estimates using daily versus bimonthly estimates of ϕ were 0.344 (CrI: 0.130, 0.575) and 0.263 (CrI: 0.167, 0.375), respectively.

Since only five of the overall 144 tag returns reported as discards in our study were from the commercial fishing sector, it was assumed in our integrated tag-return model formulation for discards (i.e., "death" of tag but fish released alive) that the reporting rate for discarded fish was the same as that for tagged fish recovered and kept (i.e., harvested) by the recreational fishing sector. The sector-specific reporting rates of standard-reward tags were estimated to be much lower than the assumed reporting rate of 1.0 for high-reward tags. The overall estimates of λ for the recreational and commercial fishing sectors were 0.577 (CrI: 0.474, 0.698) and 0.317 (CrI: 0.231, 0.426), respectively.

Mortality Estimates

NCSU multiyear tag-return study

The integrated tag-return model generated bimonthly (j = 25) estimates of sector-specific fishing mortality rates for harvested fish, F_{r_j} and F_{c_j}, the mortality rate for tags (i.e., discards), F'_j, and natural mortality, M_j. Although tag-return data were collected and modeled across 31 bimonthly periods, mortality estimates for the last six tag-recovery periods were ignored given the potential bias associated with having no known number of at-risk tags for each of those additional tag-recovery periods (i.e., no new cohorts of tag releases). However, the additional tag-recovery periods beyond the last tag-release period did inform mortality estimates for all 25 tag-release periods (i.e., provided longer-term information on tags never seen again).

Tag-return estimates of bimonthly F for harvested spotted seatrout were determined separately for the recreational and commercial fishing sectors (Figure 5). For the commercial sector, F_{c_j} ranged from 0.009 to 0.141 [relative standard deviation (RSD) = (SD/estimate) × 100; 26.2%-103.5%], and for the recreational sector, F_{r_j} ranged from 0.006 to 0.072 (RSD = 19.8%-107.0%). Commercial fishing mortality estimates were generally highest in winter and summer, while recreational fishing mortality was generally highest in spring/summer (May –August) followed by late-fall/early-winter (November-December), and lowest in winter (January-February) (Figure 5A,B). Interannual variability in bimonthly F estimates was low; however, the highest F of the time-series, 0.141 (CrI: 0.065, 0.262), occurred in January/February 2010 by the commercial fishing sector, and recreational-F was highest (0.072; CrI: 0.039, 0.116) in July/August 2012 (Figure 5*a*,*b*). Estimated mortality rates for tags (index of discards), F'_j, ranged from 0.007 to 0.055 (RSD = 23.7%-104.2%) and were generally higher in spring (March-June), except for the highest estimate (0.055; CrI: 0.027, 0.095) which occurred in November/December 2010 (Figure 5C). Estimates of overall bimonthly fishing mortality, $\hat{F}_{fish_j}$, ranged from 0.025 to 0.148 (RSD = 16.5%-70.4%) and appeared to be highest in late spring/early summer and late fall/early winter and lowest in late summer and late winter (Figure 6A).

Bimonthly estimates of M_j ranged from 0.080 to 2.678 (RSD = 15.2%-94.6%). In general, higher rates of natural mortality were estimated during winter, with the highest M_j of the time-series, 2.678 (CrI: 1.904, 3.514), occurring in November/December 2010; however, M_j during the winter of 2011/2012 was relatively low (Figure 6B). The estimated total bimonthly mortality due to both fishing and natural sources, $\hat{Z}_{fish_j}$, ranged from 0.117 to 2.764 (RSD =

14.9%-72.8%). For each bimonthly interval, M_j was relatively more important than $\hat{F}_{fish_j}$, with 56.3% to 96.9% of $\hat{Z}_{fish_j}$ due to natural losses (Figure 6C).

These instantaneous mortality rates are additive and were summed to estimate *F*, *M*, and *Z* over annual intervals typical of most management time frames. Since peak spawning of spotted seatrout in North Carolina occurs on average in late-May (NCDMF 2012), annual estimates of mortality were calculated for the May to April time periods from 2009 to 2012 (Table 6 and Figure 7). This annual time frame, as opposed to a January 1st to December 31st calendar year, also more accurately represents the seasonality in annual natural mortality likely experienced by a single cohort (e.g., winter mortality typically occurs from December to February, spanning two calendar years). For each of the three years assessed, annual *M*-estimates ranged from 1.137 to 3.954 (RSD = 10.2%-19.6%) and accounted for 81.1%-91.7% of *Z*. Annual *F*-estimates were much lower and ranged from 0.265 to 0.486 (RSD = 13.1%-17.8%). Harvest rates for the recreational and commercial fishing sectors were relatively similar across years; recreational fishers accounted for 36%, 58%, and 50% of the total harvest for 2009/2010, 2010/2011, and 2011/2012, respectively, and commercial fishers accounted for the rest. The number of discards exceeded the commercial catch in 2010/2011, and both the recreational and commercial catches in 2011/2012. Assuming a 10% catch-and-release mortality rate for all discards, discard mortality accounted from 2% (in 2009/2010) to 6% (in 2011/2012) of the combined annual *F* (i.e., harvest plus discard mortality) in each of the three years. The lowest estimated annual *Z* (1.402; CrI: 0.972, 1.863) was in 2011/2012 and the highest (4.313; CrI: 3.527, 5.193) was in 2010/2011, which translate to an annual population loss in the range of 75%-99%.

The initial survival from the capture and tagging procedure, s, was assumed to be 100%; however, an 8-10% catch-and-release mortality rate is frequently used for stock assessments of spotted seatrout (Jensen 2009; Murphy et al. 2011). Additionally, we assumed that the reporting rate of recovered high-reward tags, λ_H, was 100%. We have no reason to suspect that these assumptions were violated but tested model sensitivity to such violations nonetheless. Although estimates of Z should not change due to misspecifications in s and λ_H, the partitioning of Z into F and M will vary (Hoenig et al. 1998*a*). A decrease in s reduces the pool of at-risk tags, and given the same number of expected recoveries, estimated F (based on the expected portion of tags from the at-risk pool that are recovered) must increase while M must decrease. Similarly, incomplete reporting of high-reward tags will positively bias the reporting rate estimated for standard-reward tags (Pollock et al. 2001). Reducing λ_H implies that a greater portion of tags from the at-risk pool were recovered (i.e., both reported and not reported) which results in increased estimates of F and correspondingly decreased estimates of M. Also, since it is the product of s and λ that affects model derivation of expected tag recoveries (Hoenig et al. 1998*a*; Latour et al. 2001*a*), individually varying either auxiliary parameter by the same amount will result in similar estimates of F and M (den Heyer et al. 2013). The tag-return model annual estimates of F were more sensitive than estimates of M to slight (but reasonable) variability in s and λ_H, but the bias was minimal (Table 6). Setting either s or λ_H to 0.9 resulted in a 10-11% increase in annual F-estimates and a 1-3% decrease in annual M-estimates. Estimates of Z varied by less than 0.5%, which is within the 0.8% computational error of our OpenBUGS model simulations.

NCDMF fishery-independent gill net survey

We used data from a fishery-independent gill net survey in North Carolina to separately estimate Z_j for spotted seatrout. A total of 2,079 spotted seatrout were caught in 3,568 IGNS

samples from May 2008 to December 2012 (Figure 8), of which 2,034 were measured. These fish ranged in TL from 196 to 728 mm (mean ± SE: 433.2 ± 1.7) and were converted into fractional catches-at-age for ages that ranged from 0 to 7. The majority (81%) of spotted seatrout collected in the IGNS were age-1 (52%) and age-2 (29%). Given the dominance of age-1 fish in the recreational and commercial catches (Jensen et al. 2009), we elected to include ages 1 to 7 in our modeling analysis of survey data to estimate Z_j. In doing so, we assume that spotted seatrout within this age range share a common F and M. Additionally, relatively few age-0 spotted seatrout were caught in the IGNS from May 2008 to December 2012 (6% of total catch for all ages combined), with unusually high catches in October to December 2010 from an apparently large recruiting class dominating (i.e., 66%) the total age-0 catch over the 56 months of sampling.

Slope (β_1) and intercept (β_2) parameters of the age-selectivity logistic function (γ_a) were estimated to be -24.88 (CrI: -30.29, -20.44) and 15.49 (CrI: 12.5, 19.14), respectively, which correspond to a precipitous increase from low selectivity at age-1 to full selectivity at age-2. Seasonal availability of spotted seatrout to the IGNS was highest during the May/June bimonthly periods (α_3). Therefore, relative to an assumed constant availability multiplier for α_3 of 1.0, spotted seatrout were estimated to have been more available to the IGNS in the November/December periods (α_6 = 0.580; CrI: 0.441, 0.743) than any of the other bimonthly periods [(α_1 = 0.356; CrI: 0.272, 0.455), (α_2 = 0.458; CrI: 0.351, 0.582), (α_4 = 0.387; CrI: 0.300, 0.497), and (α_5 = 0.393; CrI: 0.304, 0.503)]. Estimates of total bimonthly mortality, Z_j, ranged from 0.043 to 1.661 (RSD = 11.1%-97.2%), and were similar in pattern and magnitude to those derived from tag-return data (Figure 9A-C). Concordantly, annual estimates of Z from survey data were comparable to tag-return estimates over the three years assessed and ranged from

1.799 (CrI: 1.386, 2.234) to 3.539 (CrI: 2.999, 4.137), which translate to annual population losses of 84%-97% (Table 6 and Figure 9D). An additional annual Z could be estimated from survey data only for 2008/2009 and was 0.781 (CrI: 0.552, 1.016; 54% annual loss).

DISCUSSION

Spotted seatrout is recreationally the most targeted and therefore, one of the most economically important, fish species in the U.S. South Atlantic and Gulf of Mexico. Although at the northern edge of the species distribution, spotted seatrout have provided a long-standing fishery for North Carolina. As such, proper management is needed in the state to ensure the long-term sustainability of this valuable fishery resource. Reliable information on vital rates, including the sources and levels of mortality, are essential to the development of such effective management strategies. Using data from the first comprehensive tag-return study of spotted seatrout in North Carolina, we estimated the relative importance of F and M to seasonal Z across multiple years. Furthermore, we estimated F separately for the recreational and commercial fishing sectors and accounted for discard mortality where tags were harvested but fish were released alive. These mortality estimates also incorporated the uncertainty associated with key auxiliary parameters (i.e., ϕ and λ), which we estimated internally through an integrated tag-return modeling approach. The overall tag-return rate of 8.4% that we observed in our study was within the range (0.8-24.9%) of those reported by many previous tagging studies on spotted seatrout, although high variability in methodologies (e.g., tag types and capture methods) implies that these rates are not directly comparable (Table 7). Still, our study suggests that the generally low tag-return rates reported by many previous spotted seatrout tagging studies, most of which

either inadequately addressed or completely ignored key auxiliary tagging parameters, may result from high *M*, high tag loss, and incomplete tag reporting.

Mortality

The recent stock assessment completed by the NCDMF concluded that the spotted seatrout population was overfished from 1991-2008 (all 18 years included in the assessment) and that overfishing is occurring (Jensen 2009). The validity of these conclusions is largely dependent on the accuracy to which *M* was accounted for in the age-structured assessment model. Underestimates of *M* will negatively bias estimates of population size and positively bias subsequent estimates of *F* (Clark 1999; Maunder and Wong 2011). The NCDMF assessment used two indirect approaches to determine *M* for spotted seatrout: (1) a Hoenig (1983) longevity-based estimate of 0.37 for all ages and (2) age-specific Lorenzen (1996) weight-based approximations ranging from a maximum of 0.41 for age-1 fish (i.e., the age of full selectivity in the recreational fishery) to a minimum of 0.21 for age-6+ fish (Jensen 2009). Our tag-return estimates of annual *M* were greater than the highest estimate used in the recent stock assessment, with discrete rates of natural loss for each year of tag-return estimates (68%-98%) being 2-3 times that estimated in the stock assessment (34%). Furthermore, whereas the assessment assumed *M* was constant across years, our estimates indicate high interannual variability in *M*.

A significant advantage of the instantaneous rates tag-return model that we used over traditional stock assessment models is that we were able to assess the seasonal (i.e., bimonthly) variability in mortality. Overall, *M* was high throughout the year but was particularly elevated during the winters of 2009/2010 and 2010/2011, which coincide with statewide reports of lethargic and moribund spotted seatrout following the rapid onset of low temperatures. In an unprecedented response to such reports, managers in North Carolina temporarily closed the

fishery for five months in early 2011 (NCDMF 2011*a*,*b*), with the expectation that reducing subsequent fishing mortality of surviving adults prior to peak spawning in summer may lead to a faster recovery of the population from winterkill (e.g., McEachron et al. 1994). Our estimate of high *M* during this winter was based on the abrupt decline in tag returns observed after this bimonthly period. Specifically, 217 tags from the 3,705 spotted seatrout released prior to the start of the January/February 2011 period (including 1,150 fish released from September 2010 through December 2010) were returned by October 31, 2013, and only 10 of these tag returns (≤5%) occurred after December 31, 2010. Although mass mortalities of spotted seatrout have been attributed to harsh winter conditions across much of the species range (Wilcox 1887; Smith 1907; Storey and Gudger 1936; Gunter 1941; Gunter and Hildebrand 1951; Simmons 1957; Tabb and Manning 1961; Moore 1976; Green et al. 1990; McEachron et al. 1994; Martin and McEachron 1996; NCDMF 2012), few have attempted to quantify winter *M* for the species. Using six-month intervals of tag-return data, external estimates of s and λ (but no account for ϕ), and maximum likelihood estimation procedures, Green et al. (1990) surmised that the elevated *M*-estimate of 2.36 in several Texas bays from November 1983 to April 1984 relative to estimates over the same months in 1981/1982 (1.36) and 1982/1983 (0.80) was the result of extreme low temperatures that persisted that winter and the absence of thermal refuge in those systems. This conclusion was also supported by observations of a massive fish kill during that winter (McEachron et al. 1994). Interestingly, estimates of *M* in our study during several summers were also elevated, including a relatively high estimate for the summer of 2012. Generally in spring, spotted seatrout emigrate from relatively shallow, low-salinity estuarine tributary creeks and move to the deeper, more saline rivers and sound of the estuary (see Section 2). This emigration coincides with the start of a protracted spawning season that continues

through September (NCDMF 2012). Higher *M* during summer may be associated with spawning-related stress (e.g., low energy and warm temperatures increase susceptibility to bacterial infections), as well as due to an increased predation risk from the larger predators common to the lower estuary and coastal ocean habitats [e.g., bottlenose dolphins (*Tursiops truncatus*)]. The large intrannual variability in *M* that was captured by and estimated from our tag-return data was not explained by the Lorenzen (1996) weight-based approach that was used in the recent stock assessment. Given that the mean and size range of spotted seatrout that we tagged was invariant across bimonthly intervals (Figure 2), the Lorenzen (1996) approximations of bimonthly *M* (approximately 0.084) were also stable. Moreover, 23 out of our 25 (92%) consecutive bimonthly estimates of *M* from tag-return data greatly exceeded these corresponding Lorenzen (1996) approximations.

We estimated bimonthly and annual *F* for spotted seatrout directly from fishery recoveries of tags by accounting for the necessary auxiliary parameters that can bias mortality estimates derived from tag-return data. Overall, *F* was relatively low in our study from September 2008 to October 2012. Our annual estimates of *F* over the three years studied were lower than the lowest *F* estimated in the recent stock assessment but such disagreement is expected given the significant differences in estimates of *M* previously discussed. However, several other characteristics of *F* should be less biased by differences in *M* and more reasonable for comparison. Our bimonthly-*F* estimates indicated that *F* was seasonal and that higher fishing pressure occurred during late-spring/early-summer and late-fall/early-winter, which is in agreement with historical (1991-2008) (NCDMF 2012) and recent (2008-2012) recreational survey statistics (http://www.st.nmfs.noaa.gov/recreational-fisheries/index). We also estimated the relative contribution of each fishing sector and fishery discards to the overall total fishing

mortality for spotted seatrout. Sector-specific differences in F in our study were small, suggesting that neither the commercial nor the recreational sector contributed disproportionately to the overall annual harvest of spotted seatrout over the years of our study. Finally, we accounted for discard mortality by separating the "death" of tags (i.e., fish released alive) from the death of fish (i.e., fish harvested) and found that annually, discards matched or exceeded commercial and recreational harvest in two of the three years. Despite the relatively high proportions of discards, we assumed that only 10% of these released fish died; therefore, discard F' had relatively little influence in our final estimates of bimonthly and annual total F (i.e., commercial harvest, recreational harvest, and 10% of discard F' combined) for spotted seatrout. Several regulation changes occurred over the course of our study that may have potentially influenced fisher behavior and contributed to the higher discard rates estimated in the latter half of our study. The minimum size limit was increased from 12 to 14 inches TL in October 2009 for part of the state's waters and in August 2011 for the entire state; however, exploratory analyses of the tag-return data did not suggest that the TL of discarded spotted seatrout varied before (mean ± SE: 368.4 ± 9.4 mm) and after (mean ± SE: 380.1 ± 7.9 mm) August 2011. Additionally, the daily recreational bag limit was reduced from 10 to 4 fish in November 2011. Although elevated levels of discards also coincided with the temporary closure of the fishery that was effective from January 14 to June 15, 2011, some tags recovered during this closed period by both fishing sectors were reported as a harvest. Our ability to gather information on discards using tag-return data was dependent upon fishers truthfully acknowledging the fate of the fish during the phone interview. The estimates of F and Z in our study would be negatively biased if more than 10% of the reported discards actually died, either due to catch-and-release mortality or to inaccurate reporting of fate (i.e., they were harvested instead of released); however, even

100% mortality of discards would not affect our overall estimate of the relative importance of *F* and *M* to *Z* for spotted seatrout in North Carolina.

Our estimates of mortality were of low precision due to the overall low number of tag returns and the resulting sparse tag-return matrix. Despite this level of uncertainty, the notable similarities between the bimonthly and annual estimates of *Z* for spotted seatrout from tag-return data versus independent survey data lend confidence that the magnitude and seasonality of our estimates of total annual population loss over the course of our study are accurate. With specific regard to the seasonal estimates of *Z*, both independent data sources captured the elevated levels during the only two of four winters where numerous reports of cold-stressed spotted seatrout were reported. These reports were largely restricted to areas of the central and northern portions of the state during the January 2010 cold front but were regionally more extensive in December 2010, which is reflected in the higher *Z* estimated by tag-return data for that winter. Estimates for that winter from survey data were less precise, particularly regarding the bimonthly period to which the model assigned the bulk of the winter mortality (i.e., over three bimonthly periods as opposed to one). Still, the *Z* estimated for the November 2010 to April 2011 time period from tag-return data (3.284; discrete loss rate of 96%) was comparable to estimate from survey data (2.621; discrete loss rate of 93%). Given the reduced sampling effort (and low sample sizes) during the 2010/2011 winter in the IGNS and the relatively large cohorts of tagged spotted seatrout released in the months preceding December 2010, the estimates of *Z* from tag-return data over this winter period are likely most accurate.

High annual population loss appears to be characteristic of spotted seatrout throughout the species' geographic distribution (Iversen and Moffett 1962; Wakeman and Ramsey 1985; Baker et al. 1986; Rutherford et al. 1989; Green et al. 1990; Wenner et al. 1990; Woodward

1990; Murphy and Taylor 1994; Woodward and Mericle 1995; Nieland et al. 2002; Jensen 2009). Although our estimates of *Z* from tag-return data for spotted seatrout in the northern range, validated by independent survey data, are among the highest ever reported for the species (discrete loss rates of 75-99%), we believe that indirect estimates of *M* used by others negatively bias many estimates of *Z* reported in the literature. Furthermore, the population dynamics of spotted seatrout in North Carolina and Virginia are likely more regularly influenced by winter conditions than stocks at the center of the species' range. The life-history traits that allow spotted seatrout populations to endure such high annual loss rates include rapid growth, early maturation, a protracted spawning season, and prolificacy.

Auxiliary Parameters, Study Limitations, and Future Considerations

We observed no acute or chronic mortality of spotted seatrout associated with tagging, but incomplete reporting and loss of internal anchor tags limited returns in this study. Inaccuracies in these three key auxiliary parameters can bias mortality estimates derived from tag returns by either reducing the pool of tags at-risk for recovery or leading to fewer recoveries than would be expected (Pollock 1991; Pollock et al. 2001; Miranda et al. 2002; Brenden et al. 2010). We determined spotted seatrout survival from tagging through long-term observations under relatively optimal conditions (i.e., tank enclosures), and our results are consistent with the few reported by others. Using field enclosures and internal anchor tags, Iversen and Moffett (1962) estimated *s* to be 0.96 within 10 d of tagging; however, it is unclear if their capture methods included gillnets in addition to hook-and-line. Green et al. (1990) elected to use a lower *s* of 0.83 that was previously estimated for spotted seatrout also held in field enclosures for 7 d after insertion of an internal anchor tag (Hegen et al. 1984). Vogelbein and Overstreet (1987) conducted a histopathological assessment of tagging-induced mortality and found minor

complications for spotted seatrout from the insertion of an internal anchor tag; no mortality or tag loss was observed up to eight weeks, although their sample size was small (n = 12). The mortality of spotted seatrout associated with hook-and-release has been well studied and is generally reported to be low (Matlock et al. 1993; Murphy et al. 1995; Duffy 2002; Stunz and McKee 2006; James et al. 2007). Given the strict landing, handling, and release requirements we imposed on taggers in our study, along with the previously determined low catch-and-release mortality for this species under less stringent conditions, we assumed there was no tagging-induced mortality in our model analysis. Our tag-return estimates of mortality were not overly sensitive to variability in s, which we ascertained by reducing s to 0.9. A possible limitation of our laboratory studies to estimate s is that the effect of water temperature at time of capture and tagging was not considered. Experimental fish were initially captured and tagged only in late-fall, and it is possible that we may have used too high a value of s for spotted seatrout during other seasons when environmental conditions were less favorable (e.g., summer water temperatures). An increase in catch-and-release mortality associated with warmer temperatures has been reported for numerous fish species; however, for spotted seatrout, this summer catch-and-release mortality is reportedly low (≤11%: Stunz and McKee 2006; James et al. 2007) or not significantly different from that in other seasons (Murphy et al. 1995).

Both our laboratory studies and analysis of double-tagged spotted seatrout recoveries suggest that immediate tag shedding was low, as expected for internal anchor tags. However, estimated chronic tag loss was high in the field. Estimates of ϕ from the recoveries of double-tagged spotted seatrout were similar using either exact days-at-liberty or by pooling double-tag recoveries across bimonthly periods, and to our knowledge these are the first field-based estimates of the chronic loss of internal anchor tags by spotted seatrout. Several other studies

report higher observed return rates of spotted seatrout tagged with internal anchor tags versus other tag types (e.g., dorsal T-bar tags) but none specifically quantified ϕ (Moffett 1961; Music and Pafford 1984; Woodward and Mericle 1995). Our results suggest that spotted seatrout expel internal anchor tags at a much higher rate (2× to 15×) than what has been reported for other frequently tagged fusiform fishes found in North Carolina estuaries, including red drum (*Sciaenops ocellatus*: Latour et al. 2001*a*) and striped bass (*Morone saxatilis*: Dunning et al. 1987; Sprankle et al. 1996). We hypothesize that the high loss rate of internal anchor tags by spotted seatrout is due to a relatively thin body wall and the absence of large scales, in conjunction with rapid growth rates. Interestingly, we observed no loss of internal anchor tags in the laboratory, similar to what was reported by Overstreet (1983) and Vogelbein and Overstreet (1987). However, post-experiment necropsies, as well as photos of recovered tagged spotted seatrout at liberty, indicated that the abdominal tissue of captive and free-roaming fish responded equally to the presence of the internal anchor tag; healing appeared to occur from the inside out and in a manner conducive to expulsion of the tag's internal anchor disc. Our observations of this tissue response were similar to those reported by Moffett (1961) and Vogelbein and Overstreet (1987). Spotted seatrout from our laboratory study were sedentary (i.e., minimal swimming activity was required) and exhibited minimal growth, which likely promoted tag retention. Captive spotted seatrout were offered a variety of diets including a high-protein pellet diet. However, only live prey and later, freshly dead prey, triggered minimal feeding behavior; thus, it is likely that our experimental fish were only feeding at just below maintenance levels. Tag expulsion may have been dampened by minimal growth of new tissue around the internal anchor tag.

The large discrepancy in our estimates of tag retention by spotted seatrout for captive versus free-roaming fish suggest that holding studies may significantly underestimate ϕ and highlight the necessity for including a double-tagging component in long-term tag-return studies rather than relying solely on short-term, or even long-term, enclosure observations. Additionally, there is indication that the return rates of tagged spotted seatrout may vary due to tag type (i.e., higher rates are associated with internal anchor tags; Table 7), and the significant loss of internal anchor tags in our study suggests that most return rates of tagged spotted seatrout are low at least partly due to high tag loss.

In fishery-dependent tag-return studies, the reporting of recovered tags by fishery participants is rarely absolute. Consequentially, this incomplete reporting, if unaccounted for, limits the use of tag-return data to better understand the sources and levels of mortality affecting fish abundance. Partitioning Z into F and M requires that λ be accurately estimated, typically through the use of high-reward tags, secretly planted tags, angler surveys, or observer coverage within a multicomponent fishery (see review in Pollock et al. 2001). Of these, high-reward tagging has been the preferred approach taken to estimate λ, especially for fisheries with a large recreational component (Denson et al. 2002; Taylor et al. 2006; Bacheler et al. 2009*c*) but also in fisheries dominated by the commercial catch (Cowen et al. 2009; Smith et al. 2009; den Heyer et al. 2013). Steps were taken to meet the fundamental assumption of this approach that all (100%) recovered high-reward tags were reported; incomplete reporting of high-reward tags would result in an overestimate of sector-specific λ in our study. First, the reporting of high-reward tags in our study was worth a monetary reward at a level (i.e., US $100) suggested to elicit a 100% reporting rate (Nichols et al. 1991; Taylor et al. 2006) and used in previous tag-return studies in North Carolina (Bacheler et al. 2009*c*) and elsewhere (Denson et al. 2002; Cowen et al. 2009;

den Heyer et al. 2013). Next, we widely advertised that spotted seatrout were being released with high-reward tags, used a color (i.e., red) that was easily distinguishable from standard-reward tags (i.e., yellow), and were consistent with the reward/color combinations used in a previously successful tag-return study of red drum in North Carolina (Bacheler et al. 2009*c*). Additionally, because fisher behavior may change with the presence of high-reward tags (Pollock et al. 2001), we released spotted seatrout with high- and standard-reward tags throughout North Carolina and Virginia and randomized our releases such that tags of both reward levels were continually at-risk across space and time for the duration of the study. Overall, given our consideration for meeting the assumptions of a high-reward tagging approach outlined by Pollock et al. (2001), we are confident that our estimates of λ are accurate. Furthermore, our tag-return estimates of mortality were not overly sensitive to a minor (but reasonable) level of incomplete reporting of high-reward tags (i.e., 90%).

Underreporting of standard-reward tags was high in our study. We estimated sector-specific λ for the recreational and commercial fisheries and found that recreational fishers reported a greater proportion (1.8×) of spotted seatrout tags they recovered than commercial fishers. The 0.26 difference in sector-specific λ was similar to that (0.33) estimated for the North Carolina red drum fishery in a previous tag-return study using high-reward tags (Bacheler et al. 2009*c*). Our estimate of λ for recreational fishers (0.58) was higher than the 0.33 reported by Green et al. (2003) for spotted seatrout in Texas using a planted tag approach but lower than that (0.77) estimated from the relative returns of high- and standard-reward tagged red drum in North Carolina (Bacheler et al. 2009*c*). Our estimate of λ for commercial fishers (0.32) was also lower than the 0.44 reported by Bacheler et al. (2009*c*) and much lower than the near complete reporting (0.89-0.92) estimated by Smith et al. (2009) for a regional southern flounder

(*Paralichthys lethostigma*) gillnet fishery in North Carolina, although the authors of that study developed strong working relationships with commercial fishers in the New River that likely resulted in a high-level of study participation. Several factors could have contributed to both our observed underreporting rates and the sector-specific differences in λ; however, the two most likely deterrents to participation in our study by fishers were (1) the relative trade-off between the time it took to report a tag versus the standard reward offered (i.e., many fishers may have been uninterested in $5, a hat, or a T-shirt) and (2) the perception that the tag-return data would eventually result in tighter regulations, rather than the actual overall benefit of providing critical data needed for best management practices. The latter is particularly relevant given that the development and implementation of the first fishery management plan for spotted seatrout in North Carolina occurred over the course of our study and resulted in new harvest limits for both fishing sectors, beginning in October 2009 with an increase in the minimum size limit and continuing through at least November 2011 with a reduction in daily bag limits for recreational fishers and a new daily catch limit for commercial fishers.

The bimonthly interval of our tag-return model provided valuable information about the seasonality in F and M but some consideration for potential violations of key model assumptions is needed. First, tag-return models assume that all marked fish are released instantaneously at the beginning of each interval (Ricker 1975; Youngs and Robson 1975). However, our limitation to the use of hook-and-line to capture spotted seatrout for tagging, as well as the necessity to distribute our tagging effort coastwide, prevented strict adherence to this assumption. Marked fish were released continually across our bimonthly intervals and consequently, fish tagged later in bimonth-j were only subject to a fraction of Z during that initial bimonthly release interval. Monthly intervals (Bacheler et al. 2009*c*; Smith et al. 2009) and even

a scaling factor for partial mortality during the month of release (Latour et al. 2001*a*; Smith et al. 2009) have been used to better satisfy this assumption given the continual release of marked fish. These approaches were not possible in our study due to an inability to catch, tag, and release spotted seatrout each month (e.g., low catches in February of each year) and the use of multiple taggers that resulted in continual rather than batch releases of marked fish each month. We do not believe that our violation of the assumption of instantaneous releases is of practical concern given that the rate of decline ($Z_j + \phi$) of tagged spotted seatrout over a bimonthly interval was low, except for some intervals of high M_j (i.e., winter), and that the fraction of tags that were returned each interval was small relative to the number at-risk. Additionally, the similar bimonthly estimates of Z_j derived from tag-return data and from IGNS data, given their independence, suggests that the tag-return model was not overly sensitive to violations of this assumption.

Two other key model assumptions particularly relevant to our tag-return data were that (1) tagged fish mixed with the untagged population and (2) all tagged fish shared the same survival and recovery probabilities. Our tagging effort was implemented such that we were able to tag spotted seatrout across the entire distribution of the population, which in theory should allow for sufficient mixing of marked and unmarked fish. The spatial distribution of recaptures indicates that tagged fish were well mixed across the study area. Furthermore, relatively few fishers (48 out of 477; 10%) recovered and reported more than one tagged spotted seatrout, and most of these multiple recoveries occurred over separate occasions. Permanent emigration from the study area, such as the migration of older individuals to areas inaccessible to fishing or where fishing effort is relatively low (e.g., ocean), can result in differing survival and recovery probabilities over time, especially for cohorts tagged early on in a multiyear study (Latour et al.

2001*a*,*b*). Such emigration would inflate estimates of Z_j in our study, and given that M is indirectly estimated from the decline in tag returns over time (i.e., tags never seen again) not explained by F and the auxiliary parameters, most of the positive bias associated with permanent emigration is captured in the estimates of M_j. Historical fishing effort and landings data collected in North Carolina and Virginia suggest that the existence of a large offshore population of spotted seatrout is unlikely (NCDMF 2012). Thus, we are confident that our tag-return estimates of mortality were not biased by permanent emigration from the estuarine and nearshore coastal environments where all tagging and tag-recoveries in our study occurred. Estimates of Z_j from IGNS data would also be subject to this same bias.

CONCLUSION

Comprehensive tag-return studies compliment traditional stock assessment approaches by providing independent and reliable information on the sources and levels of mortality affecting abundance. The results of our multiyear tag-return study provide new information on the relative importance of F and M to Z for spotted seatrout in North Carolina. Although our results and those of the recent state assessment both indicate high annual loss of the spotted seatrout population each year, direct estimates of F from tag-return data suggest the population dynamics of spotted seatrout in North Carolina are driven predominantly by natural sources of mortality rather than harvest. Due to continual coastwide tagging, rigorous laboratory and field efforts to precisely estimate and account for bias associated with key auxiliary tagging parameters, the use of accepted tag-return modeling techniques, and validation from independent data, we believe our estimates of spotted seatrout mortality accurately reflect the seasonal dynamics of annual loss in North Carolina. We conclude that indirect estimates of M commonly derived from

longevity and weight-based parameters are unsuitable for estimating *M* for spotted seatrout and that future assessments of the North Carolina stock would be improved by consideration of more direct estimates of and annual variability in *M*. Continued comprehensive tagging of spotted seatrout in North Carolina is needed to fully describe the range of *M* (e.g., variability in winter severity) that occurs at the species' northern latitudinal limit. Improved precision of mortality estimates from future tag-return studies of spotted seatrout would be achieved by increasing the overall number of tags returned, specifically through efforts to increase tag retention (e.g., use alternative tag type or multiple tags), increase reporting rates of recovered tags (e.g., use only high-reward tags), or increase the size of the tagged population relative to the untagged population (i.e., tag more fish).

Table 1. List of symbols frequently used in this section. The parameters listed here are described in greater detail in the text.

Symbol	Description
Z_j	Instantaneous total mortality rate in bimonth *j*
M_j	Instantaneous natural mortality rate in bimonth *j*
F_j	Instantaneous fishing mortality rate in bimonth *j* of harvested tags
F'_j	Instantaneous fishing mortality rate in bimonth *j* for tags of discards
S_{ij}	Bimonth-*j* survival for single tags released in bimonth *i*
S'_{ij}	Bimonth-*j* survival (both tags intact) for double tags released in bimonth *i*
δ	Previously estimated discard (hook-and-release) mortality rate
λ	Tag-reporting rate
s	Survival from tagging and handling
Q_t	Probability of tag retention at time *t* after release
ρ	Probability of tag retention immediately after tagging
ϕ	Chronic tag-loss rate
R_{ij}	Observed recoveries in bimonth *j* of single-tag releases in bimonth *i* for harvested fish
R'_{ij}	Observed recoveries in bimonth *j* of single-tag releases in bimonth *i* for discarded fish
$R_{TT_{ij}}$	Observed recoveries in bimonth *j* of double-tag releases (retaining both tags) in bimonth *i* for harvested fish
$R_{T_{ij}}$	Observed recoveries in bimonth *j* of double-tag releases (retaining only one of two tags) in bimonth *i* for harvested fish
$R'_{TT_{ij}}$	Observed recoveries in bimonth *j* of double-tag releases (retaining both tags) in bimonth *i* for discarded fish
$R'_{T_{ij}}$	Observed recoveries in bimonth *j* of double-tag releases (retaining only one of two tags) in bimonth *i* for discarded fish
C_{ij}	Catch of cohort *i* in bimonth *j* during fishery-independent survey
α_p	Multiplier for seasonal (*p*) availability to fishery-independent survey
γ_a	Fishery-independent survey selectivity for age *a*
L	Likelihood function

Table 2. Bimonthly releases of tagged spotted seatrout by North Carolina State University personnel and collaborating fishing guides in North Carolina and Virginia waters from September 2008 through October 2012.

		Tag-Release Category			
Bimonthly Period		Single Standard Reward	Double Standard Reward	Single High Reward	Total
Sep./Oct.	2008	150	42	30	222
Nov./Dec	2008	267	91	68	426
Jan./Feb.	2009	99	45	26	170
Mar./Apr	2009	65	24	13	102
May/Jun.	2009	148	29	23	200
Jul./Aug.	2009	42	20	11	73
Sep./Oct.	2009	186	93	46	325
Nov./Dec	2009	158	37	39	234
Jan./Feb.	2010	16	22	3	41
Mar./Apr	2010	67	29	20	116
May/Jun.	2010	127	44	34	205
Jul./Aug.	2010	46	40	13	99
Sep./Oct.	2010	550	212	136	898
Nov./Dec	2010	336	168	90	594
Jan./Feb.	2011	63	16	15	94
Mar./Apr	2011	86	47	26	159
May/Jun.	2011	60	19	14	93
Jul./Aug.	2011	391	175	106	672
Sep./Oct.	2011	330	159	90	579
Nov./Dec	2011	295	142	80	517
Jan./Feb.	2012	109	48	32	189
Mar./Apr	2012	82	51	17	150
May/Jun.	2012	149	66	34	249
Jul./Aug.	2012	77	40	24	141
Sep./Oct.	2012	18	8	8	34
Total		3,917	1,667	997	6,582

Table 3. Total length (cm) of spotted seatrout for single internal anchor tag (T), dummy transmitter (V), and control (C) (i.e., no tag or transmitter) treatments by tank replicate during the 2008/2009 laboratory experiment.

Treatment	Tank 1 (cm)	Tank 2 (cm)	Tank 3 (cm)	Tank 4 (cm)
T	26.7	27.9	27.9	28.4
T	29.2	29.2	28.6	28.6
T	30.5	29.8	30.5	29.8
T	38.7	43.2	38.1	43.8
V	31.7	30.5	31.7	31.7
V	33.0	33.0	34.3	34.9
V	43.2	44.4	39.4	43.8
C	26.7	27.9	28.4	29.2
C	29.2	29.2	29.2	29.2
C	31.1	29.2	29.8	30.5
C	45.7	48.3	41.3	44.4
		Average (±SD) (cm)		
T	31.3 (5.2)	32.5 (7.2)	31.3 (4.7)	32.6 (7.5)
V	36.0 (6.3)	36.0 (7.4)	35.1 (3.9)	36.8 (6.3)
C	33.2 (8.5)	33.6 (9.8)	32.2 (6.1)	33.3 (7.4)
Combined	33.2 (6.5)	33.9 (7.6)	32.6 (4.8)	34.0 (6.6)

Table 4. Total length (cm) of spotted seatrout for single internal anchor tag (T), double internal anchor tag (TT), and control (C) (i.e., no tag or transmitter) treatments by tank replicate during the 2010 laboratory experiment.

Treatment	Tank 1 (cm)	Tank 2 (cm)	Tank 3 (cm)
T	28.1	29.7	30.0
T	28.6	29.7	30.0
T	29.9	29.9	30.1
T	30.0	31.3	30.2
T	31.7	31.6	30.4
T	32.1	32.4	30.6
T	33.5	32.9	32.6
TT	29.5	31.0	30.5
TT	31.5	31.0	30.6
TT	31.5	31.0	31.4
TT	31.5	31.2	32.0
TT	33.5	32.1	32.3
TT	35.0	32.2	33.0
TT	35.6	33.6	33.9
C	27.9	28.7	26.6
C	28.2	29.0	28.1
C	28.6	29.6	28.3
C	29.8	30.5	30.2
C	31.3	31.0	31.0
C	32.6	32.0	34.0
C	34.6	34.5	36.9
		Average (±SD) (cm)	
T	30.6 (2.0)	31.1 (1.3)	30.6 (0.9)
TT	32.6 (2.2)	31.7 (1.0)	32.0 (1.2)
C	30.4 (2.5)	30.8 (2.0)	30.7 (3.6)
Combined	31.2 (2.3)	31.2 (1.5)	31.1 (2.2)

Table 5. The number of double-tagged spotted seatrout released in North Carolina and Virginia waters that were recovered and reported from September 2008 through October 2013 (n = 155 total), relative to days-at-liberty (T = double-tagged fish recovered and retaining only one of two tags; TT = double tagged fish recovered and retaining both tags).

Days-at-liberty	Count		Days-at-liberty	Count		Days-at-liberty	Count	
	T	TT		T	TT		T	TT
1		2	79	1		179		1
2		1	81	1		180	1	
3		1	84	1	1	181	1	
5		2	85	1		184		1
6		3	87		1	189		1
7		1	88		1	200	1	
10		3	89	1		201		1
11		1	92	1		203	1	1
12		1	93		2	204		1
13		1	94		2	214		1
14		1	95		1	241		1
16		1	98		1	249		1
20	1	2	99		1	251		1
21		1	101	1		255	1	
23		2	102	1		256		1
25		3	104		2	258		1
26		1	106	1		259	1	
28		1	107		1	265	1	
30		1	108	1	1	268		1
31		2	110	1	1	279		1
32		1	114		1	280		1
35		1	121		1	282	1	
38		1	123		1	290		1
39		1	124		1	303		1
40		1	126		1	309		1
41		1	128		1	338	1	
43		1	129	1	1	356		1
44		2	133		1	357		1
45		2	134		1	368		1
47		1	142		1	372	1	
49		1	143		1	380	1	
50		1	148	1		383	1	
51		1	149		2	403		1
54		1	152		1	427	1	
55		1	154	1		429	1	
56		2	160		1	442		1
60	1	2	168		1	449		1
62	1	3	172		1	460		1
63	1		174		1	578	1	
72		1	176	1		598	1	
73		1	177		1	635		1
74		1	178		1	685		1

Table 6. Summary of annual parameter estimates from the integrated tag-return model and survey model from May 2009 to April 2012. For the tag-return model, tag loss (ϕ) and sector-specific incomplete reporting of standard-tag recoveries (λ_S) were determined jointly with rates of fishing (F), natural (M), and total mortality (Z) based on the recoveries of tagged spotted seatrout from September 2008 through October 2012 and accounting for a 10% discard mortality rate on fisher releases. Estimates from three separate models with varying levels of assumed initial tagging survival (s) and reporting rate of high-reward tags (λ_H) are presented.

					May 2009 – April 2010			May 2010 – April 2011			May 2011 – April 2012		
Tag-Return Model		ϕ	Rec. λ_S	Com. λ_S	F	M	Z	F	M	Z	F	M	Z
$s = 1.0$, $\lambda_H = 1.0$	mean	0.263	0.577	0.317	0.486	2.247	2.733	0.360	3.954	4.313	0.265	1.137	1.402
	lower	0.167	0.473	0.231	0.340	1.637	2.060	0.257	3.207	3.527	0.204	0.719	0.972
	upper	0.375	0.698	0.426	0.680	2.903	3.453	0.490	4.782	5.193	0.341	1.585	1.863
$s = 0.9$, $\lambda_H = 1.0$	mean	0.263	0.578	0.319	0.536	2.181	2.717	0.398	3.906	4.304	0.294	1.104	1.398
	lower	0.166	0.475	0.232	0.374	1.584	2.055	0.283	3.166	3.518	0.227	0.623	0.968
	upper	0.376	0.700	0.430	0.747	2.828	3.430	0.541	4.727	5.170	0.375	1.553	1.863
$s = 1.0$, $\lambda_H = 0.9$	mean	0.262	0.521	0.287	0.536	2.180	2.716	0.399	3.916	4.315	0.294	1.102	1.396
	lower	0.167	0.426	0.209	0.375	1.577	2.049	0.284	3.182	3.537	0.227	0.693	0.969
	upper	0.374	0.633	0.387	0.743	2.836	3.444	0.545	4.737	5.191	0.376	1.552	1.861
Survey Model							Z			Z			Z
	mean						2.070			3.539			1.799
	lower						1.804			2.999			1.386
	upper						2.344			4.137			2.234

Table 7. Summary of previous spotted seatrout tag-return studies whose published reports were available (i.e., not necessarily an exhaustive summary table). Tag types: IA = internal anchor tag; TB = T-bar tag; DT = Dart tag; CS = California spaghetti tag; BC = body cavity tag; MS = Monel strap tag. Capture methods: HL = hook-and-line; GN = gill net; TN = trammel net; CN = cast net; SN = stop net; PN = pound net; HS = haul seine; TL = trotline. Note: Some reports share tag-return data and are marked by an asterisk (*).

State	Years	Tag Type	Capture Method	# Tagged	# Returned	Return Rate (%)	Source
TX	1950-1975	MS, IA	HL, GN, TN, TL	20,517	382	1.9	Matlock 1992
	1975-1982	IA	HL, GN, TN	12,349	910	7.4	Marwitz 1986
	1975-1999*	IA	HL, GN, TN	23,213	1,433	6.2	Bowling and Sunley 2003*
	1976-1981*	IA	HL	2,040	176	8.6	Baker et al. 1986*
	1982-1983*	IA	HL	488	54	11.1	Baker and Matlock 1993*
VA	1995-2012	TB, IA	HL	46,571	1,969	4.2	Musick and Gillingham 2013
FL	1958-1960	BC	HL, GN, TN	2,990	308	10.3	Moffett 1961
	1958-1960	IA	HL, GN, TN	2,355	269	11.4	Moffett 1961
	1961	IA	HL, GN, TN	5,409	1,349	24.9	Iversen and Moffett 1962
	1961*	IA	HL, GN, CN	513	119	23.2	Hutton et al. 1962*
	1964*	CS	HL, GN, TN	208	11	5.3	Beaumariage and Wittich 1966*
	1964*	IA	HL, GN, TN	299	40	13.4	Beaumariage and Wittich 1966*
	1965*	CS	HL, GN, TN	281	19	6.8	Beaumariage 1969*
	1965*	IA	HL, GN, TN	315	35	11.1	Beaumariage 1969*
	1961-1965	CS, IA	HL, GN, TN	3,957	537	13.6	Beaumariage 1969*
	1986-1988, 1990-1992	IA	HL, TN	927	14	1.5	Stevens and Sulak 2001
	1990-1999	DT	HL, GN, TN, HS	364	6	1.7	Tremain et al. 2004
SC	1978-2009	DT	HL	14,516	348	2.4	Wiggers 2010
	1986-1993	IA	HL, SN, TN	6,284	604	9.6	Wenner and Archambault 1996
LA	1969-1976	TB	(not reported)	2,834	22	0.8	Adkins et al. 1979
	1976-1977	TB	HL, GN, TN	2,604	30	1.2	Adkins et al. 1979
	1976-1980	TB	HL, GN, PN	5,290	107	2.0	Rogillio 1980
	1976-1983	TB	HL, GN	4,569	61	1.3	Arnoldi 1984
	1980-1985	TB	HL, GN, PN	5,249	418	8.0	Rogillio 1985
GA	1979-1982	TB, IA	HL, GN, TN, CN, HS	3,381	456	13.5	Music and Pafford 1984
	1986-1989	IA	TN	2,332	180	7.7	Woodward et al. 1990
	1991-1995	IA	GN, TN	1,066	60	5.6	Woodward and Mericle 1995
MS	1978-1980	IA	HL, GN, TN, HS	133	14	10.5	Overstreet 1983
	1995-1999	DT	HL	15,206	408	2.7	Hendon et al. 2002
NC	1996-1999	DT	HL	240	5	2.1	NC CCA (NC Sea Grant documentation)
	2008-2013	IA	HL	6,582	553	8.4	This study

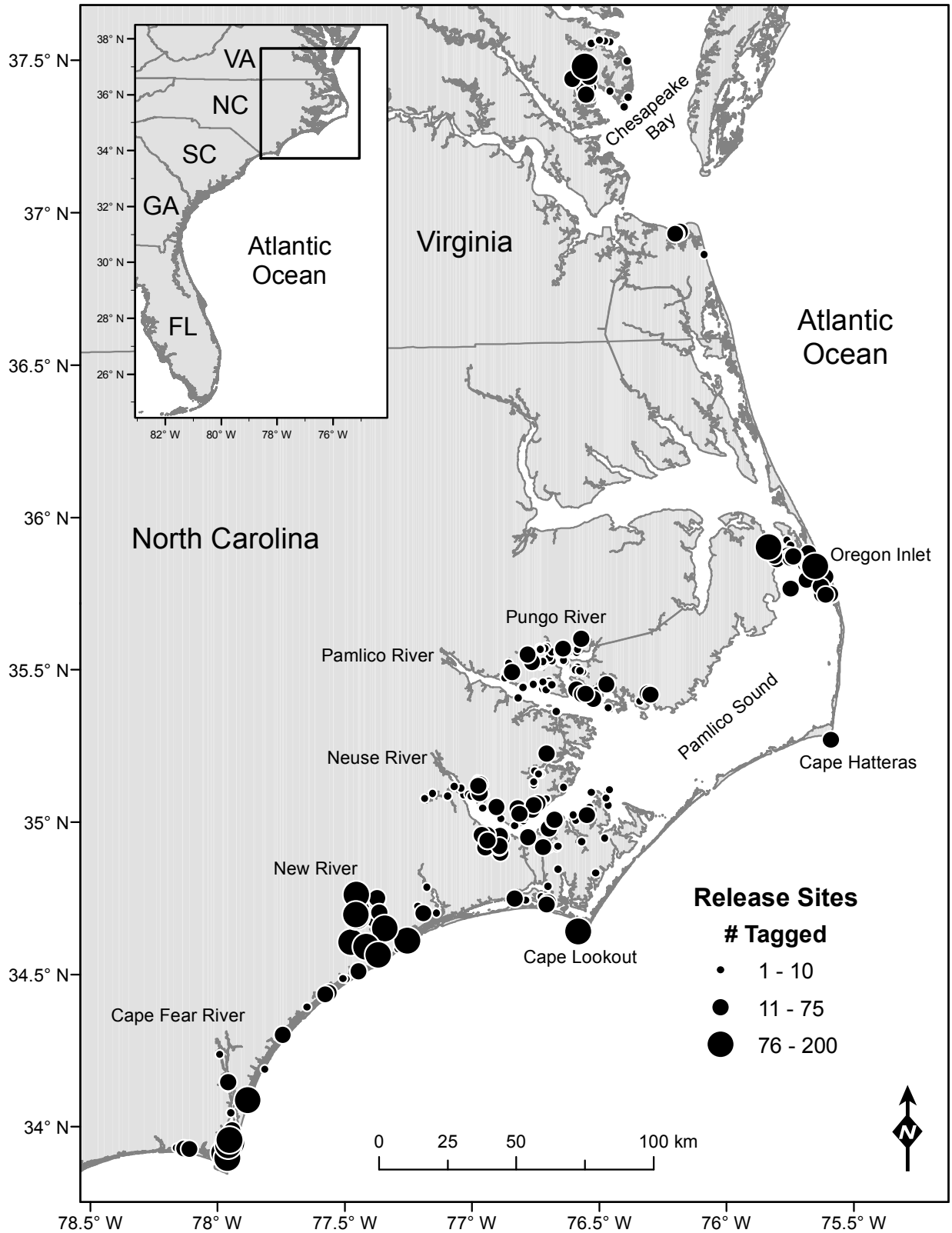


Figure 1. Locations in North Carolina and Virginia waters where spotted seatrout (N = 6,582) were tagged and released from September 2008 through October 2012.

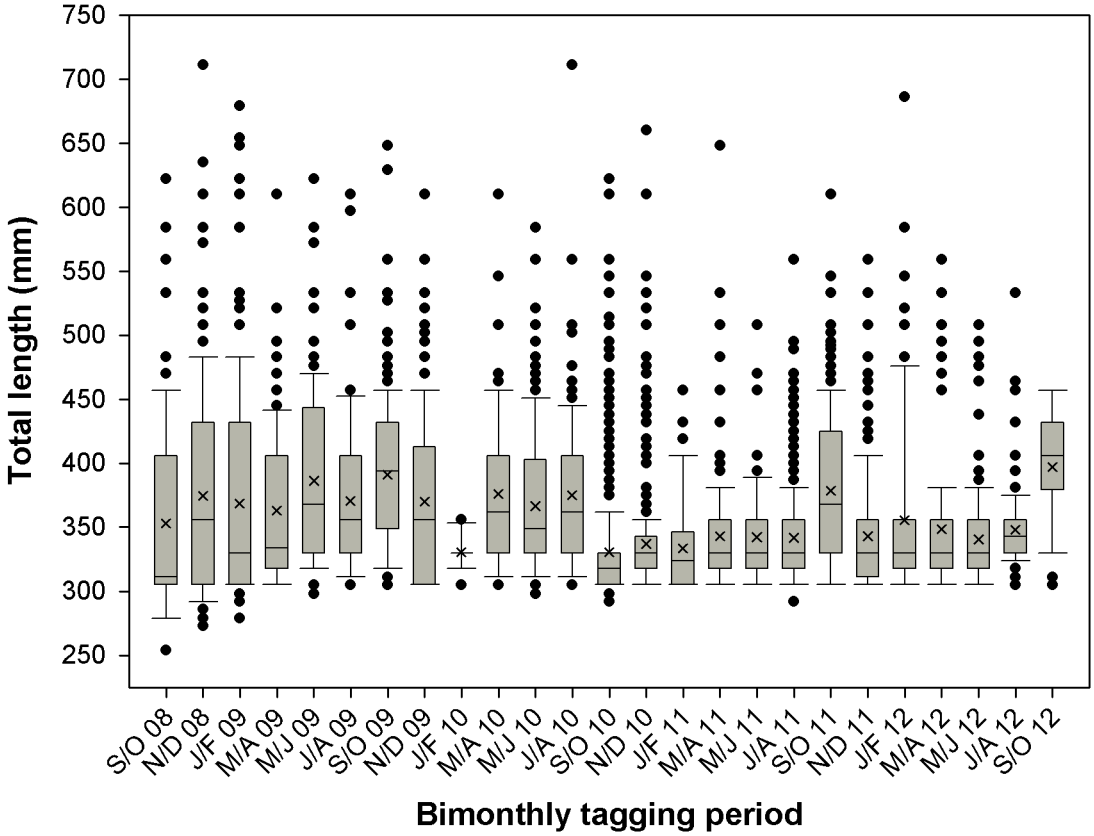


Figure 2. Box-and-whisker plots of the total length of tagged spotted seatrout at time of release for each bimonthly tagging period in North Carolina and Virginia waters from September 2008 through October 2012. The shaded box represents the interquartile range (IQR), with the upper and lower bounds of the box representing the 75th and 25th percentiles, respectively. The horizontal line inside the box represents the median and the box whiskers extend to the maximum and minimum observations within ±1.5(IQR) (i.e., the 90th and 10th percentiles, respectively). Black dots represent observations that lie outside ±1.5(IQR). The overall mean total length for each bimonthly tagging period is also shown, depicted by an x-symbol.

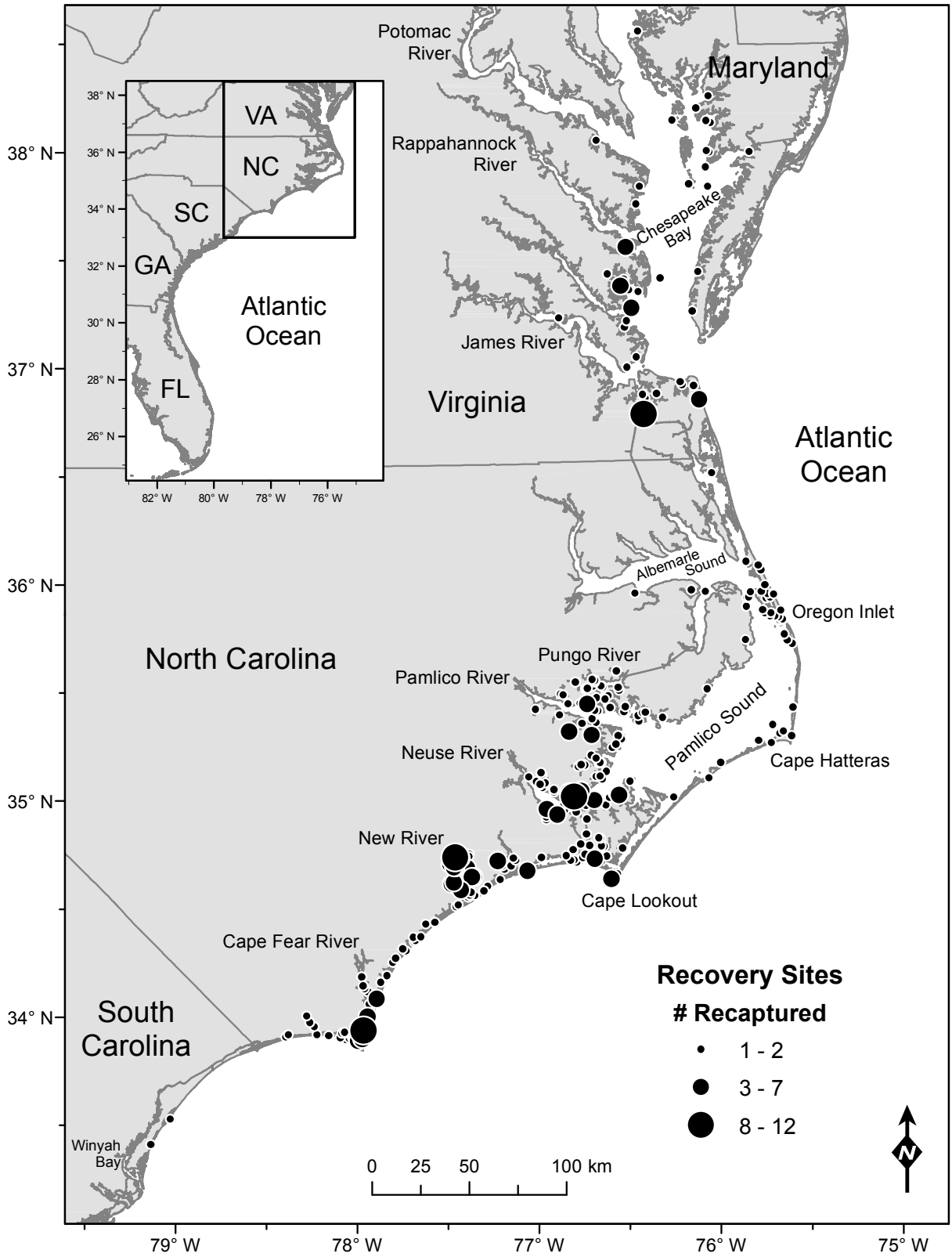


Figure 3. Locations where spotted seatrout tagged in North Carolina and Virginia waters were recovered and reported from September 2008 through October 2013 (n = 553).

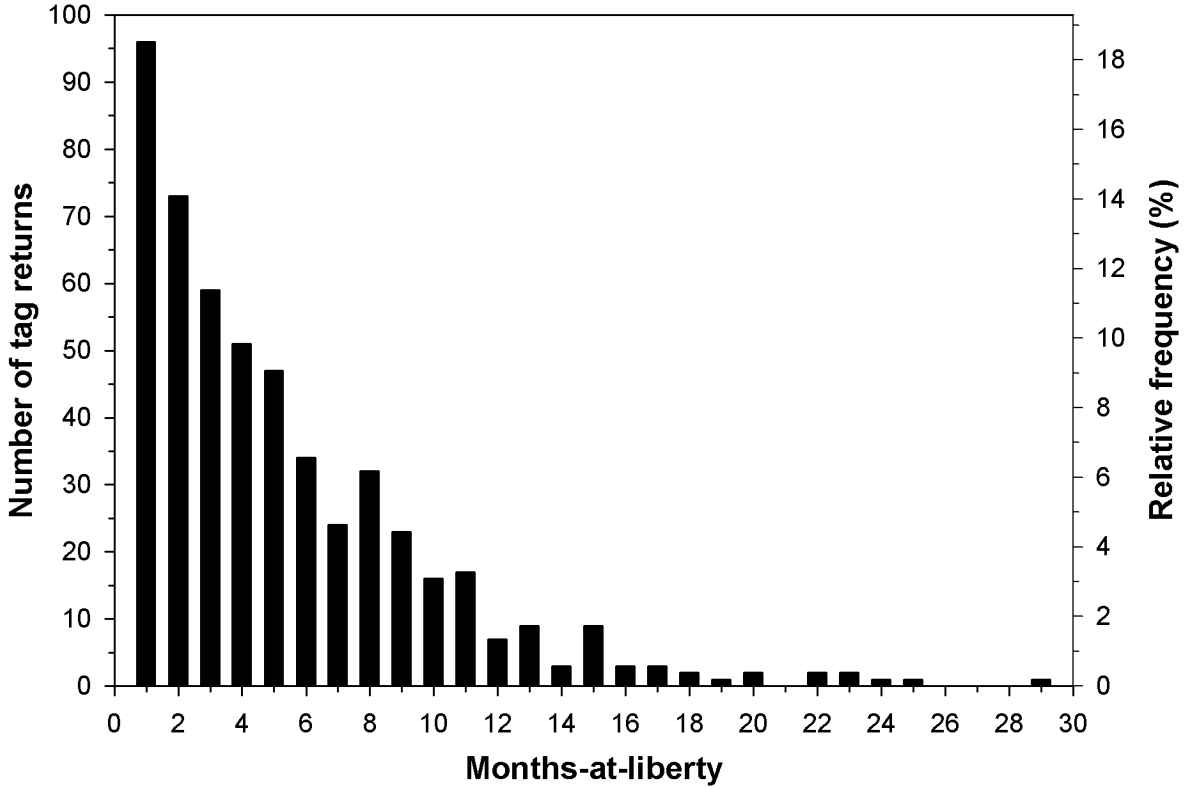


Figure 4. The number of spotted seatrout tagged in North Carolina and Virginia waters that were recovered and reported from September 2008 through October 2013 (n = 518 total), relative to months-at-liberty (i.e., 30-d intervals from day of release; 1 = 1 to 30 d, 2 = 31 to 60 d, etc.). Information on the exact date of recapture reported by fishers was insufficient for the remaining 35 tag recoveries, which were not included in this histogram.

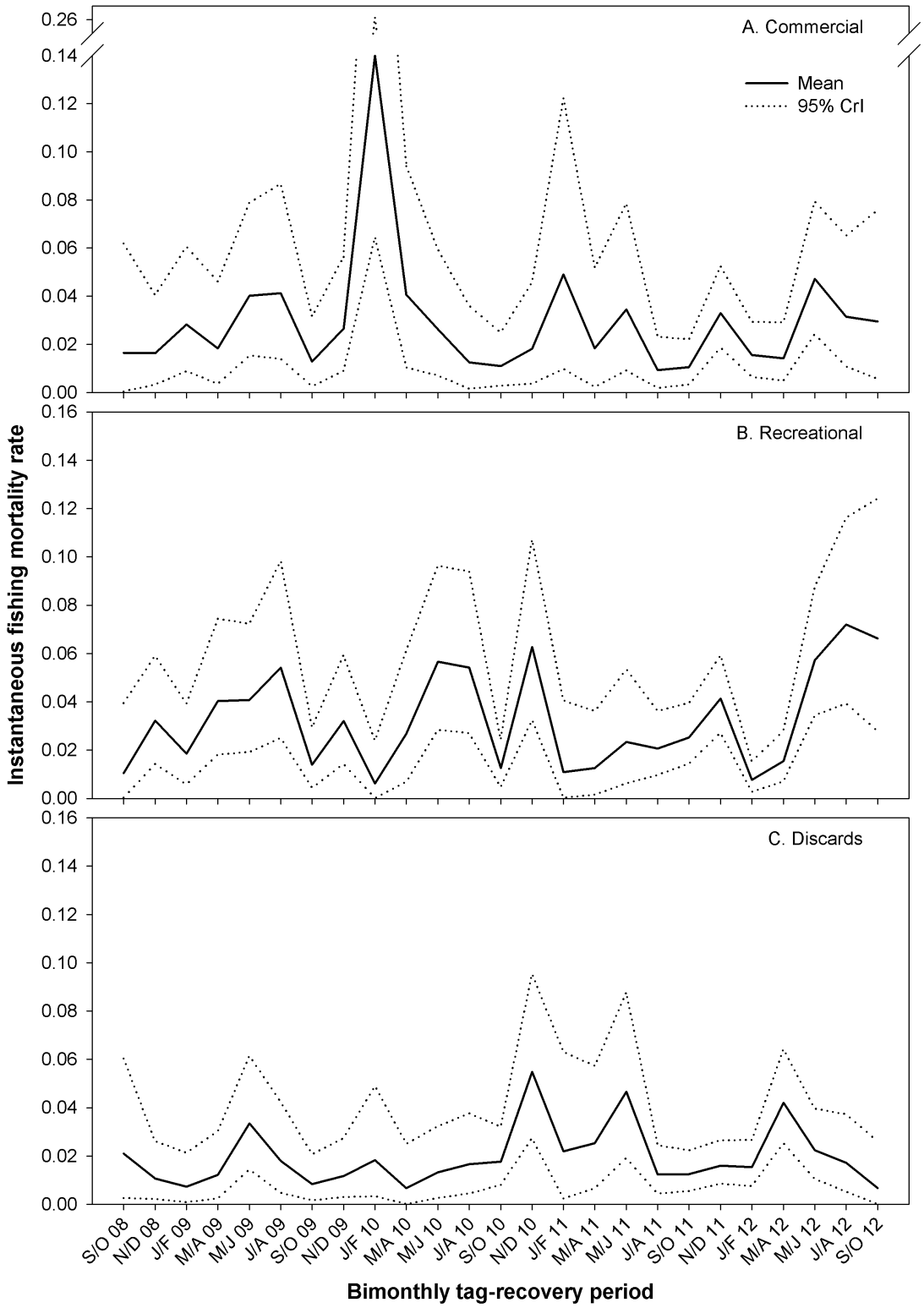


Figure 5. Sector-specific instantaneous fishing mortality rates estimated across 25 bimonthly tag-recovery periods (September 2008 to October 2012) from spotted seatrout tagged in North Carolina and Virginia. Estimates are shown separately for mortality due to commercial harvest (A), recreational harvest (B), and discards (i.e., death of tags but fish released alive) (C).

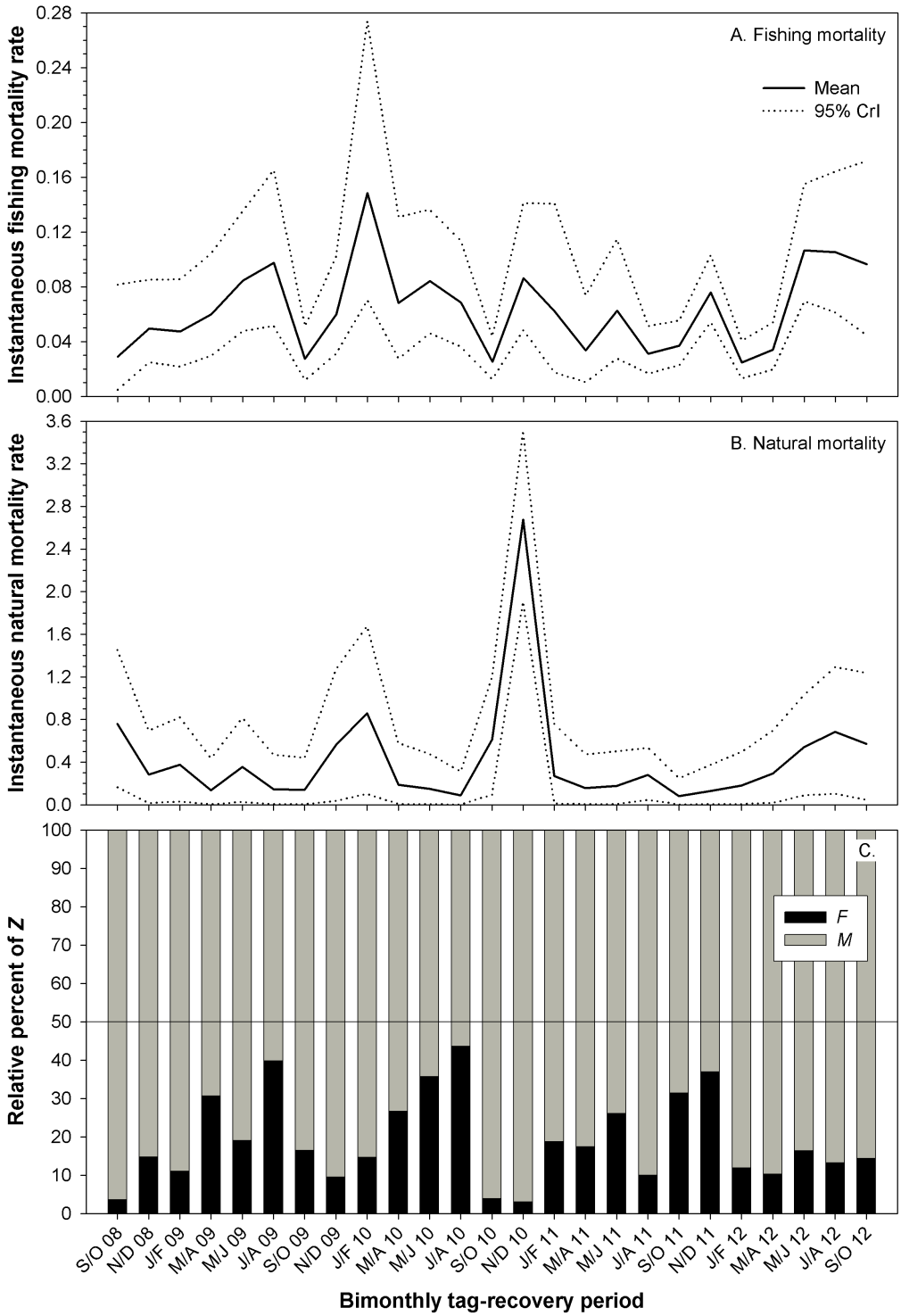


Figure 6. Instantaneous combined fishing mortality rate that accounts for a 10% discard mortality rate (A), instantaneous natural mortality rate (B), and the relative importance of the fishing and natural components of total mortality, *Z* (C), estimated across 25 bimonthly tag-recovery periods (September 2008 to October 2012) from spotted seatrout tagged in North Carolina and Virginia. Note: There is a difference in y-axis scaling between Plots A and B. A reference line for equal (50%) contribution of *F* and *M* to *Z* is provided in Plot C.

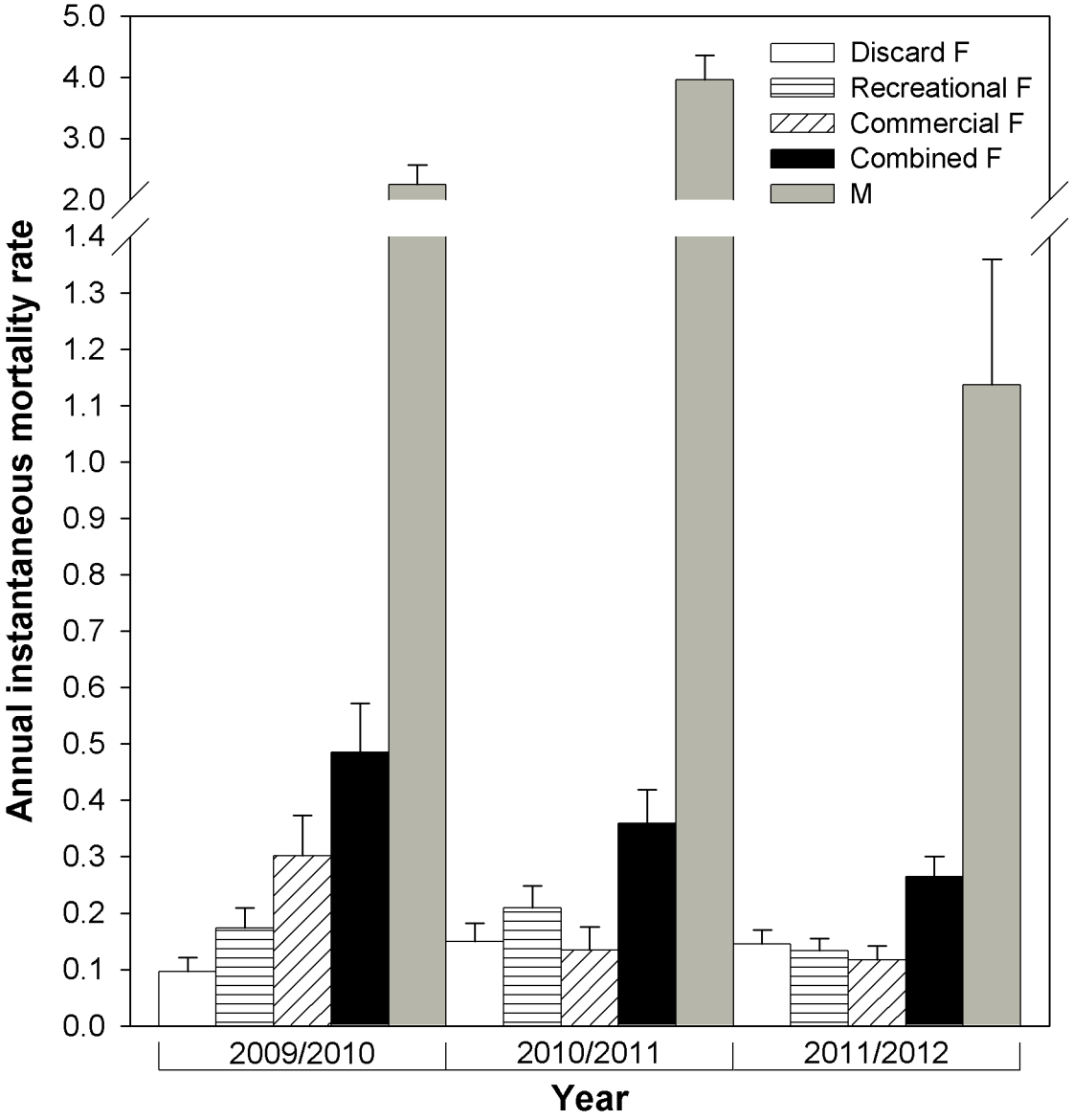


Figure 7. Annual instantaneous rates of discard mortality (i.e., death of tags but fish released alive), sector-specific fishing mortality (i.e., harvest), combined fishing mortality (harvest plus an assumed 10% for discard mortality), and natural mortality, estimated from the recoveries of spotted seatrout tagged in North Carolina and Virginia spanning three years: May 2009-April 2010, May 2010-April 2011, May 2011-April 2012. Bars are posterior means with associated standard deviations of the posterior distribution.

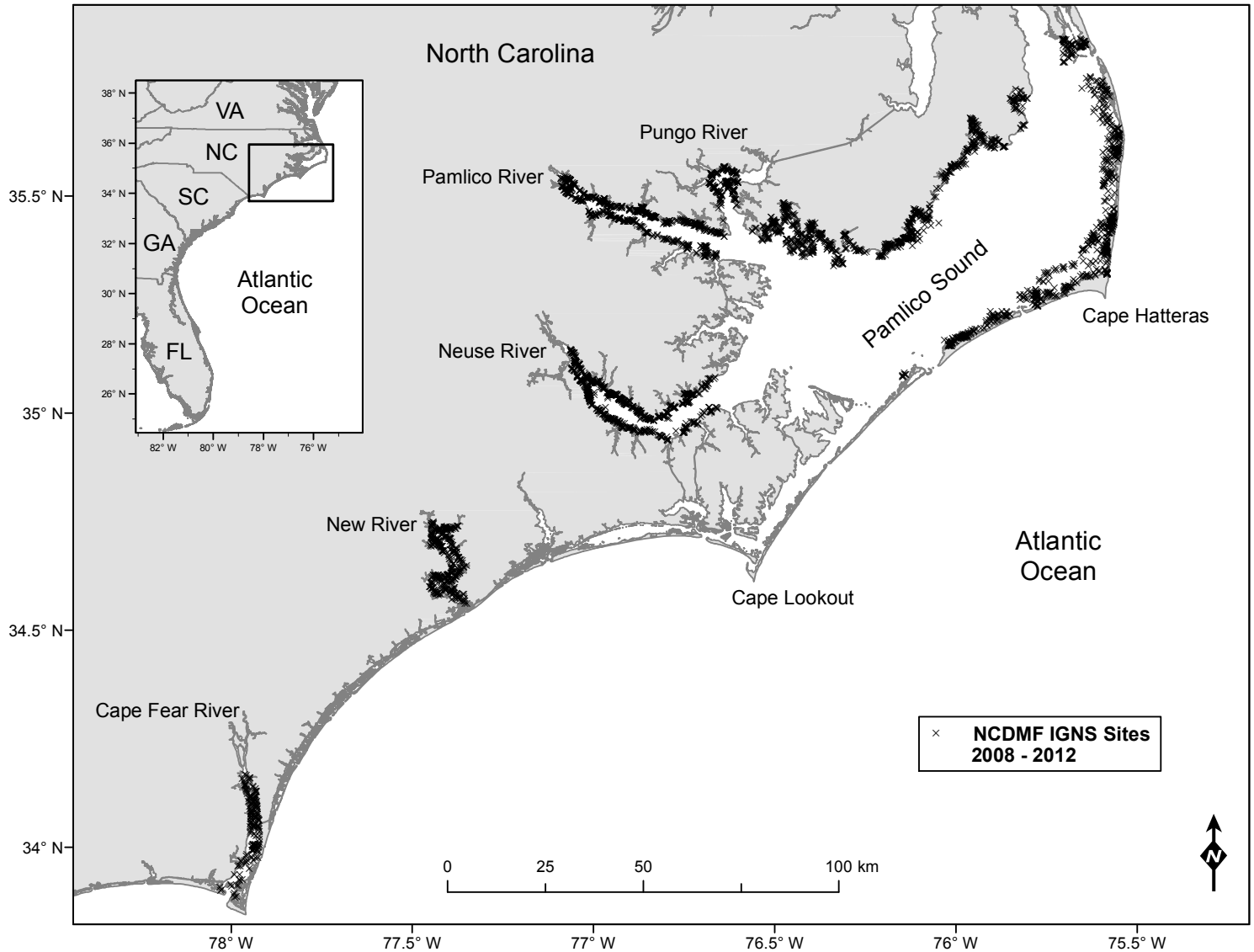


Figure 8. Independent gill net survey sites sampled by the North Carolina Division of Marine Fisheries between May 2008 and December 2012.

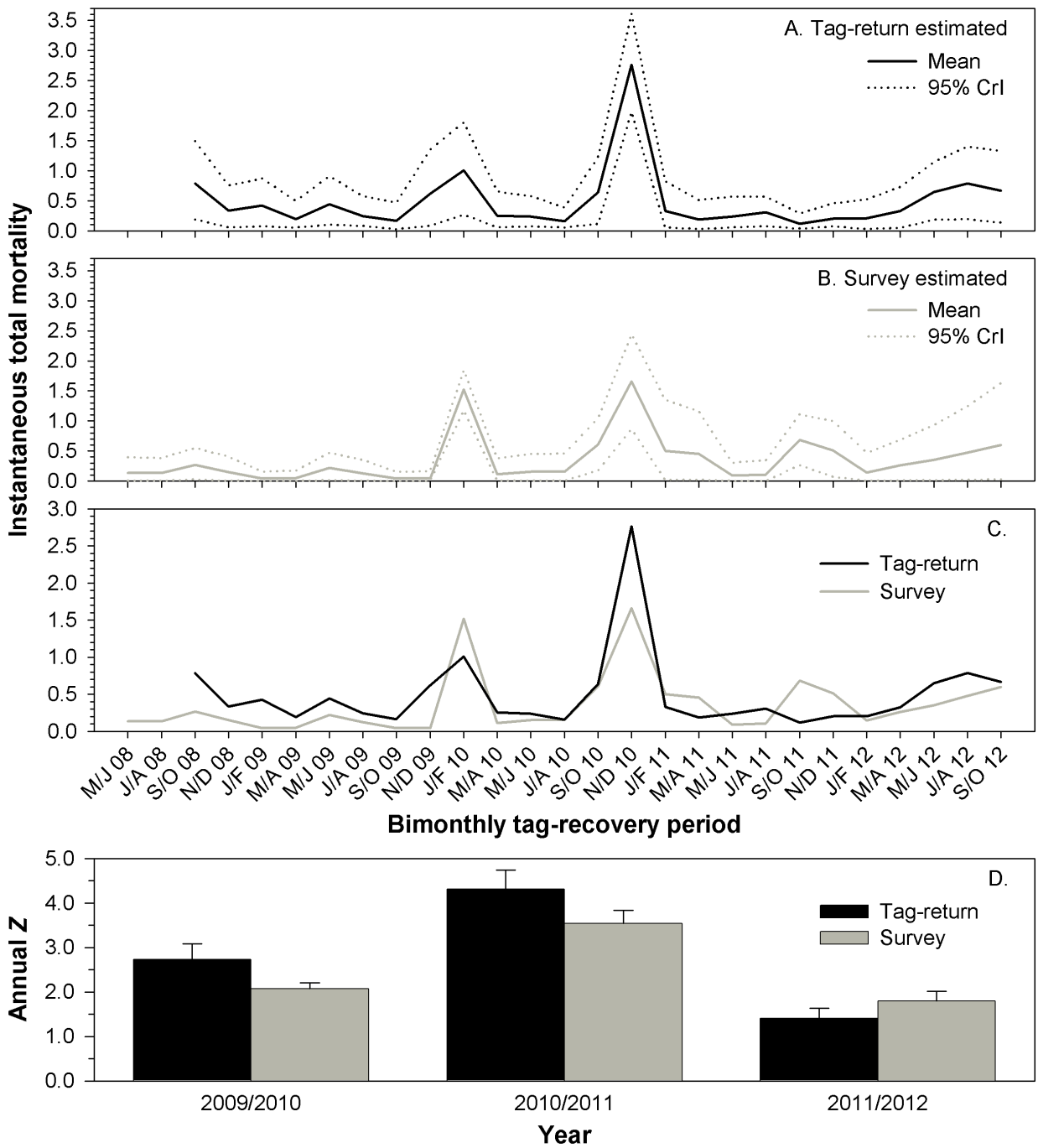


Figure 9. Instantaneous total mortality rates (*Z*) estimated across 25 bimonthly tag-recovery periods (September 2008 to October 2012) from spotted seatrout tagged in North Carolina and Virginia by North Carolina State University (A) and 27 bimonthly sampling periods (May 2008 to October 2012) from fishery-independent gill net survey data collected by the North Carolina Division of Marine Fisheries (B). Mean estimates of the posterior distributions for both tag-return and survey models are overlaid for easier comparison of the variability in seasonal pattern and magnitudes (C). Annual estimates of *Z* are presented as posterior means (bars) with associated standard deviations of the posterior distribution (D).

SECTION 2

WINTER ACOUSTIC TELEMETRY

INTRODUCTION

Arctic cold fronts periodically expose fishes, including spotted seatrout, in relatively shallow temperate estuarine ecosystems to rapid temperature declines. In the absence of thermal refugia, the main limitation being proximity to deeper water or ocean access, fish are subject to acute cold stress often resulting in mortality. Episodic mass mortalities of spotted seatrout have been attributed to harsh winter conditions across much of the species' range; hereafter referred to as winterkill (Wilcox 1887; Smith 1907; Storey and Gudger 1936; Gunter 1941; Gunter and Hildebrand 1951; Simmons 1957; Tabb and Manning 1961; Moore 1976; Green et al. 1990; McEachron et al. 1994; Martin and McEachron 1996; NCDMF 2012). However, the anecdotal information on cold tolerance that exists for spotted seatrout provides an unclear and geographically restricted understanding of the thermal and other environmental conditions that lead to winterkill of this species. In Florida, air temperatures of 7 to 9 °C reportedly lowered water temperatures similarly and were lethal for spotted seatrout (Tabb 1958); however, others have observed more directly that spotted seatrout in Florida can survive exposure to 6 °C water (Gilmore et al. 1978). In Texas, spotted seatrout mortality was observed in areas where water temperatures reached lows of 3 to 4 °C (Gunter and Hildebrand 1951). Similarly, and from the same general geographical region, Moore (1976) reported that spotted seatrout were stressed when waters reached 7 °C and did not survive exposure to temperatures below 5 °C; however, spotted seatrout in Texas are apparently not stressed at temperatures above 10 °C (McEachron et al. 1994).

The understanding of cold tolerance in spotted seatrout is incomplete and largely speculative; thus, there is a need for a direct study of winterkill in this species. An investigation of spotted seatrout mortality associated with acute cold stress is particularly relevant at the northern extent of the species' range where lethal winter conditions are most frequent. Approaching this upper latitudinal limit, acute cold stress of spotted seatrout has been observed for at least three centuries in North Carolina (Lawson 1709; Smith 1907; NCDMF 2012). Periodic declines in the state's abundance of spotted seatrout have been attributed in part to winterkill in 1996, 2000, 2001, and 2003 (Jensen 2009).

Cold tolerance of fishes has traditionally been assessed in the laboratory under controlled experimental conditions (Beitinger et al. 2000) and there is a paucity of literature on the use of field-based approaches to directly study winterkill in temperate fishes (Donaldson et al. 2008). *In situ* studies of fish cold tolerance present numerous challenges, most notable of which is the ability to link a history of the thermal dynamics experienced by individuals to some stressful endpoint (e.g., death). Detailed and continuous monitoring of fish and their environment is essential given the episodic and acute nature of winterkills (i.e., the frequency and duration of mortality events are largely unpredictable). Ultrasonic telemetry data are increasingly being used to estimate both fish movement (Haeseker et al. 1996; Bacheler et al. 2009*a*,*b*) and mortality (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Waters et al. 2005; Thompson et al. 2007; Bacheler et al. 2009*c*; Friedl et al. 2013). The general approach involves relocating telemetered individuals in a defined study area through active and passive tracking until one of four possible final fates is determined: natural mortality, harvest, emigration, or transmitter failure (e.g., expired battery). Concurrently monitoring the abiotic environment of

the study area allows for direct testing of the effects of water quality (e.g., temperature) on the survival of telemetered fish.

Interannual variability in fish abundance can be driven in part by significant overwinter loss of standing stock (Hurst 2007). At northern latitudinal limits, highly variable winter conditions and preponderance for severe cold relative to elsewhere in the species' range likely result in extensive overwinter loss of spotted seatrout and significantly influence abundance levels (see Section 1). Thus, determining the importance of winterkill to the population dynamics of North Carolina spotted seatrout is essential to management of this valuable fishery resource. Furthermore, adequate empirical data on thermal minimum limitations are fundamental to future research both predicting the effects of overwinter mortality on spotted seatrout abundance throughout the species' distribution and projecting climate-related changes in that distribution. Here, we directly examined acute cold stress and mortality of spotted seatrout through *in situ* monitoring of localized variability in abiotic conditions and telemetered fish movements during winter in North Carolina.

METHODS

Telemetry study sites

Telemetry of spotted seatrout occurred throughout three winters from 2009 to 2012 within overwintering habitats of the Pungo and Neuse rivers, both major tributaries of Pamlico Sound, North Carolina, and included Pantego Creek, Pungo Creek, Slocum Creek, and Hancock Creek (Figure 1). These study areas are relatively shallow embayment tributaries with mostly uniform depths averaging 1-3 m with some areas of deeper water (e.g., 3-6 m). Due to their distance from ocean access, lunar tides are negligible in these tributaries, and wind mixing and

precipitation regulate salinities at depth between oligohaline to mesohaline conditions (Giese et al. 1979). Harvest of spotted seatrout is limited to the recreational fishing sector in three of the study tributaries; however, a large section of Pungo Creek is open to commercial harvest as well. Hydrographical features of these areas, including their shape and size, permit the frequent tracking of telemetered fish by active and passive techniques on manageable temporal and spatial scales (see below). Additionally, these tributaries are historically abundant with spotted seatrout during winter and periodically prone to winterkill conditions.

Transmitter implantation

From 2009 to 2012, during the periods of November to February, spotted seatrout were captured primarily using hook-and-line; however, many fish for telemetry in the Neuse River study areas were obtained by electrofishing. Healthy individuals (i.e., no physical signs of stress from capture techniques) and those meeting an established minimum total length requirement of 356 mm were kept as telemetry-tagging candidates. All candidate spotted seatrout were immediately placed in onboard holding tanks (at least 100 l in size) containing ambient water; water quality was maintained through frequent water changes, continuous aeration, and supplemental oxygenation. Uniquely coded ultrasonic transmitters (VEMCO, Bedford, Nova Scotia; V13-1H, 13 x 36 mm, approximately 10.5 g in air, 69-kHz frequency, 30 to 90-s random transmission rate, approximate 196-d battery life) were surgically implanted into telemetry candidates; some larger candidates (total length > 457 mm) in the Neuse River study areas received larger transmitters (VEMCO, Bedford, Nova Scotia; V16-4H, 16 x 68 mm, approximately 23.5 g in air, 69-kHz frequency, 60 to 120-s random transmission rate, approximate 641-d battery life). The surgical procedure employed for implanting fish with transmitters was successfully implemented in other studies (Haeseker et al. 1996; Bacheler et al.

2009*a*,*b*,*c*; Friedl et al. 2013) and tailored specifically for spotted seatrout with the assistance of staff from North Carolina State University's (NCSU) College of Veterinary Medicine (CVM) (e.g., Harms and Lewbart 2011). Individual spotted seatrout were anesthetized in 75 l of aerated water with 150 mg l^{-1} tricaine methanosulfonate (MS-222). Upon loss of equilibrium (usually 3-5 minutes), total length (TL; mm) and wet weight (WW; g) measurements were taken, and the fish was placed ventral side up in a V-notch of an open-cell foam surgical platform fitted onto a 38-l cooler equipped with a re-circulating water pump. Water containing 75 mg l^{-1} MS-222 was continuously pumped over the gills for the duration of the surgery to maintain sedation. An approximately 12-mm long incision was made midway along the ventral midline between the pelvic girdle and the vent, using a sterile size-10 surgical blade. To prevent damage to visceral organs, care was taken to avoid penetrating the peritoneum with the surgical blade. Upon reaching the peritoneum through the muscle wall, sterile curved-tip hemostatic forceps with blunt ends were used to break through the membrane so that a transmitter could be inserted. The incision was closed with three to four simple interrupted sutures (PDS™ II synthetic absorbable suture in 3-0 thread size with FS-1 reverse cutting needle, Ethicon Endo-Surgery, Inc., Somerville, NJ, USA) after transmitter insertion to the abdominal cavity, and an antiseptic salve was applied to the suture site. Fish were returned to a 50-l aerated tank for recovery and then released once equilibrium was reestablished and normal swimming behavior was observed, typically within 10 minutes after surgery.

Telemetry relocations

We monitored telemetered spotted seatrout movement within, as well as emigration from and immigration to, each study area using a fixed array of submersible receivers (VEMCO VR2 and VR2W; hereafter referred to as VR2/W) (Figure 1). Preliminary analyses found nearly

100% detection of V13-1H and V16-4H transmitters at 300 and 400 m, respectively, by VR2/W receivers in our study areas. Consequently, VR2/W receivers at the mouths of study creeks were conservatively positioned 400 m apart from one another and within 200 m of shore (Figure 1) to fully observe all emigration and immigration events by telemetered spotted seatrout. Additional VR2/W receivers were systematically stationed in areas upstream of the mouth array to monitor broad daily movement patterns within each study creek. Iron auger anchors (1.5 m length) with attached stainless steel cable (6.35 mm diameter) and a terminal surface identification float served as moorings for most VR2/W receivers. For deeper listening stations (> 3.0 m), concrete blocks (34 kg weight) were substituted for auger anchors. Receivers were secured to a rope (PRODAC®, Orion Ropeworks, Inc., Winslow, ME, USA; 12.7 mm diameter, approximately 76.0 cm length), which was attached to moorings via a stainless steel carabiner; the other end of the rope had a subsurface float to maintain receiver in a vertical position approximately 0.3 to 0.5 m above the bottom. Receiver stations varied in depth from 1.5 to 4.9 m. Each VR2/W receiver continuously logged the unique transmitter ID code, date, and time of all telemetered spotted seatrout that were within the range of detection for the duration of the study. Bottom water temperature was recorded at 15-minute intervals by data loggers (Hobo® Water Temperature Pro v2, Onset Computer Corp., Bourne, MA, USA; ± 0.2 °C accuracy) deployed at several VR2/W stations across the study tributaries and at a uniform depth of approximately 1.5 m (Figure 1). Cumulative degree day (CDD) combines temperature and time into a single measure that characterizes minimum thermal tolerance defined by prolonged exposure to some base (e.g., sublethal) low temperature (Wuenschel et al. 2012). We chose a threshold temperature of 7 °C based on laboratory results (not presented). For each telemetry season and study system, the cumulative degree days below 7 °C (CDD < 7 °C) was calculated as:

$$CDD < 7°\text{C} = \sum_{t=1}^{t=n} \left(7.0 - Temp_t\right),$$

where $Temp_t$ is the daily mean water temperature of day t and n is the total number of consecutive days with fish at-risk.

Telemetered spotted seatrout were also manually relocated within each study area at least every 14 d (more frequently when water temperatures were ≤ 7 °C) using an ultrasonic receiver (VEMCO VR100) equipped with an omnidirectional hydrophone (VEMCO VH165). Manual tracking in each study creek involved navigating by research vessel to fixed listening stations (n = 15-30) approximately 100 to 500 m apart, depending on hydrography. The distance between listening stations was dependent on changes in depth or shoreline orientation since these can inhibit the detection of a transmitting acoustic signal. Upon general relocation, a unidirectional hydrophone (VEMCO VH110) was regularly used to determine a more precise position of an individual telemetered spotted seatrout. Schooling of spotted seatrout was common, occasionally resulting in overlapping acoustic transmissions by telemetered individuals; therefore, we listened at each station until the VR100 receiver successfully registered all present unique transmitter identification codes. Time-of-day, latitude-longitude coordinates, depth, and water clarity (i.e., Secchi depth) were recorded at each listening station. Additionally, we measured both bottom (up to 3.1 m) and surface (at 0.3 m) temperature (°C) and salinity (ppt) with a temperature-conductivity meter (YSI® Model 85, YSI, Inc., Yellow Springs, OH, USA). If the acoustic signal of any telemetered spotted seatrout was missed during a manual-tracking event, it was considered to be present in the study area at that time if a VR2/W receiver detected it and the fish was determined to not be emigrating (i.e., most recent detection was on outer-most VR2/W array at tributary mouth and occurred prior to manual-tracking event). The tracking of

telemetered spotted seatrout each year continued until all fish in a study area died, were harvested, or permanently emigrated (see next section for description of telemetered fish fates).

Interpretation and analysis of telemetry data

Hightower et al. (2001) established conditions for interpreting the fate of a telemetered fish based on its movements following release. Possible fates include surgery-related mortality, natural mortality, harvest, or emigration. Telemetered spotted seatrout were assumed to be alive if their positions varied between manual relocation events. Alternatively, natural death was assumed for fish whose location remained stationary across multiple searches. A censorship period of 7 d following release ensured that any surgery-related effects on immediate survival and behavior (e.g., higher emigration rates) were not misinterpreted as natural deaths or normal movement patterns. Telemetered spotted seatrout that were not relocated after repeated manual searches of a study area and that also remained undetected by the VR2/W receiver array (i.e., did not move within or emigrate from the study area), were assumed to have been harvested (see below for exception when water temperatures were ≤ 7 °C). Natural mortality inferred from stationary transmitters could be misinterpreted if telemetered fish experienced discard mortality (i.e., death associated with a recreational or commercial release) and this is a potential bias in our study. However, given that all telemetered spotted seatrout were of legal harvestable size and that relatively few telemetered fish were harvested (see Results), we believe the potential for this bias was low. Similarly, repeated relocation of a transmitter signal in a constant position could result from fish expulsion of the transmitter while in the study area; the potential for this bias is low (see results below from a laboratory experiment on surgery survival and transmitter retention, for which the methodology is described in Section 1). If a transmitter failed prematurely, this would be misinterpreted as a harvest. While there is no precise way to assess

transmitter failure beyond ensuring full functionality prior to releasing a telemetered fish, the likelihood of this bias in our study was small given that transmitters from all stationary natural and surgery-related mortalities (V13-1H, n = 8) continued to transmit throughout the manufacturer-guaranteed battery life. Several other telemetry studies have also assumed with confidence that the probability of VEMCO transmitter expulsion or failure was negligible (see Hightower et al. 2001; Heupel and Simpfendorfer 2002; Bacheler et al. 2009*a*,*b*,*c*; Friedl et al. 2013), including for spotted seatrout (Callihan et al. 2013). Avian predation could also be misinterpreted as a fishery removal of a telemetered spotted seatrout from our study areas. Spotted seatrout are a dominant prey species for ospreys (*Pandion haliaetus*); however, the sizes of telemetered spotted seatrout in our study are near the maximum of fish prey sizes previously observed for ospreys in similar systems (Glass and Watts 2009). More importantly, ospreys overwinter in areas south of North Carolina (Watts and Paxton 2007) and are uncommon in our study areas over the time periods in which telemetry took place. Bald eagles (*Haliaeetus leucocephalus*) are year-round residents in our study areas but are not known in similar systems to consume spotted seatrout (Markham 2004). Other birds (i.e., gulls and pelicans), as well as semiaquatic mammals (i.e., otters), may opportunistically feed on lethargic and moribund spotted seatrout suffering from acute cold stress, and in such case could remove a telemetered spotted seatrout from the water. Given the inefficiency by recreational and commercial fishers to catch spotted seatrout during low temperatures using traditional gears (e.g., hook-and-line, gill net), the relatively low fishing effort observed in the study areas during cold episodes, and that only immobilized telemetered spotted seatrout provide feeding opportunities for avian predators in our study area, we assumed that any removal of a telemetered spotted seatrout during cold

conditions (i.e., water temperatures ≤ 7 °C) indirectly resulted from acute cold stress and was therefore interpreted as a natural mortality.

We used the Pollock et al. (1989) modification of the Kaplan and Meier (1958) product-limit method, a nonparametric maximum likelihood approach to estimating survivorship curves, to describe the general patterns in survival for telemetered spotted seatrout during each winter study period. This modification allows for staggered entry of newly tagged individuals over time either from new releases or from immigration back to the study area by tagged individuals that previously emigrated. At any time of census, t_j, the Kaplan-Meier (K-M) estimator of survival probability, $S(t)$, is conditional on r_j, the number of spotted seatrout at risk at t_j (i.e., have not died or been censored prior to t_j), and d_j, the number of spotted seatrout that died at t_j, such that:

$$\hat{S}(t) = \begin{cases} 1 & \text{if } t < t_1 \\ \prod_{t_j \le t} \left[\frac{r_j - d_j}{r_j} \right] & \text{if } t_1 \le t \end{cases} .$$

The standard error of the K-M estimator was calculated as the square root of Greenwood's (1926) formula for variance:

$$\text{var}\left[\hat{S}(t)\right] = \hat{S}(t)^2 \sum_{t_j \le t} \frac{d_j}{r_j(r_j - d_j)} .$$

As proposed by Kalbfleisch and Prentice (2002), 95% confidence intervals were calculated as:

$$\hat{S}(t)\exp\left(e \pm 1.96 \sqrt{\frac{\sum_{t_j \le t} \frac{d_j}{r_j(r_j - d_j)}}{\ln\left[\hat{S}(t)\right]}} \right) .$$

In our study, death of a telemetered spotted seatrout after the 7-d censorship period could result from either natural sources or from harvest. Given these competing risks and that our primary

objective was to study spotted seatrout survival relative to low temperature, we obtained marginal survival curves (i.e., only natural deaths considered) by censoring all fishing mortalities and emigrations on the day in which they occurred. Graphical comparisons of daily marginal survival versus mean daily water temperature were made within and among both river systems during each winter study period. All K-M analyses were performed in R version 2.15.2 (R Core Team 2012) using the SURVIVAL package (Therneau 2012).

In addition to the sources of bias affecting the determination of fates for telemetered fish described earlier, several other assumptions apply to our modeling of telemetry data. First, we assumed that all marked fish alive in the study area at time *i* had the same survival rate to time *i*+1. We also assumed that marked and unmarked fish had the same survival rates. Next, we assumed that movement patterns could be used to determine whether a tagged fish remained alive or had died due to natural mortality (Jepsen et al. 1998; Hightower et al. 2001; Heupel and Simpfendorfer 2002; Waters et al. 2005; Thompson et al. 2007; Bacheler et al. 2009*c*; Friedl et al. 2013). Finally, we assumed that all emigrating fish were detected and could be censored from analyses.

RESULTS

Laboratory experiment – postsurgical survival and transmitter retention

Over 225 d of daily monitoring (see methodology in Section 1), we observed no postsurgical mortality for eight spotted seatrout (mean ± SE: 326.0 ± 5.2 mm TL; 349.5 ± 20.5 g WW; 3.1 ± 0.2 % transmitter weight: fish weight) surgically implanted with dummy V13 transmitters, or for four others (mean ± SE: 427.0 ± 11.3 mm TL; 797.5 ± 42.7 g WW; 3.2 ± 0.2 % transmitter weight: fish weight) receiving dummy V16 transmitters. Necropsies of all fish

performed at the termination of the experiment revealed that all telemetered fish were slightly emaciated. However, there was minimal evidence of deleterious effects (e.g., infection or necrosis) from the presence of a transmitter; only one fish implanted with a V13 transmitter was judged by CVM staff to exhibit signs of infected and necrotic tissue but this was only around the surgery wound. Transmitter retention was high, with only one telemetered spotted seatrout expelling the transmitter over the course of the retention experiment. This V13 transmitter loss occurred 40 d post-surgery. Closer inspection revealed that the simple continuous suture knot loosened, resulting in complete unraveling of the sutures, dehiscence, and expulsion of the transmitter. This fish was not treated (i.e., the sutures were not repaired) but was closely monitored throughout the remainder of the experiment, during which it survived and the wound healed naturally. Therefore, we determined that V13-1H and V16-4H transmitters did not adversely affect the survival of spotted seatrout (≥ 356 mm TL and ≥ 457 mm TL, respectively) and that 100% transmitter retention necessitates the use of a simple interrupted suture technique; consequently, simple interrupted suturing was used for all surgeries of the field telemetry study.

Interpretation and analysis of telemetry data

The daily movements and fates of 118 telemetered adult spotted seatrout were determined across three winters in North Carolina (Table 1). Ultrasonic transmitters were surgically implanted in 37 spotted seatrout (mean ± SE: 430.1 ± 4.7 mm TL; 741.3 ± 24.9 g WW; 1.5 ± 0.1 % transmitter weight: fish weight) during winter 2009-2010, 10 spotted seatrout (mean ± SE: 379.6 ± 8.2 mm TL; 500.5 ± 45.9 g WW; 2.2 ± 0.2 % transmitter weight: fish weight) during winter 2010-2011, and 26 spotted seatrout (mean ± SE: 414.7 ± 8.1 mm TL; 735.9 ± 43.2 g WW; 1.6 ± 0.1 % transmitter weight: fish weight) during winter 2011-2012 in the two study tributaries of the Pungo River, and 45 spotted seatrout (mean ± SE: 460.0 ± 7.1 mm TL; 965.3 ± 42.6 g

WW; 1.5 ± 0.1 % transmitter weight: fish weight) during winter 2011-2012 in the two study tributaries of the Neuse River. During all three telemetry study periods and in all study areas, VR2/W receivers logged a combined 2,294,598 detections from all 118 telemetered spotted seatrout. Manual relocation percentages of telemetered fish were also high during all three winter study periods. In winters of 2009-2010, 2010-2011, and 2011-2012, 34 of 37 (92%), 10 of 10 (100%), and 64 of 71 (90%) telemetered spotted seatrout were manually tracked, respectively.

Automated and manual relocations within the first 7 d upon release were censored to account for surgery-related effects on the behavior and survival of telemetered spotted seatrout. Consequently, 10 fish were excluded from our overall analysis due to an inferred surgery death (n = 1), permanent emigration (n = 8), or a confirmed fishing mortality (n = 1) during a censorship period (Table 1). The remaining 108 telemetered spotted seatrout considered at-risk and included in our overall analysis were separated into the following assumed fates: fishing mortality (n = 8), natural mortality (n = 13), and emigration (n = 87) (Table 1). Specifically, of the 34 at-risk fish during winter 2009-2010 in two tributaries of the Pungo River, there was 1 unconfirmed harvest and 7 assumed natural deaths (Table 1, Figure 2). Two of the 7 assumed natural mortalities were judged based on a lack of transmitter movement and the other 5 based on permanent loss of transmitter signal during cold episodes (e.g., scavenger or hand harvest of cold-stunned fish). There was no presumed harvest of telemetered spotted seatrout during winter 2010-2011 in the Pungo River tributaries; however, 6 of 9 at-risk fish were assumed to die naturally based on either a lack of movement (n = 5) or a loss of signal during a cold episode (n = 1) (Table 1, Figure 3). Tributaries of two separate river systems were studied during winter 2011-2012. Of the 24 at-risk fish in the Pungo River tributaries, there were 4 unconfirmed

harvests and no natural deaths, and of the 41 at-risk fish in the Neuse River tributaries, 4 harvested telemetered spotted seatrout were confirmed through returned transmitters from anglers and there were no natural deaths (Table 1, Figure 4).

Throughout two of the three winter telemetry seasons, the exception being 2010-2011, the majority of telemetered adult spotted seatrout survived and emigrated from the study tributaries around mid-February to mid-March (Table 1, Figures 2-4). Beginning on the first day after the 7-d censorship period, the mean (± SE) days-at-risk were 52.7 ± 3.8, 11.1 ± 2.1, 90.8 ± 8.0 in the Pungo River tributaries for 2009-2010, 2010-2011, and 2011-2012 winters, respectively, and 97.7 ± 5.7 in the Neuse River tributaries for the 2011-2012 winter.

Fine-scale (i.e., 15-minute) measurements of water temperature were reduced to daily mean temperatures and used to compare long-term thermal profiles in each study tributary across telemetry seasons (Figure 5A). Low temperatures that were found to be lethal to spotted seatrout in the laboratory at either acute (3 °C) or chronic (5 °C) exposure (results of this separate study are not presented here) were reached in the Pungo River tributaries during the winters of 2009-2010 and 2010-2011. Thermal stress for spotted seatrout was apparently higher in the winter of 2010-2011 (CDD < 7 °C = 144.3) than in the winter of 2009-2010 (CDD < 7 °C = 80.4) and both winters were likely more stressful than the winter of 2011-2012. The winter of 2011-2012 was considerably warmer (CDD < 7 °C = 0.6) and the thermal profile for tributaries of the Pungo River was similar to that of the Neuse River tributaries (CDD ≤ 7 °C = 0.9), with the exception that the Neuse River was generally warmer (mean ± SE: 1.0 ± 0.1 °C) than the Pungo River on a given day. Collectively, the observed variability in daily mean maximum and minimum temperatures across the December 1 to February 28 time period ranged from 0.25 to 3.75 °C d^{-1},

with a distributional peak at approximately 1.0 to 1.5 °C d^{-1} (Figure 5B). In the Pungo River tributaries, this variability was unrelated to daily mean temperature (i.e., colder days were neither more nor less variable than warmer days; $R^2 = 0.008$, $p = 0.141$, n = 270) (Figure 5C). Ten rapid-onset-of-cold events were closely examined and found to vary in duration from 16 to 160 h and in rate of temperature decline from approximately 0.1 to 0.3 °C h^{-1} (Figure 5D). Furthermore, temperatures declined the fastest in events of shorter duration and the level of decline (i.e., the difference in water temperature between the beginning and end of an event) was generally highest in events of longer duration.

Stratification of temperature and salinity was observed. At depths of up to 3.1 m, temperature stratified by as much as 6.4 °C but in general, bottom and surface waters were within (mean absolute difference ± SE) 1.0 ± 0.03 °C of each other (Figure 6A). Of particular relevance is the temperature stratification when either bottom or surface water conditions were thermally stressful (i.e., ≤ 5 °C based on controlled laboratory results). In these cases, bottom water temperature ranged from -4.5 °C colder to 3.0 °C warmer than surface water, with a mean absolute difference (± SE) of 0.8 ± 0.1 °C. For all winter telemetry seasons, salinity levels in each study tributary were generally mesohaline, with some listening stations in upper reaches classified as oligohaline. In the Pungo River tributaries, mean (± SE; n = total number of measurements taken) bottom salinity during each of the 2009-2010, 2010-2011, and 2011-2012 telemetry seasons were 8.4 (± 0.1; n = 743), 12.2 (± 0.1; n = 264), and 13.9 (± 0.1; n = 215) ppt, respectively. In the Neuse River tributaries during telemetry of 2011-2012, mean bottom salinity was 11.2 (± 0.1; n = 325) ppt. Collectively and at depths of up to 3.1 m, bottom salinity was as much as 14.0 ppt higher than at the surface; however, mean (± SE) salinity stratification of the water column was 3.1 ± 0.1 ppt (Figure 6B).

K-M estimates of marginal winter survival for adult spotted seatrout in North Carolina were determined daily *in situ* based on an at-risk pool of telemetered fish that varied over time due to additions (i.e., new releases and immigration), uncensored losses (i.e., natural mortality), and censored losses (i.e., harvest and emigration) of tagged individuals (Figure 7). During the winter of 2009-2010, the probability of survival was reduced either during or immediately following when daily mean temperatures were below 5 °C, and the highest mortality was observed in the second week of February (Figure 7A). However, during the second week of January when temperatures reached lows of 3 °C and below, survival was high. Coincidentally, most at-risk fish during this time period were not relocated by either VR2/W receivers or through manual searches but were found later as temperatures increased (Figure 2). During the winter of 2010-2011, temperatures decreased rapidly beginning in December and the six fish at risk when daily mean temperatures were below 3 °C, all died (Figure 7B). In contrast to the previous two winters, daily mean temperatures during the winter of 2011-2012 in the Pungo River, as well as in the Neuse River, never reached the critical lows of 3 and 5 °C and no natural mortalities were observed; spotted seatrout marginal survival in both study areas was 100% over the 6-month period (Figure 7C,D).

DISCUSSION

Directly observing natural deaths is difficult, especially in open, dynamic systems (Vetter 1988; Quinn and Deriso 1999). Acoustic telemetry permitted our *in situ* determination of spotted seatrout mortality in overwintering estuarine tributaries relative to environmental variability. We were able to monitor daily movements and survival for up to 175 d (approximately 6 months) and found that both natural mortality and emigration from our study creeks were largely driven

by temperature. In general, when water temperatures at depths of 1.5 m fell below 5-7 °C, telemetered spotted seatrout responded by either emigrating from the study creeks, occupying deeper thermal refuges within the study creeks (i.e., > 1.5 m), or remaining in the relatively shallow habitats at approximately 1.5 m. In the latter case, our data provide strong evidence of spotted seatrout natural mortality due to acute cold stress. We were limited in our study by the lack of spatial monitoring of the thermal environment, especially in deeper and less saline areas that likely provided refuge during extreme cold. Furthermore, the high degree of variability in both temperature and salinity that we observed in the water column throughout the study creeks during manual tracking suggest that our real-time monitoring of temperature at only one or two stationary receivers per creek were an imprecise record of the thermal history experienced by each telemetered fish. Similar studies in the future should increase the spatial coverage of environmental monitoring, particularly in areas that may provide refuge from environmental stressors. Additionally, VEMCO transmitters more advanced than the ones used in this study are now available and capable of logging temperature, depth, and acceleration. These archival transmitters provide a tremendous advantage with regards to studying the influence of temperature on survival; however, their high costs (approximately twice as much as non-archival transmitters) and the requirement to recapture the fish (transmitter) in order to retrieve the logged information, limit the use of these transmitters in studies with budgetary constraints or in open systems where recaptures are low due to emigration, sampling inefficiency, or low exploitation.

The patterns in survival that we observed over the three separate study periods support the general patterns in seasonal instantaneous natural mortality rate (*M*) estimated from tag-return data (see Figure 6B in Section 1). We observed winter kill of telemetered fish in the 2009/2010 and 2010/2011 study periods and specifically during months of high estimated *M*

from conventional tagging. We observed no natural mortality in either the Pungo River or Neuse River study creeks during the 2011/2012 period, which coincides with the low estimates of winter *M* from conventional tagging relative to the previous two winters. Also of interest and in support of tag-return mortality estimates, relatively few harvests of telemetered spotted seatrout were inferred in our study. Considering the popularity of these particular creeks among recreational anglers, the high level of fishing effort we regularly observed during manual tracking events, and that fish in these overwintering creeks were spatially confined, it was surprising how few of our telemetered fish were caught. On numerous occasions we observed (i.e., manually relocated acoustic signal) multiple telemetered spotted seatrout in the immediate presence of recreational fishers. Similarly, stationary receivers recorded telemetered spotted seatrout successfully navigating set gill nets in Pungo Creek. These direct observations and the low number of inferred harvests of telemetered fish imply that exploitation of spotted seatrout in these systems was low. Finally, in 2012 we observed a mass emigration of nearly all telemetered fish from study creeks in both the Pungo River and the Neuse River during the latter half of March. The timing of these observed emigrations is in agreement with what is known about the reproductive condition and onset of spawning behavior for spotted seatrout in North Carolina (NCDMF 2012) and areas south (Brown-Peterson 2003); the emigrations observed from the Pungo River study creeks in February 2010 were likely influenced by a second bout of low temperatures that persisted for nearly a month. Additionally, this mass March/April emigration that we observed in 2012 supports the seasonal availability parameter estimates for the NCDMF gill net survey that we estimated in a separate survey model analysis of instantaneous total mortality rate (see Section 1) and coincides with the extensive migrations north each spring and summer exhibited by conventionally tagged spotted seatrout (see Section 3).

Table 1. Summary of telemetry study results including numbers of fish tagged and released, total length (mm) ranges, beginning and end dates of daily data availability, assumed fates, and days-at-risk ranges for telemetered spotted seatrout that were tracked during three consecutive winters in two adjacent tributaries of the Pungo River, NC, and during one winter in two adjacent tributaries of the Neuse River, NC. Number of individuals for a given fate is presented with the proportion of the total number tagged (in parentheses) for that winter and river system.

	Pungo R.			Neuse R.
Telemetry study results	2009-2010	2010-2011	2011-2012	2011-2012
Number tagged	37	10	26	45
Total length [min. – max.]	372 – 502	360 – 440	361 – 495	362 – 540
Date of first fish release [mm/dd]	12/01	11/18	11/02	11/07
Date of last fish at-risk [mm/dd]	03/18	12/16	05/30	05/22
Surgery-related mortality	0	1 (0.10)	0	0
Permanent emigration within 7 d	3 (0.08)	0	2 (0.08)	3 (0.07)
Fishing morality				
Total	1 (0.03)	0	4 (0.15)	4 (0.09)
Confirmed	0	0	0	4 (0.09)*
Unconfirmed	1 (0.03)	0	4 (0.15)	0
Natural mortality				
Total	7 (0.19)	6 (0.60)	0	0
Stationary transmitter	2 (0.05)	5 (0.50)	0	0
Removal during cold episodes	5 (0.14)	1 (0.10)	0	0
Emigration after 7 d	26 (0.70)	3 (0.30)	20 (0.77)	38 (0.84)
Days at risk [min. – max.]	7 – 101	3 – 22	11 – 173	2 – 172

*One of these four confirmed fishing mortalities occurred during a 7-d censorship period; proportion is of total number tagged.

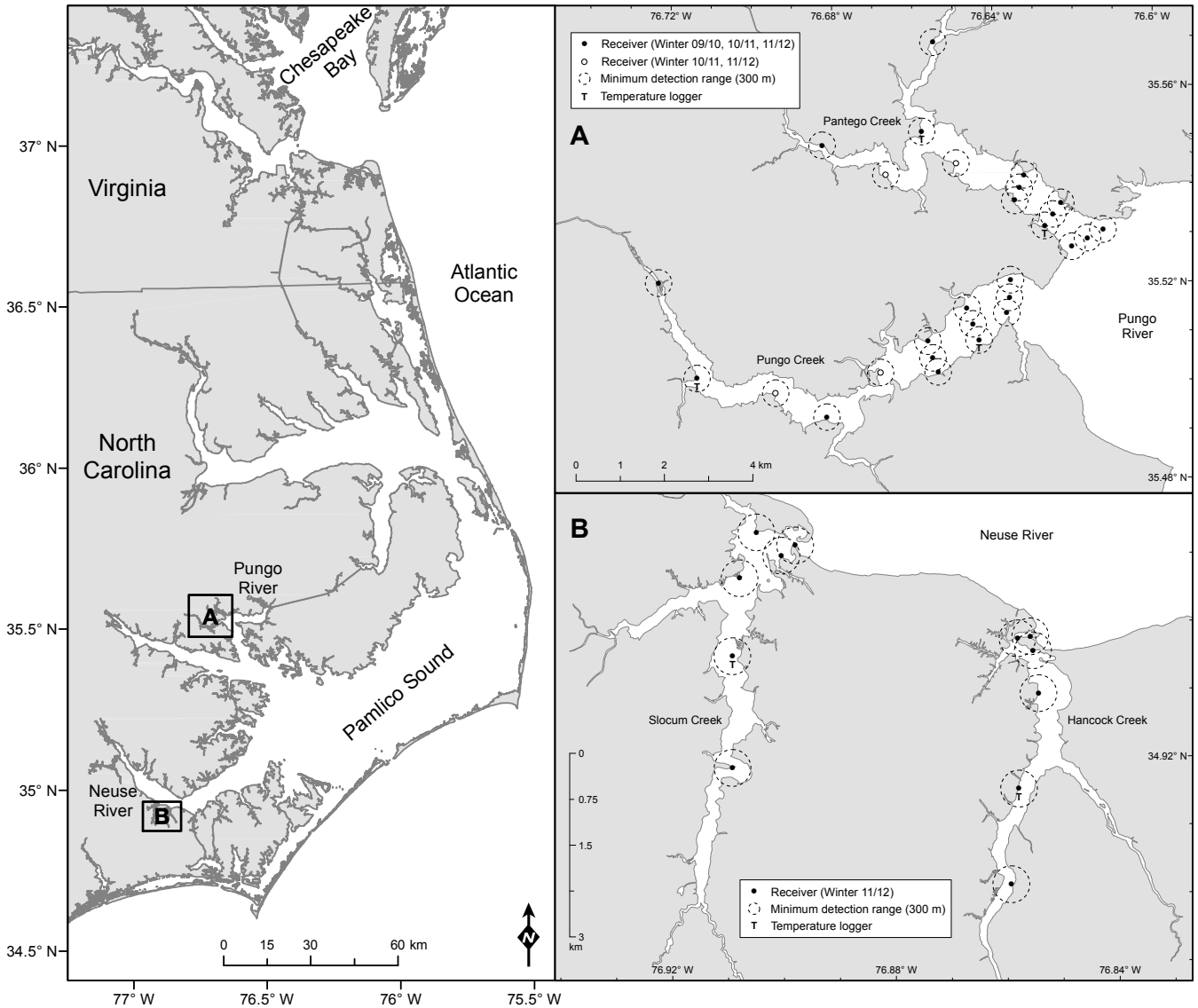


Figure 1. Study sites in North Carolina (A = Pungo River tributaries; B = Neuse River tributaries) where spotted seatrout were monitored with ultrasonic telemetry across three separate winters: 2009/2010, 2010/2011, and 2011/2012.

Figure 2. Relocation histories for 37 telemetered spotted seatrout released in two adjacent tributaries of the Pungo River, NC from December 2009 to March 2010. Each row characterizes the automated and manual detections and assumed fates for an individual tagged fish each day, including a 7-d censorship period following postsurgical release. Fates are coded as natural mortality determined from stationary transmitter (NM1), natural mortality determined from removal of transmitter during cold temperatures (NM2), unconfirmed fishing mortality (UF), immigration (I), and emigration (E).

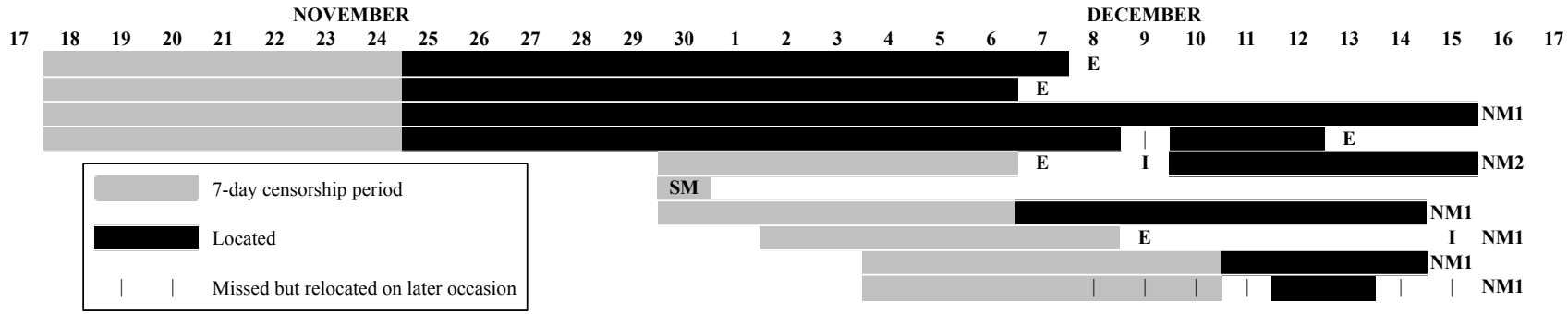
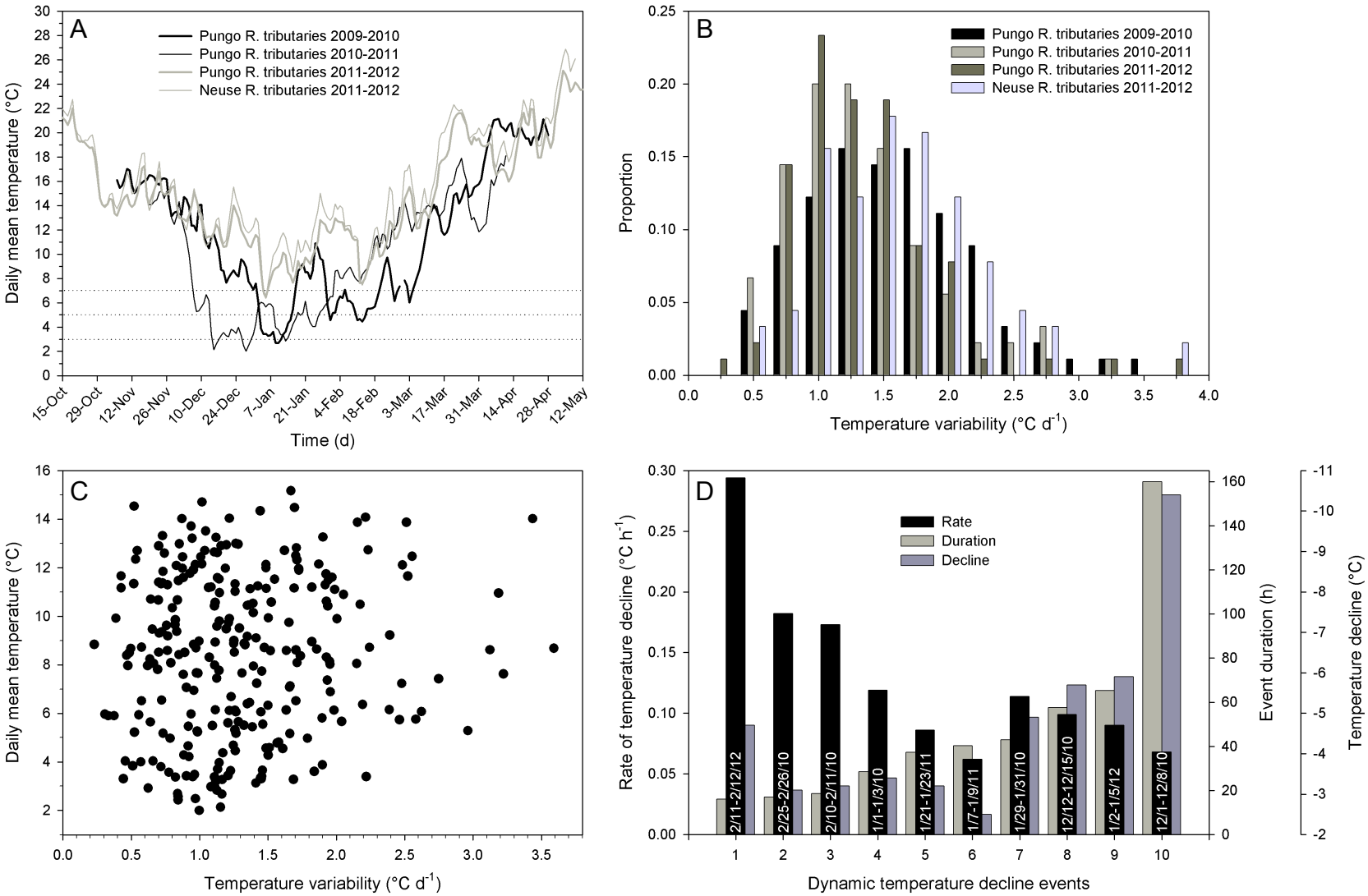


Figure 3. Relocation histories for 10 telemetered spotted seatrout released in two adjacent tributaries of the Pungo River, NC from November to December 2010. Each row characterizes the automated and manual detections and assumed fates for an individual tagged fish each day, including a 7-d censorship period following postsurgical release. Fates are coded as surgery-related mortality (SM), natural mortality determined from stationary transmitter (NM1), natural mortality determined from removal of transmitter during cold temperatures (NM2), immigration (I), and emigration (E).

Figure 4. Relocation histories for 26 telemetered spotted seatrout released in two adjacent tributaries of the Pungo River, NC and for 45 telemetered spotted seatrout released in two adjacent tributaries of the Neuse River, NC, from November 2011 to May 2012. Each row characterizes the automated and manual detections and assumed fates for an individual tagged fish each day, including a 7-d censorship period following postsurgical release. Fates are coded as natural mortality (NM), unconfirmed fishing mortality (UF), confirmed fishing mortality (F), immigration (I), and emigration (E).

Figure 5. Water temperature data collected by automated loggers in study tributaries of the Pungo River (2009-2010, 2010-2011, and 2011-2012) and Neuse River (2011-2012) in North Carolina. (A) Daily mean temperature (°C) spanning the late-fall to early-spring time period across three spotted seatrout winter telemetry seasons; temperature measurements taken at a uniform depth of approximately 1.5 m in each study tributary. References (dotted lines) to low temperature treatments that affected survival under controlled laboratory conditions are also presented. (B) Daily variability in mean maximum and minimum temperatures (°C d^{-1}) across the December 1 to February 28 time period. (C) The relationship between daily temperature variability (°C d^{-1}) and daily mean temperature (°C) across the December 1 to February 28 time period in 2009-2010, 2010-2011, and 2011-2012 in the Pungo River study tributaries only (n = 270). (D) The rate of temperature decline (°C h^{-1}) and duration (h) of 10 rapid-onset-of-cold events, along with the level of decline in temperature during each event (-°C). The dates over which each event spans are also presented.


A
Pungo R. tributaries 2009-2010
Pungo R. tributaries 2010-2011
Pungo R. tributaries 2011-2012
Neuse R. tributaries 2011-2012
Daily mean temperature (°C)
Time (d)
15-Oct
29-Oct
12-Nov
26-Nov
10-Dec
24-Dec
7-Jan
21-Jan
4-Feb
18-Feb
3-Mar
17-Mar
31-Mar
14-Apr
28-Apr
12-May
B
Pungo R. tributaries 2009-2010
Pungo R. tributaries 2010-2011
Pungo R. tributaries 2011-2012
Neuse R. tributaries 2011-2012
Proportion
Temperature variability (°C d-1)
C
Daily mean temperature (°C)
Temperature variability (°C d-1)
D
Rate
Duration
Decline
Rate of temperature decline (°C h-1)
Event duration (h)
Temperature decline (°C)
2/11-2/12/12
2/25-2/26/10
2/10-2/11/10
1/1-1/3/10
1/21-1/23/11
1/7-1/9/11
1/29-1/31/10
12/12-12/15/10
1/2-1/5/12
12/1-12/8/10
Dynamic temperature decline events

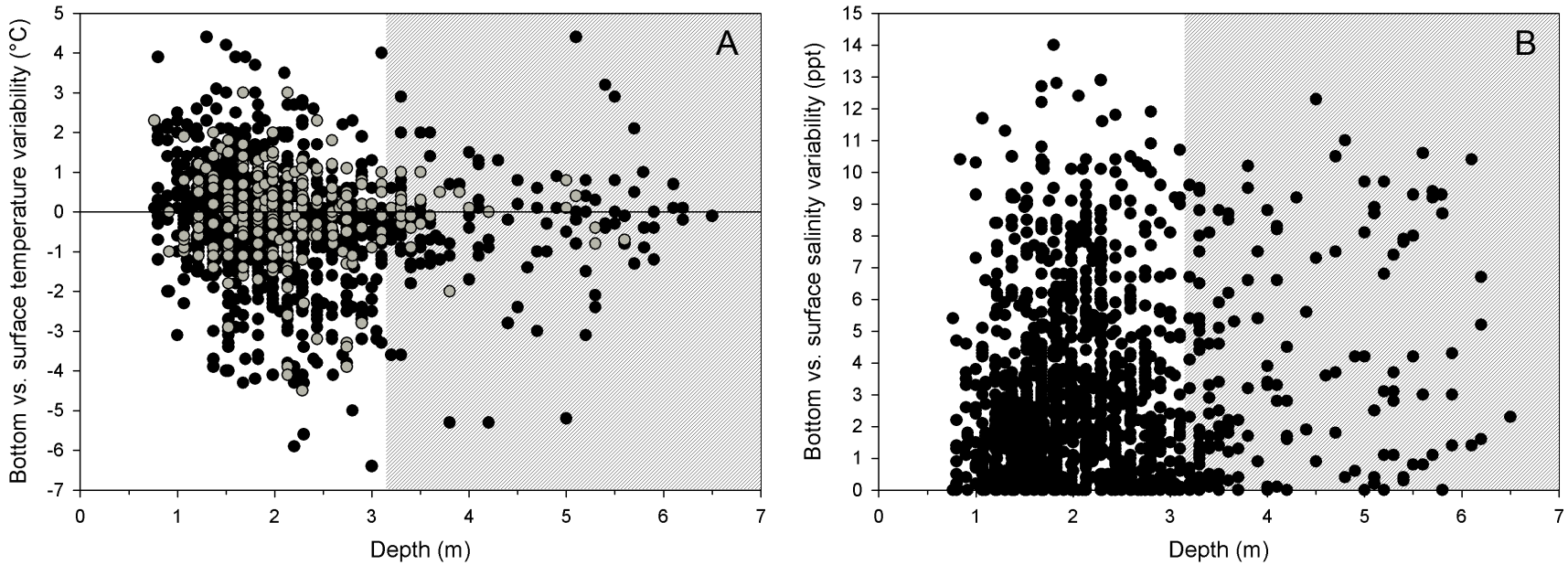
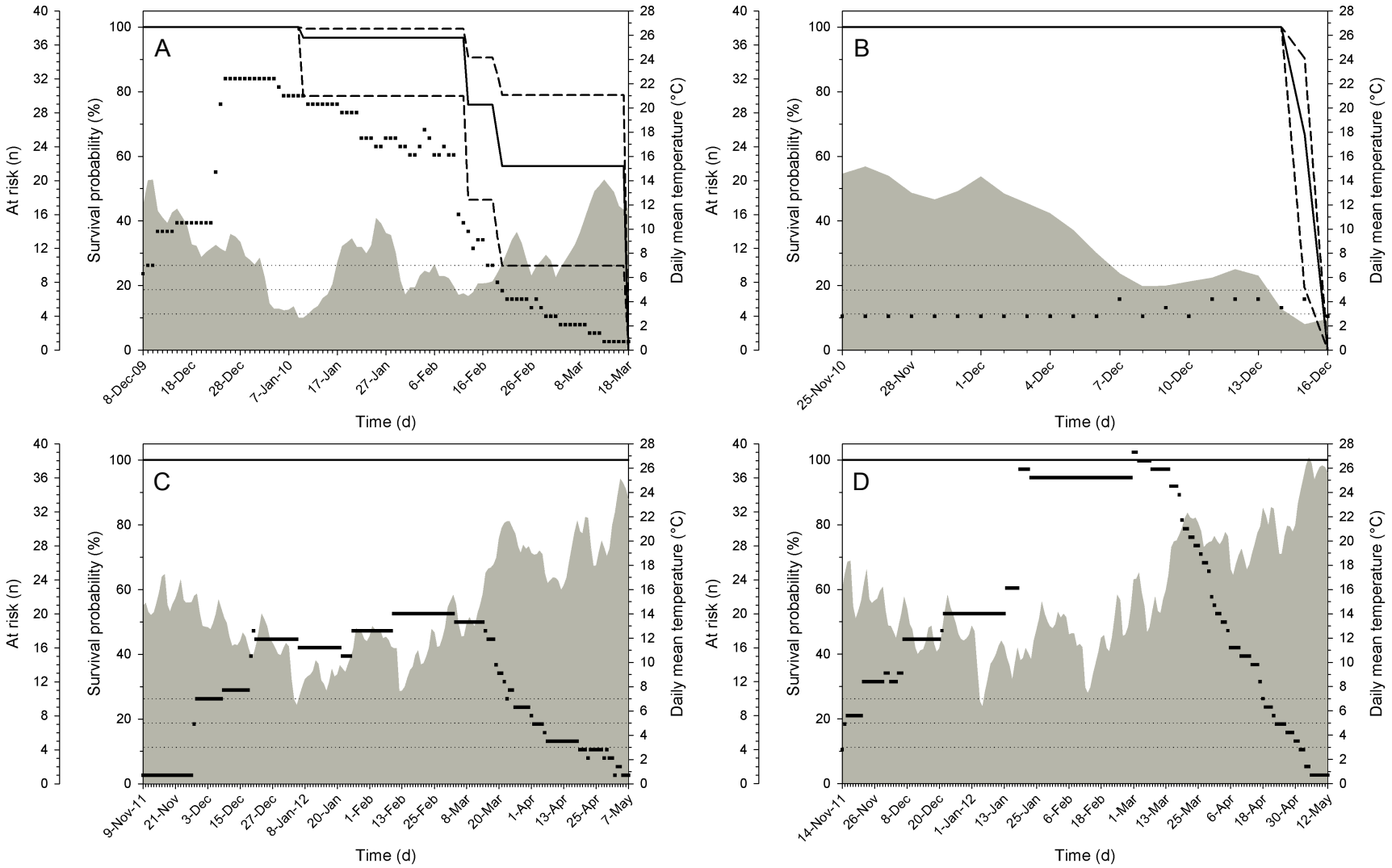


Figure 6. Stratification of temperature (A) and salinity (B), defined as bottom (up to 3.1 m) versus surface (at 0.3 m) variability in these abiotic parameters (e.g., bottom minus surface temperature), recorded during manual tracking events that were pooled across three telemetry seasons. For example, a value of -3 °C means that the bottom temperature was 3 °C colder than at the surface. Measurements in patterned areas were recorded at listening stations where depths exceeded the 3.1 m water quality instrument cable capability; therefore, full stratification of the water column in temperature and salinity likely differ from that which is presented. Gray points in Plot A represent sampling events where either bottom or surface water temperature measurements were ≤ 5 °C (i.e., the temperature at which significant mortality was observed under controlled laboratory conditions).

Figure 7. Daily Kaplan-Meier estimates of marginal survival (i.e., only natural deaths considered; solid line) with 95% pointwise confidence intervals (dashed lines) for telemetered spotted seatrout relative to daily mean water temperature (°C) (gray shaded area) in study tributaries of the Pungo River (A: 2009-2010; B: 2010-2011; C: 2011-2012) and Neuse River (D: 2011-2012) in North Carolina. The daily numbers of fish at risk (squares) are shown, along with references (dotted lines) to low temperature treatments that affected survival under controlled laboratory conditions. Differences in scale of x-axes reflect the ranges in time over which telemetered spotted seatrout were at risk in each study tributary during a given telemetry season.


A
B
C
D
At risk (n)
Survival probability (%)
Daily mean temperature (°C)
Time (d)
8-Dec-09
18-Dec
28-Dec
7-Jan-10
17-Jan
27-Jan
6-Feb
16-Feb
26-Feb
8-Mar
18-Mar
25-Nov-10
28-Nov
1-Dec
4-Dec
7-Dec
10-Dec
13-Dec
16-Dec
9-Nov-11
21-Nov
3-Dec
15-Dec
27-Dec
8-Jan-12
20-Jan
1-Feb
13-Feb
25-Feb
8-Mar
20-Mar
1-Apr
13-Apr
25-Apr
7-May
14-Nov-11
26-Nov
8-Dec
20-Dec
1-Jan-12
13-Jan
25-Jan
6-Feb
18-Feb
1-Mar
13-Mar
25-Mar
6-Apr
18-Apr
30-Apr
12-May

SECTION 3

MOVEMENT PATTERNS INFERRED FROM TAGGING

INTRODUCTION

The level of mixing among individuals across a species' geographic range, generally defined as connectivity, is central to the development of conservation and management strategies for marine and estuarine fish populations. Connectivity can occur over multiple spatial and temporal scales and during any point in life history (i.e., larval, juvenile, or adult stages). Populations identified for management (i.e., unit stocks) are frequently based on the broad-scale movements and exchange of adults. Numerous techniques have been used to differentiate adults into discrete stocks, including the use of artificial tags (e.g., mark-recapture methodology) and natural tags (e.g., parasite markers, otolith chemistry, tissue stable isotopes, and genetics). In particular, mark-recapture data allow for the most direct analyses of the spatiotemporal variability in movement rates and migration patterns of marine and estuarine fishes.

For spotted seatrout (*Cynoscion nebulosus*), a relatively short-lived, estuarine-dependent species abundant throughout the U.S. South Atlantic and Gulf of Mexico, numerous tag-return studies suggest that movements are spatially limited, with few migrations by marked individuals away from natal estuaries (VanderKooy 2001; Bortone 2003). In general, tagged spotted seatrout in the Gulf of Mexico were seldom recaptured beyond 50 km from point of release (Moffett 1961; Iversen and Tabb 1962; Beaumariage 1969; McEachron and Matlock 1980; Rogillio 1980; Rogillio 1982; Overstreet 1983; Arnoldi 1984; Baker et al. 1986; Baker and Matlock 1993; Bourgeois et al. 1995; Hendon et al. 2002); however, movement over greater distances ranging from 150 to 500 km were estimated in a few tag-return cases (Moffett 1961; Iversen and Tabb 1962; Bowling and Sunley 2003). Similarly, tagging studies conducted along

the U.S. South Atlantic coast revealed that the vast majority of marked spotted seatrout were recaptured within 25 km of release sites (Music and Pafford 1984; Wenner et al. 1990; Woodward et al. 1990; Woodward and Mericle 1995; Wenner and Archambault 1996; Johnson et al. 1999; Tremain et al. 2004; Wiggers 2010) but some fish were capable of migrating up to 200 km, although these long-range movements were also rare (Music and Pafford 1984; Wenner et al. 1990; Woodward et al. 1990; Wenner and Archambault 1996; Wiggers 2010).

Temporal differences in the movements of adult spotted seatrout are also apparently similar across much of the species' range. Migrations between upper- and lower-estuarine (including the coastal zone) habitats are largely seasonal and thought to be driven, in part, by prey availability and reproduction cycles (Rogillio 1982; Overstreet 1983; Arnoldi 1984; Music and Pafford 1984; Baker et al. 1986; Woodward et al. 1990; Helser et al. 1993; Wenner and Archambault 1996). The influence of temperature on foraging and spawning behaviors, along with the relatively low tolerance of spotted seatrout to cold (see Sections 1 and 2), support the view, pervasive throughout the literature on this species, that the large-scale movements of spotted seatrout are predominantly related to temperature change.

Based on the restricted home ranges of spotted seatrout that have been identified by tag-return data, populations are generally assumed to be resident, which implies stock structuring. Movements are largely confined to interjurisdictional boundaries, and unit stocks are typically assessed and managed at the state level (VanderKooy 2001; VanderKooy and Muller 2003; ASMFC 2012). Further evidence of stock structuring has been found in several analyses of the spatial heterogeneity (i.e., geographic restrictions to gene flow) in spotted seatrout (see extensive reviews of earlier research in Bortone 2003 and Ward et al. 2007). Recently, Anderson and Karel (2009) sequenced the mtDNA control region of samples of spotted seatrout taken along the

Texas coast and found an isolation-by-distance (IBD) effect (i.e., a negative correlation between increasing geographic distance and genetic similarity in populations). A reanalysis of the mtDNA data, combined with a new analysis using six nuclear microsatellite loci, suggests more definitively that Texas spotted seatrout can be separated into multiple genetically distinct subpopulations (Anderson and Karel 2010). In Florida, at least five subpopulations of spotted seatrout are thought to exist based on mtDNA analysis alone (Wilson et al. 2002), and other studies employing just microsatellite data support an IBD model across the Gulf of Mexico, where populations in Texas and Louisiana are genetically less similar to populations in Florida (Gold et al. 2003; Ward et al. 2007). Elsewhere along the U.S. South Atlantic coast, however, research addressing the genetic connectivity of spotted seatrout is limited. Based on just two microsatellite loci, Wiley and colleagues (2003) concluded that spotted seatrout sampled from Chesapeake Bay were separate from those sampled in Georgia and South Carolina. In a more recent analysis of 13 microsatellite markers, significant population differentiation was found between North Carolina spotted seatrout and those in Georgia and South Carolina, where gene flow was also best characterized by an IBD pattern (O'Donnell 2013).

Spotted seatrout are uncommon north of Chesapeake Bay (Welsh and Breder, Jr. 1923; Pattillo et al. 1997; Bortone 2003; ASMFC 2012). Although movement characteristics and, to a lesser degree, stock structure, have been heavily studied in the center and southern portions of the species' geographic distribution, connectivity in the northern range (i.e., North Carolina latitudes and north), including movement rates, migration patterns, and the spatial scale of management, is poorly understood. The influence of the abiotic environment on the movement and survival of fishes is considered highest at the edges of a species' range (Miller et al. 1991), and it is not known if these edge effects result in movement rates different from those previously

described for spotted seatrout, especially considering that the species in the northern range is likely more vulnerable to extreme cold. Migrations to overwintering habitats may be extensive and would likely traverse interjurisdictional boundaries, contribute to stock mixing, and affect management strategies for spotted seatrout in the northern range.

Here, we examine both the regional- (i.e., statewide) and coastwide-scale movements of spotted seatrout at the species' northern latitudinal limit in order to assess connectivity and stock composition. Specifically, data from a multiyear tag-return study conducted in North Carolina and Virginia were used to describe the movement patterns of spotted seatrout.

METHODS

A North Carolina State University (NCSU) tagging initiative was begun in September 2008 to study the movement and mortality of spotted seatrout in North Carolina. Marked fish were released through October 2012; however, tag-return data were collected and analyzed through October 2013. Spotted seatrout for tagging (≥ 305 mm TL) were collected using predominantly hook-and-line and occasionally by electrofishing. Healthy individuals (i.e., exhibiting no physical signs of trauma from capture) were externally marked with internal anchor tags (Floy Tag, Inc., Washington, USA; Model FM-95W) that were labeled with a unique identification number, contact information, and instructions to return the tag for a reward. In order to meet spatial and temporal objectives for tagging effort, a select group of ten guide-service professionals were trained and compensated for assisting NCSU personnel with the tagging of spotted seatrout. These paid taggers were selected for their proficiency in catching spotted seatrout, the high percentage of their fishing charter business spent targeting spotted seatrout, the majority of days each year they commit to fishing, and their extensive knowledge of

the regional waterscape. Recorded information associated with each individual release included tag number, date, total length (measured to the nearest quarter inch), and geographic coordinates (latitude and longitude). Recapture information was collected during a phone interview with fishers returning tags and consisted notably of the tag number, date and location of capture, and fish total length (primarily in inches). Latitude and longitude coordinates for recapture locations of spotted seatrout tagged by NCSU were occasionally provided by fishers but primarily assigned according to fishers' direct geographical descriptions. For more details regarding the NCSU tagging methods see Section1 of this report.

Spotted seatrout were continually tagged and released throughout the estuarine and nearshore coastal waters of North Carolina and in select areas of Virginia. Tagging effort was distributed among six broad geographical regions (Figure 1). In Virginia, spotted seatrout were predominantly tagged and released in the tributaries of Mobjack Bay and Lynnhaven Bay, both part of Region 1, Chesapeake Bay (see Figure 1 in Section 1). In North Carolina, the five regions of tagging effort included: Region 2) the northern Outer Banks (i.e., the North Carolina/Virginia border south to Ocracoke Inlet, including eastern and northern Pamlico Sound, coastal waters for this region, and Albemarle Sound); Region 3) the Pamlico River estuary (i.e., Pamlico River, Pungo River and western Pamlico Sound); Region 4) the Neuse River estuary (i.e., Ocracoke Inlet south to Bogue Inlet, including the Neuse River, Bay River, southern Pamlico Sound, and adjacent waters of Core and Bogue Banks); Region 5) the New River estuary (i.e., coastal and estuarine waters from Bogue Inlet south to Carolina Beach Inlet, including the White Oak and New Rivers); Region 6) the Cape Fear River estuary (i.e., the coastal and estuarine waters from Carolina Beach Inlet south to the North Carolina/South Carolina border, including the Cape Fear River). The delineation of these regions was based on

a preliminary analysis of historical landings data and preconceptions that movements would be primarily restricted to within these general boundaries. The compensation of taggers promoted uniform tagging effort across the five study regions and ensured that marked fish were released each month within North Carolina. However, the distribution of tags was largely dependent upon the regional availability and abundance of spotted seatrout, and as such, tag releases varied spatially and temporally throughout the four-year study.

Tag-return data were combined across years under the assumption that interannual variability in movement patterns was minimal. Regional-scale movements of spotted seatrout in North Carolina and Virginia were examined by first qualitatively assessing the overall spatial patterns in tag recoveries, and then delineating boundaries for analysis that appeared to best generalize, without oversimplifying, those patterns. The six regional boundaries used to distribute tagging effort also appeared to characterize movement patterns well and thus, were used for further analysis (Figure 1). The distance (km) and direction (i.e., whole circle bearing of movement vector: North: 0-90°, 271-359°; South: 91-270°) moved by tagged spotted seatrout were determined from the latitude and longitude of mark and recapture locations. Euclidean pathways (i.e., single straight line vector) are a standard measure of connectivity distances. We calculated the net displacement (i.e., shortest distance between mark and recapture locations) of tagged spotted seatrout as the linear distance (i.e., Euclidean pathway) using ArcGIS 10.1 (ESRI®, Redlands, CA, USA).

RESULTS

Overall, 6,582 spotted seatrout were tagged in North Carolina and Virginia waters by NCSU from September 2008 through October 2012 (see Figure 1 of Section 1). Approximately

8% (n = 553 unique fish) of these fish were recovered and reported over five years (through October 31, 2013). Only one tagged spotted seatrout was caught multiple times (i.e., twice) in our study. For movement analysis, we used associated recovery information on the second recapture of this fish (e.g., 85 days at liberty) since the first recapture event occurred after only two days at liberty. Recoveries of tagged spotted seatrout occurred primarily throughout North Carolina estuarine and coastal waters and in Chesapeake Bay (see Figure 3 of Section 1). Days-at-liberty could be determined for 518 of the total tag recoveries and ranged from 1 to 848 (mean ± SD: 145.8 ± 136.2; see Figure 4 of Section 1). Precise information on recapture location was sufficient to determine the linear distance traveled by 525 of the total tag recoveries, which was estimated up to a maximum of 424.5 km (approximately 229 nautical miles). Over half (56%) of the recovered and returned tagged spotted seatrout were recaptured within 20 km (approximately 11 nautical miles) from where they were originally tagged, including 19% recaptures within 2 km (approximately 1 nautical mile) of the tagging location (Figure 2). Interestingly, 25% of tag recoveries occurred more than 100 km (approximately 54 nautical miles) from the original point of release, and half of these fish moved distances in excess of 180 km (approximately 97 nautical miles). The linear distance moved by spotted seatrout between tagging and recovery locations was weakly correlated with days at liberty ($R^2 = 0.034$, $p < 0.01$) and fish total length at recapture ($R^2 = 0.072$, $p < 0.01$) (Figure 3).

Differences in tag recoveries and associated information on movement were examined across the six broad geographical regions. Tag-return rates were similar across all regions and ranged from 6-10%. The size range of spotted seatrout tagged (overall mean ± SD: 354.4 ± 56.3 mm; overall range: 254-711 mm) and the days at liberty were also similar across regions (Table 1). Linear distances moved by spotted seatrout tagged in Region 3 (Pamlico River estuary) and

Region 6 (Cape Fear River estuary) were relatively lower on average than for fish tagged in Region 4 (Neuse River estuary) and Region 5 (New River estuary), and all were much lower than those estimated for fish tagged in Region 2 (northern Outer Banks) (Table 1). Most (74-96%) fish tagged in a given region were recaptured from the same region, with the exception of Region 2 (northern Outer Banks) where only 28% of spotted seatrout tagged in that area were recovered from that area (Table 2). Most (50%) of the recaptures of spotted seatrout tagged in Region 2 (northern Outer Banks) that occurred outside of that area were from regions to the south, particularly Region 5 (New River estuary; 30%); however, 22% of fish tagged in Region 2 were recovered in Region 1 (Chesapeake Bay). Only one (4%) of the fish tagged in Region 1 (Chesapeake Bay) was recovered south and in Region 2 (northern Outer Banks). Movement outside of Region 3 (Pamlico River estuary) was limited (16% for recoveries of fish tagged in that region) and most exchange appeared to be with Region 4 (Neuse River estuary). In Regions 4 (Neuse River estuary) and 5 (New River estuary), 24% and 19% of tag recoveries from fish released in those areas, respectively, were from regions to the north. Limited movements outside of Region 6 (Cape Fear River estuary) were observed (12% for recoveries of fish tagged in that region) and most of these outside recoveries were from more northerly regions. Overall, for recaptures of spotted seatrout tagged in North Carolina (n = 499 with sufficient information on recovery region), 49 (9.8%) were from outside of the state's jurisdictional boundaries. Forty-seven (96%) of these interjurisdictional recoveries were from Chesapeake Bay, including 39 (80%) in Virginia waters and 8 (16%) in Maryland waters. Only two (0.4%) spotted seatrout tagged in North Carolina were recaptured in South Carolina.

Regional-scale movement patterns were visually assessed relative to the linear distance moved by tagged spotted seatrout. We considered localized movements to be linear distances

less than or equal to 20 km (approximately 11 nautical miles), and as stated earlier, more than half of reported tag recoveries in our study were limited to where the fish was originally tagged and released. These localized movements resulted in minimum exchange across our regional boundaries. Linear distances greater than 20 km but up to 100 km (approximately 54 nautical miles) were considered relatively small-scale in our study and produced mixing predominantly between neighboring regions (or adjacent estuarine systems) (Figure 4). Large-scale movements, the linear distances greater than 100 km but up to 180 km (approximately 97 nautical miles), resulted in the largest observed exchange of spotted seatrout across regions within North Carolina; however, most of these large-scale movements were from fish in Region 2 (northern Outer Banks) moving either north or south (Figure 5). These large-scale movements also resulted in limited exchange across interjurisdictional boundaries, except for spotted seatrout tagged near state lines (i.e., fish tagged around Oregon Inlet and the Cape Fear River). Finally, coastwide movements of spotted seatrout that moved linear distances greater than 180 km resulted in the majority (i.e., 39 of the 49 fish tagged in North Carolina and recaptured in other states; 80%) of interjurisdictional exchange observed in our study (Figure 6). Most (70%) of these coastwide movements were north from regions in North Carolina to Region 1 (Chesapeake Bay), with the remaining 30% predominately southward movements from Region 2 (northern Outer Banks).

DISCUSSION

The Atlantic States Marine Fisheries Commission (ASMFC) currently manages spotted seatrout under an Omnibus Amendment to the Interstate Fisheries Management Plan for the species (ASMFC 2012), which sets minimum regulations by which each member state must

abide. Given limited data on migration rates of spotted seatrout in the U.S. South Atlantic, it is assumed that populations within each Atlantic member state are mostly resident, as has been shown for populations in the northern Gulf of Mexico and along the Atlantic coast of Florida (Iversen and Tabb 1962; Baker et al. 1986; Hendon et al. 2002; Tremain et al. 2004). Therefore, the ASMFC recommends that these unconfirmed subpopulations in Atlantic estuaries be assessed separately (ASMFC 2012). Nevertheless, populations in both North Carolina and Virginia were considered one unit stock in North Carolina's recent age-structured assessment based on an early analysis of tag-return data from the Virginia Game Fish Tagging Program (VGFTP) (Jensen 2009). Further review of these VGFTP data and consideration of the results from our multiyear tag-return study in North Carolina do not unequivocally imply homogeneity in stock structure. Between 1995-2012, 91 of 1,883 (4.8%) tag returns for spotted seatrout from the VGFTP were from North Carolina (Susanna Musick, VGFTP, pers. comm.). In our study, we found that 9.4% of spotted seatrout tagged in North Carolina (i.e., 47 of 499 recoveries that were reported with sufficient information on recovery region) were recaptured in Chesapeake Bay, including the jurisdictional waters of both Virginia and Maryland. Interestingly, our tag-return data, along with historic tag-return data from South Carolina, show less than 1% of tagged spotted seatrout migrate over the North Carolina and South Carolina jurisdictional boundary (John Archambault and Robert Wiggers, SCDNR, pers. comm.). This low level of mixing between neighboring systems is also found in populations of spotted seatrout further south (see Introduction).

The higher movement levels of spotted seatrout between North Carolina and Virginia are expected as winter temperatures within Chesapeake Bay are much colder relative to southern estuaries. The relatively low tolerance of spotted seatrout for cold temperatures (see Section 2)

limits the northern extent of the species' latitudinal range (e.g., Chesapeake Bay). Tagging data from the northern range document consistent seasonal migration patterns of spotted seatrout between North Carolina and Chesapeake Bay. VGFTP tag-return data confirm that spotted seatrout tagged in Chesapeake Bay migrate southward to North Carolina each fall and winter. Similarly, our NCSU tag-return data confirm that spotted seatrout move from North Carolina to Chesapeake Bay during spring months, with Virginia and Maryland tag returns documented only during summer months (i.e., spawning season). The timing of these recaptures suggests that these fish may be returning to Chesapeake Bay for summer feeding and spawning. Whether or not these fish were themselves spawned in Chesapeake Bay is unknown but likely; natal homing has been shown for other sciaenids including red drum (*Sciaenops ocellatus*: Patterson et al. 2004; Rooker et al. 2010) and a congener of spotted seatrout, weakfish (*Cynoscion regalis*: Thorrold et al. 2001). Weakfish, for example, migrate south and offshore of North Carolina to overwinter but return each spring and early summer to natal estuaries to spawn.

The possibility of temperature-driven latitudinal mixing in populations of spotted seatrout from Chesapeake Bay to southern North Carolina is unique to the northern extent of the species' distribution. In terms of population structure, the two most likely scenarios are: (1) genetic homogeneity resulting from temperature-driven mixing during winter that carries over into the spawning season, or (2) two distinct genetic groups mix during winter and separate and home to natal estuaries for spawning in spring. Tagging data, including the results of our study, suggest the latter but stock boundaries (used for management and conservation of spotted seatrout in North Carolina) can be more accurately identified from a comprehensive analysis of the genetic mixing between populations in North Carolina and surrounding estuaries (Carvalho and Hauser 1994; Ward 2000; Laikre et al. 2005; Schwartz et al. 2006).

Table 1. Regional and total numbers of spotted seatrout tagged and the reported subsequent recoveries from September 2008 through October 2013. Summary statistics for fish size (total length; mm), days at liberty, and linear distance moved (i.e., Euclidean pathway; km) are also provided. Note: Some samples sizes are lower than the total 553 tag returns due to incomplete reporting of all information necessary to estimate either exact days at liberty or exact region of recovery.

Release Region	Total Tagged	Total Returns	Percent Returned	Total length of releases (mm)			Days at liberty				Distance (km)			
				Mean	SD	Range	n	Mean	SD	Max	n	Mean	SD	Max
(1) Chesapeake Bay	432	26	6.0	360.6	59.5	292-622	25	161.4	183.0	725	26	37.6	42.3	180.1
(2) NOBX	1,616	134	8.3	347.0	46.9	273-622	122	145.2	137.8	715	121	128.8	81.1	311.9
(3) Pamlico R.	714	46	6.4	339.5	52.2	254-622	45	146.0	115.1	460	44	24.1	47.6	303.0
(4) Neuse R.	1,357	125	9.2	350.4	63.0	273-686	116	141.6	127.4	578	121	44.5	79.4	367.2
(5) New R.	1,460	146	10.0	362.8	61.4	279-711	134	156.4	150.2	848	137	48.4	82.2	341.0
(6) Cape Fear R.	1,003	76	7.6	367.5	48.6	305-559	76	129.1	114.9	442	76	27.8	72.9	424.5
Combined	6,582	553	8.4	354.4	56.3	254-711	518	145.8	136.2	848	525	60.5	84.9	424.5

Table 2. Regional differences in the recoveries of tagged spotted seatrout from September 2008 through October 2013. Shown is the number of tagged spotted seatrout in each region that were recovered in that region (gray squares) or elsewhere. Parenthetical numbers are the percentage of recovered fish from a release region that were recaptured in a given recovery region. Also provided is the number and percent of tagged fish that moved north and south of the release region; directionality was determined from the whole circle bearings of movement vectors (North: 0-90°, 271-359°; South: 91-270°). No fish were tagged in South Carolina (SC) but recoveries did occur in this region. Note: Combined samples size is lower than the total 553 tag returns due to incomplete reporting of all information necessary to estimate the exact region of recovery.

		Recovery region							Directionality	
Release region	n	1	2	3	4	5	6	SC	North	South
(1) Chesapeake Bay	26	25 (0.96)	1 (0.04)							1 (0.04)
(2) NOBX	121	26 (0.22)	34 (0.28)	9 (0.07)	36 (0.30)	15 (0.12)	1 (0.01)		26 (0.22)	61 (0.50)
(3) Pamlico River	44	1 (0.02)		37 (0.84)	6 (0.14)				1 (0.02)	6 (0.14)
(4) Neuse River	121	11 (0.09)	6 (0.05)	12 (0.10)	90 (0.74)	2 (0.02)			29 (0.24)	2 (0.02)
(5) New River	137	7 (0.05)	8 (0.06)	5 (0.04)	6 (0.04)	105 (0.77)	5 (0.04)	1 (0.00)	26 (0.19)	6 (0.04)
(6) Cape Fear River	76	2 (0.03)		1 (0.01)	3 (0.04)	2 (0.03)	67 (0.88)	1 (0.01)	8 (0.11)	1 (0.01)
Combined	525	72 (0.14)	49 (0.09)	64 (0.12)	141 (0.27)	124 (0.24)	73 (0.14)	2 (0.00)	90 (0.17)	77 (0.15)

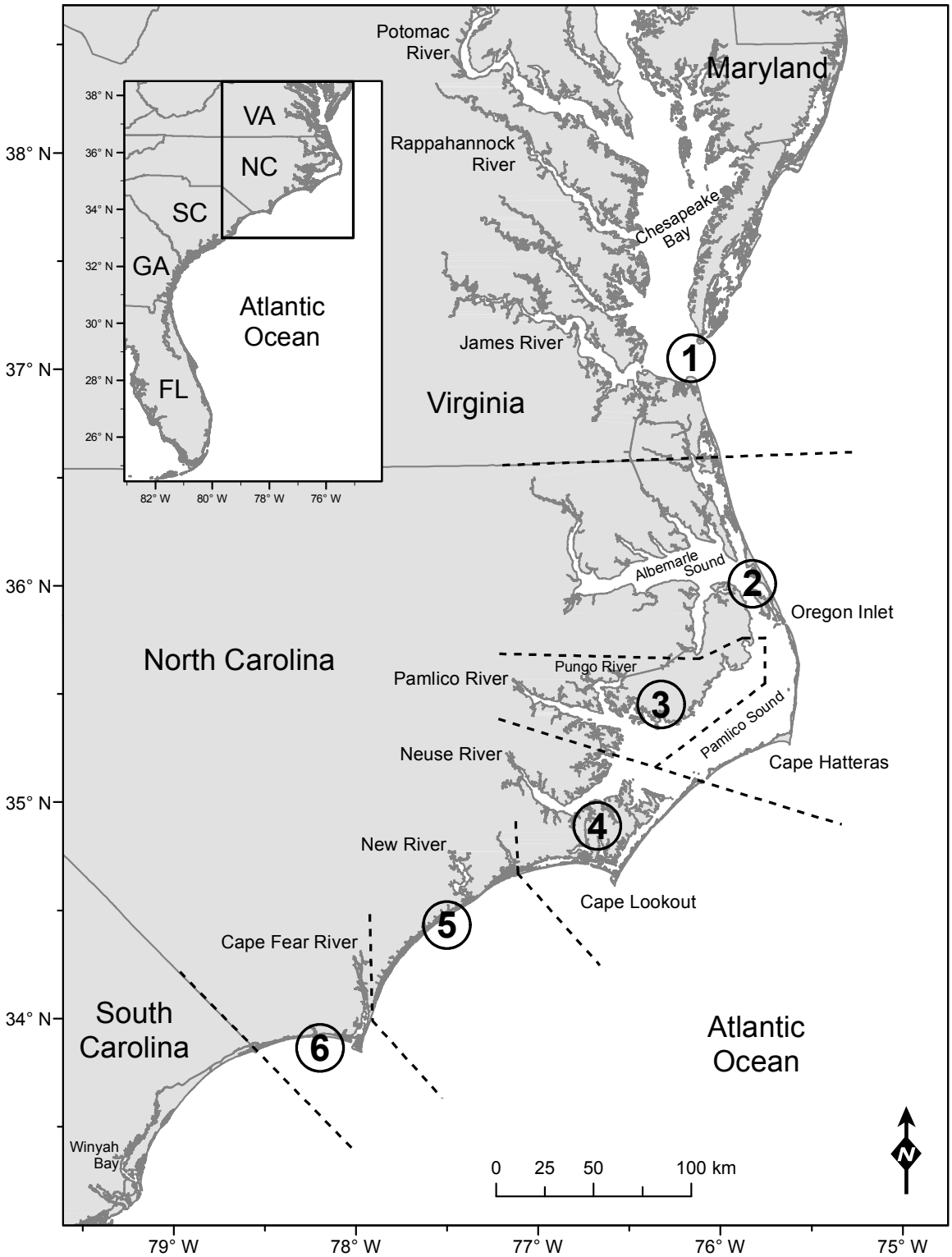


Figure 1. Regional boundaries (dashed lines) used to distribute tagging effort and to examine the movement patterns of spotted seatrout from September 2008 though October 2013. North Carolina, Virginia, Maryland (e.g., Potomac River), and South Carolina state lines are interjurisdictional boundaries for management.

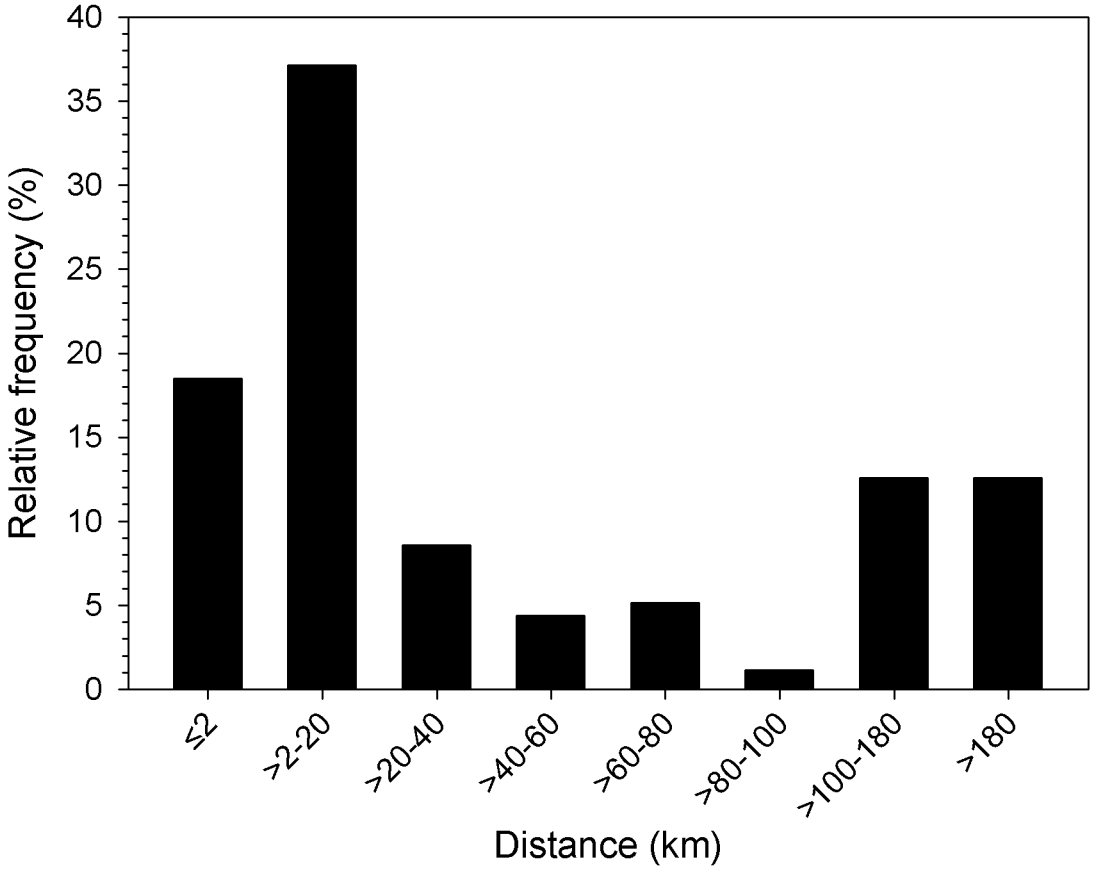


Figure 2. Frequency distribution of the linear distance (i.e., Euclidean pathway; km) moved by spotted seatrout between tagging and recovery locations. Of the 553 total tag returns in this study, 525 were reported with sufficient information to accurately estimate distance traveled.

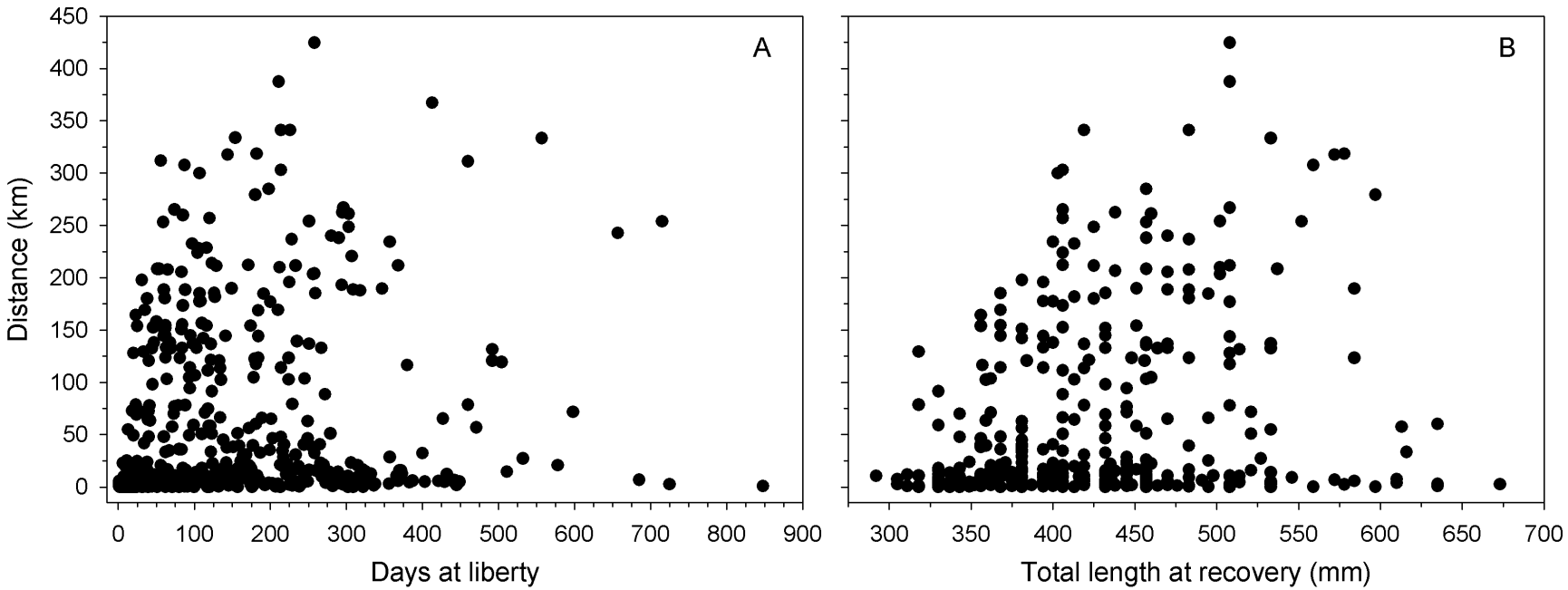


Figure 3. Correlation plots of the linear distance (i.e., Euclidean pathway; km) moved by spotted seatrout between tagging and recovery locations relative to (A) days at liberty (n = 507) and (B) fish total length at recapture (n = 370; mm). Samples sizes for each plot are lower than the total 553 tag returns due to incomplete reporting of all information necessary to estimate either exact days at liberty or fish size at time of recovery.

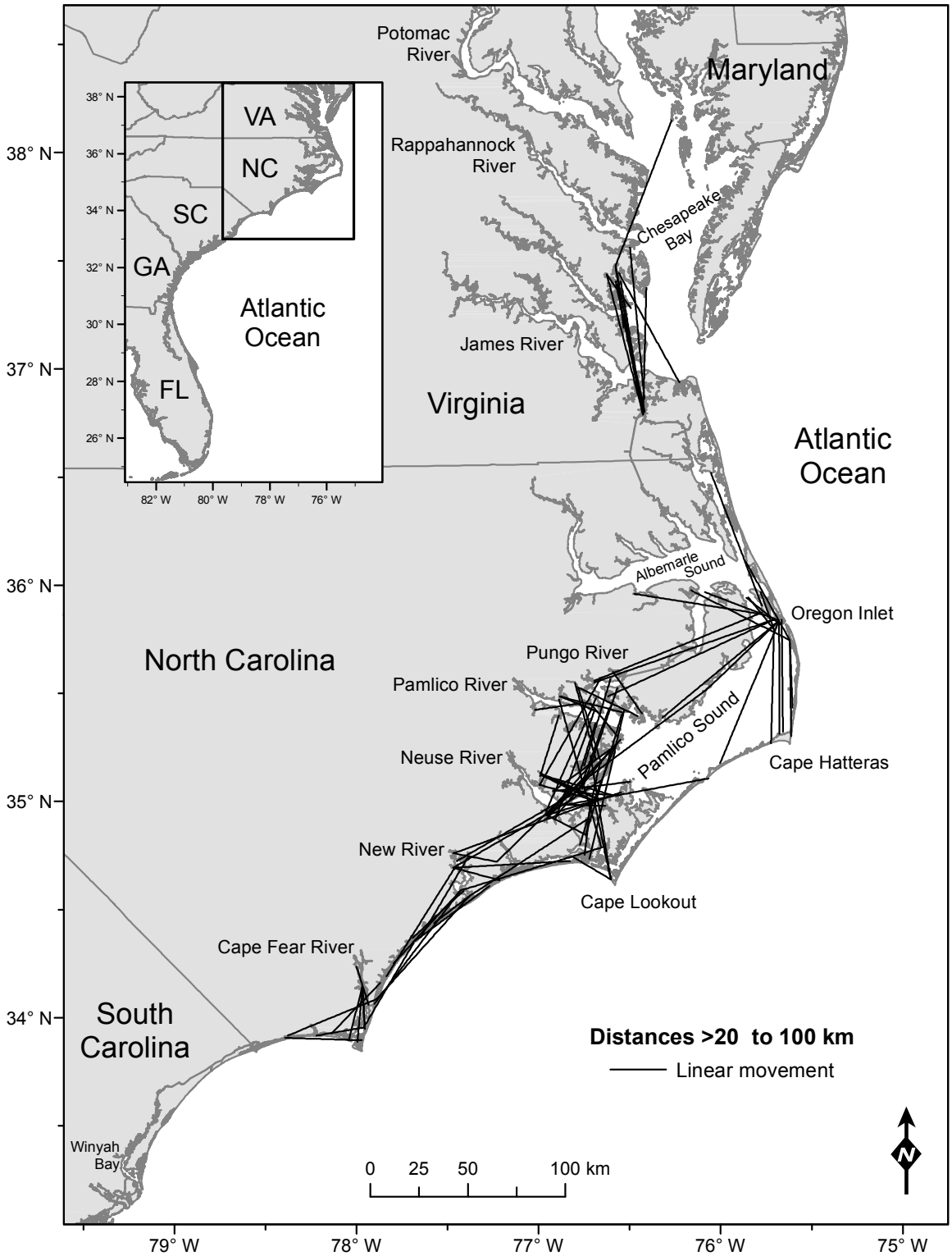


Figure 4. Small-scale (i.e., distances greater than 20 km and up to 100 km) linear movements of spotted seatrout (black vectors) determined from tag-return data collected from September 2008 through October 2013.

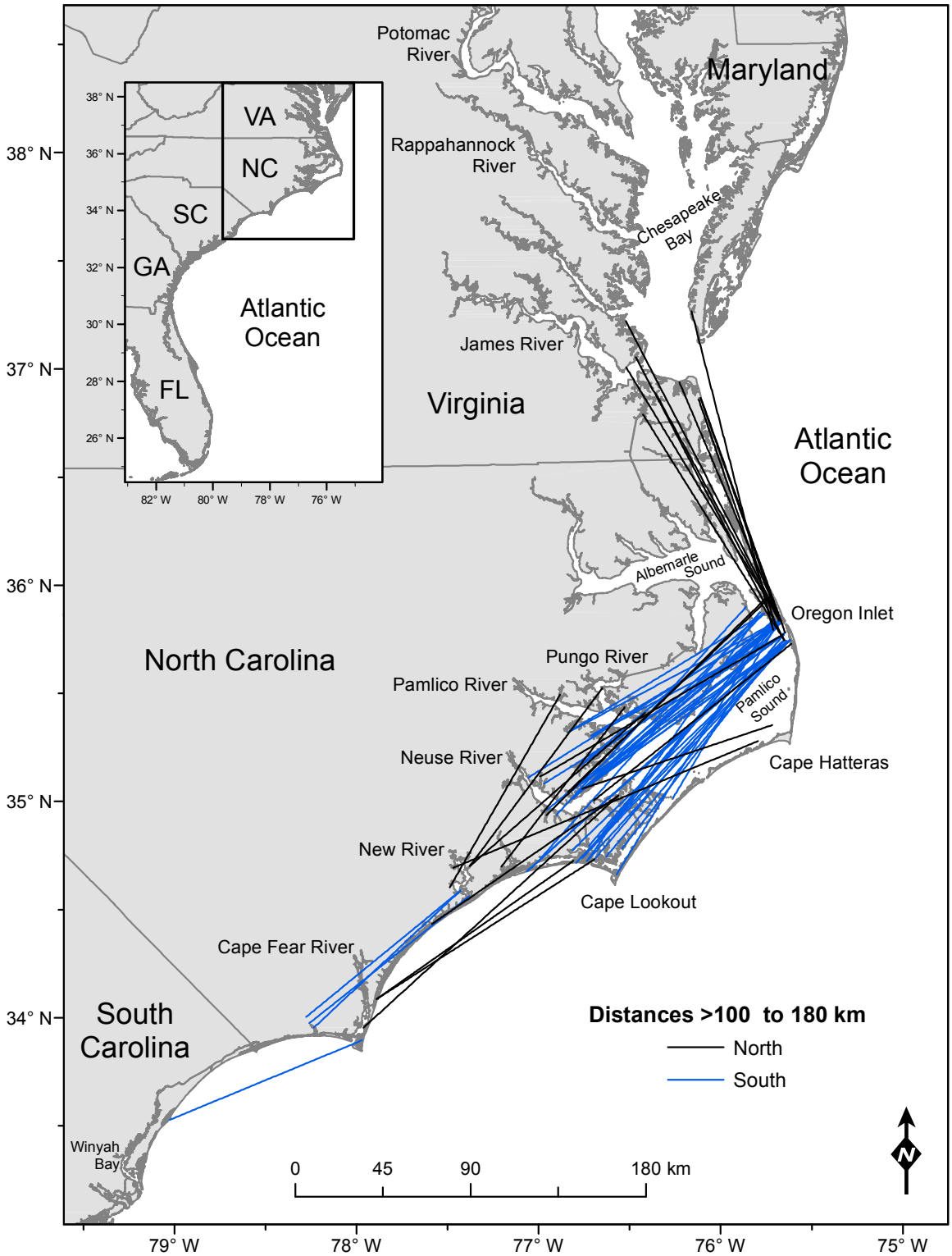


Figure 5. Large-scale (i.e., distances greater than 100 km and up to 180 km) linear movements of spotted seatrout (solid vectors) determined from tag-return data collected from September 2008 through October 2013. Black vectors indicate movements north from tagging locations and blue vectors indicate movements south.

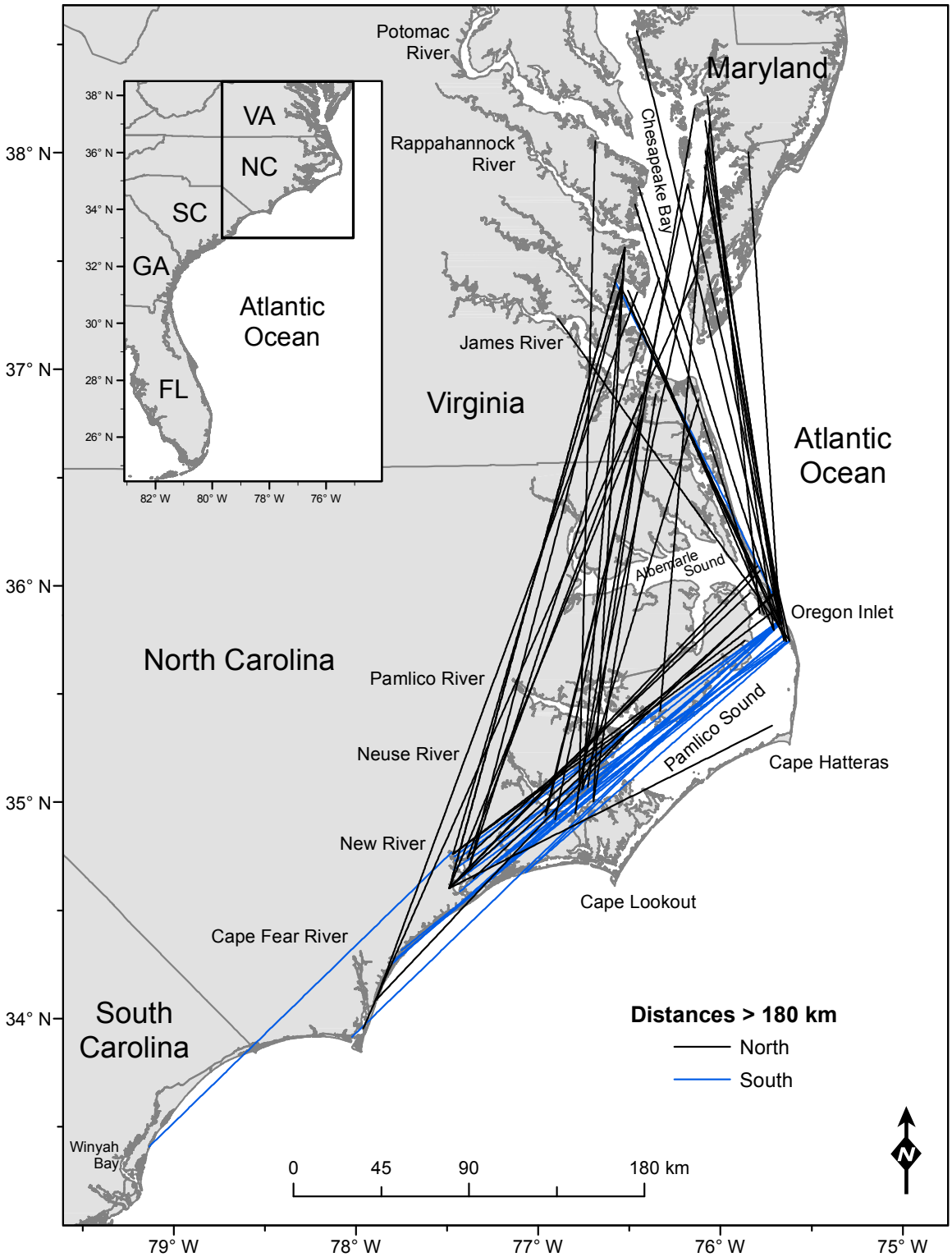


Figure 6. Coastwide (i.e., distances greater than 180 km) linear movements of spotted seatrout (solid vectors) determined from tag-return data collected from September 2008 through October 2013. Black vectors indicate movements north from tagging locations and blue vectors indicate movements south.

REFERENCES (ALL SECTIONS)

Adkins, G., J. Tarver, P. Bowman, and B. Savoie. 1979. A study of the commercial finfish in coastal Louisiana. Louisiana Department of Wildlife and Fisheries. Technical Bulletin 29: 1-87.

Anderson, J. D., and W. J. Karel. 2009. A genetic assessment of current management strategies for spotted seatrout in Texas. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 1: 121-132.

Anderson, J. D., and W. J. Karel. 2010. Population genetics and dynamics of spotted seatrout in the estuarine waters of Texas. Fisheries and Aquaculture Journal. FAJ-2: 1-19.

Arnoldi, D.C. 1984. Aspects of the biology of spotted seatrout in Calcasieu Lake, Louisiana, with management implications. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 38: 470-479.

Atlantic States Marine Fisheries Commission (ASMFC). 2012. Omnibus Amendment to the Interstate Fishery Mgmt. Plans for Spanish Mackerel, Spot, and Spotted Seatrout. Arlington, Virginia, USA. 161 pp.

Bacheler, N. M., J. E. Hightower, L. M. Paramore, J. A. Buckel, and K. H. Pollock. 2008. An age-dependent tag return model for estimating mortality and selectivity of an estuarine-dependent fish with high rates of catch and release. Transactions of the American Fisheries Society 137(5): 1422-1432.

Bacheler, N. M., L. M. Paramore, J. A. Buckel, and J. E. Hightower. 2009*a*. Abiotic and biotic factors influence the habitat use of an estuarine fish. Marine Ecology Progress Series 377: 263-277.

Bacheler, N. M., L. M. Paramore, S. M. Burdick, J. A. Buckel, and J. E. Hightower. 2009*b*. Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry. Fishery Bulletin 107: 405-419.

Bacheler, N. M., J. A. Buckel, J. E. Hightower, L. M. Paramore, and K. A. Pollock. 2009*c*. A combined telemetry-tag return approach to estimate fishing and natural mortality rates of an estuarine fish. Canadian Journal for Fisheries and Aquatic Sciences 66: 1230-1244.

Baker, W. B., G. C. Matlock, L. W. McEachron, A. W. Green, and H. E. Hegen. 1986. Movement, growth, and survival of spotted seatrout tagged in Bastrop Bayou, Texas. Contributions in Marine Science 29: 91-101.

Baker, W. B., and G. C. Matlock. 1993. Movement of spotted seatrout tagged in Trinity Bay, Texas. Northeast Gulf Science 13(1): 29-34.

Barrowman, N. J., and R. A. Myers. 1996. Estimating tag-shedding rates for experiments with multiple tag types. Biometrics 52: 1410-1416.

Beaumariage, D. S., and A. C. Wittich. 1966. Returns of the 1964 Schlitz tagging program. Florida Board of Conservation Marine Laboratory, St. Petersburg, Florida, USA. Technical Series 47. 51 pp.

Beaumariage, D. S. 1969. Returns of the 1965 Schlitz tagging program including a cumulative analysis of previous results. Florida Board of Conservation Marine Laboratory, St. Petersburg, Florida, USA. Technical Series 59. 38 pp.

Beitinger, T. L., W. A. Bennett, and R. W. McCauley. 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environmental Biology of Fishes 58: 237-275.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Vol. 19 of Fishery Investigations Series 2. United Kingdom Ministry of Agriculture, Fisheries, and Food, London, England. 533 pp.

Bortone, S. A. (Ed.). 2003. Biology of the spotted seatrout. CRC Press, Boca Raton, Florida, USA. 312 pp.

Bourgeois, M. J., V. Guillory, and H. Blanchet. 1995. A biological and fisheries profile for Louisiana spotted seatrout, *Cynoscion nebulosus*. Louisiana Department of Wildlife and Fisheries, Marine Fisheries Division, Baton Rouge, Louisiana, USA. Fishery Management Plan Series No. 3, Part 1. 101 pp.

Bowling, B. G., and A. L. Sunley. 2003. A summary of fish tagging on the Texas coast: November 1975-December 1999. Texas Parks and Wildlife Department, Coastal Fisheries Division, Austin, Texas, USA. Management Data Series No. 219. 40 pp.

Brenden, T. O., M. L. Jones, and M. P. Ebener. 2010. Sensitivity of tag-recovery mortality estimates to inaccuracies in tag shedding, handling mortality, and tag reporting. Journal of Great Lakes Research 36: 100-109.

Brodziak, J., J. Ianelli, K. Lorenzen, and R. D. Methot Jr. (Eds.). 2011. Estimating natural mortality in stock assessment applications. NOAA Technical Memorandum NMFS-F/SPO-119.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data: a handbook. United States Fish and Wildlife Service, Resource Publication No. 156. Washington, D.C., USA.

Brown-Peterson, N. J. 2003. The reproductive biology of spotted seatrout. *In*: Biology of the spotted seatrout. S. A. Bortone (Ed.). CRC Press, Boca Raton, Florida, USA. pp. 99-133.

Callihan, J. L., J. H. Cowan, Jr., and M. D. Harbison. 2013. Sex differences in residency of adult spotted seatrout in a Louisiana estuary. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 5: 79-92.

Carvalho, G. R., and L. Hauser. 1994. Molecular genetics and the stock concept in fisheries. Reviews in Fish Biology and Fisheries 4: 326-350.

Clark, W. G. 1999. Effects of an erroneous natural mortality rate on a simple age-structured stock assessment. Canadian Journal of Fisheries and Aquatic Sciences 56: 1721-1731.

Cowen, L., S. J. Walsh, C. J. Schwarz, N. Cadigan, and J. Morgan. 2009. Estimating exploitation rates of migrating yellowtail flounder (*Limanda ferrufinea*) using multistate mark-recapture methods incorporating tag loss and variable reporting rates. Canadian Journal of Fisheries and Aquatic Sciences 66: 1245-1255.

den Heyer, C. E., C. J. Schwarz, M. K. Trzcinski. 2013. Fishing and natural mortality rates of Atlantic halibut estimated from multiyear tagging and life history. Transactions of the American Fisheries Society 142: 690-702.

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. Fishery Bulletin 100(1): 35-41.

Donaldson, M. R., S. J. Cooke, D. A. Patterson, and J. S. Macdonald. 2008. Cold shock and fish. Journal of Fish Biology 73(7): 1491-1530.

Duffy, J. 2002. Catch-and-release mortality studies of spotted seatrout and red drum in coastal Alabama. *In*: Catch and release in marine recreational fisheries. J. A. Lucy and A. L. Studholme (Eds.). American Fisheries Society, Bethesda, Maryland, USA. pp. 110-113.

Dunning, D. J., Q. E. Ross, J. R. Waldman, and M. T. Mattson. 1987. Tag retention by, and tagging mortality of, Hudson River striped bass. North American Journal of Fisheries Management 7(4): 535-538.

Fabrizio, M. C., J. D. Nichols, J. E. Hines, B. L. Swanson, and S. T. Schram. 1999. Modeling data from double-tagging experiments to estimate heterogeneous rates of tag shedding in lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 56: 1409-1419.

Friedl, S. E., J. A. Buckel, J. E. Hightower, F. S. Scharf, and K. H. Pollock. 2013. Telemetry-based mortality estimates of juvenile spot in two North Carolina estuarine creeks. Transactions of the American Fisheries Society 142: 399-415.

Giese, G. L., H. B. Wilder, and G. G. Parker, Jr. 1979. Hydrology of major estuaries and sounds in North Carolina. United States Geological Survey Water Resources Investigation 79-46. Raleigh, North Carolina, USA. 175 pp.

Gilmore, R. G., L. H. Bullock, and F. H. Berry. 1978. Hypothermal mortality in marine fishes of south-central Florida January, 1977. Northeast Gulf Science 2(2): 77-97.

Glass, K. A., and B. D. Watts. 2009. Osprey diet composition and quality in high- and low-salinity areas of lower Chesapeake Bay. Journal of Raptor Research 43(1): 27-36.

Gold, J. R., L. B. Stewart, and R. Ward. 2003. Population structure of spotted seatrout (*Cynoscion nebulosus*) along the Texas Gulf Coast, as revealed by genetic analysis. *In*: Biology of the spotted seatrout, S. A. Bortone (ed.). CRC Press. Boca Raton, Florida, USA. pp. 17-29.

Green, A. W., L. W. McEachron, G. C. Matlock, and E. Hegen. 1990. Use of abdominal streamer tags and maximum-likelihood techniques to estimate spotted seatrout survival and growth. American Fisheries Society Symposium 7: 623-630.

Greenwood, M. 1926. The "errors of sampling" of the survivorship tables. Appendix 1. In: Report on Public Health and Medical Subjects. No. 33, London, UK: Her Majesty's Stationery Office.

Gulland, J. A. 1983. Fish stock assessment: a manual of basic methods. Wiley, New York, New York, USA.

Gunter, G. 1941. Death of fishes due to cold on the Texas coast, January, 1940. Ecology 22(2): 203-208.

Gunter, G., and H. H. Hildebrand. 1951. Destruction of fishes and other organisms on the south Texas coast by the cold wave of January 28-February 3, 1951. Ecology 32(4): 731-736.

Haddon, M. 2001. Modeling and quantitative methods in fisheries. Chapman and Hall/CRC, Boca Raton, Florida, USA. 406 pp.

Haeseker, S. L., J. T. Carmichael, and J. E. Hightower. 1996. Summer distribution and condition of striped bass within Albemarle Sound, North Carolina. Transactions of the American Fisheries Society 125: 690-704.

Hampton, J. 1996. Estimates of tag-reporting and tag-shedding rates in a large-scale tuna tagging experiment in the western tropical Pacific Ocean. Fishery Bulletin 95: 68-79.

Harms, C. A., and G. A. Lewbart. 2011. The veterinarian's role in surgical implantation of electronic tags in fish. Reviews in Fish Biology and Fisheries 21: 25-33.

Hearn, W. S., G. M. Leigh, and R. J. Beverton. 1991. An examination of a tag-shedding assumption, with application to southern bluefin tuna. ICES Journal of Marine Science 48(1): 41-51.

Hearn, W. S., K. H. Pollock, and E. N. Brooks. 1998. Pre-and post-season tagging models: estimation of reporting rate and fishing and natural mortality rates. Canadian Journal of Fisheries and Aquatic Sciences 55(1): 199-205.

Hegen, H. E., G. E. Saul, and G. C. Matlock. 1984. Survival of handled and tagged spotted seatrout held in wood and wire cages. Texas Parks and Wildlife Department, Coastal Fisheries Branch, Austin, Texas, USA. Management Data Series No. 61. 13 pp.

Helser, T. E., R. E. Condrey, and J. P. Geaghan. 1993. Spotted seatrout distribution in four coastal Louisiana estuaries. Transactions of the American Fisheries Society 122: 99-111.

Henderson-Arzapalo, A., P. Rago, J. Skjeveland, M. Mangold, P. Washington, J. Howe, and T. King. 2009. An evaluation of six internal anchor tags for tagging juvenile striped bass. North American Journal of Fisheries Management 19: 482-492.

Hendon, J. R., J. R. Warren, J. S. Franks, and M. V. Buchanan. 2002. Movements of spotted seatrout (*Cynoscion nebulosus*) in Mississippi coastal waters based on tag-recapture. Gulf of Mexico Science 2: 91-97.

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.

Hewitt, D. A., D. M. Lambert, J. M. Hoenig, R. N. Lipcius, D. B. Bunnell, and T. J. Miller. 2007. Direct and indirect estimates of natural mortality for Chesapeake Bay blue crab. Transactions for the American Fisheries Society 136: 1030-1040.

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.

Hightower, J. E., and K. H. Pollock. 2013. Tagging methods for estimating population size and mortality rates of inland striped bass populations. American Fisheries Society, Bethesda, Maryland, USA. Symposium 80: 249-262.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York, New York, USA. 570 pp.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 82: 898-903.

Hoenig, J. M., N. J. Barrowman, W. S. Hearn, and K. H. Pollock. 1998*a*. Multiyear tagging studies incorporating fishing effort data. Canadian Journal of Fisheries and Aquatic Science 55(6):1466-1476.

Hoenig, J. M., N. J. Barrowman, K. H. Pollock, E. N. Brooks, W. S. Hearn, and T. Polacheck. 1998*b*. Models for tagging data that allow for incomplete mixing of newly tagged animals. Canadian Journal of Fisheries and Aquatic Science 55(6): 1477-1483.

Hurst, T. P. 2007. Causes and consequences of winter mortality in fishes. Journal of Fish Biology 71(2): 315-345.

Hutton, R.F, R.M. Ingle, and R.W. Topp. 1962. Results of the tagging of salt water fishes in Florida. Florida Board of Conservation Marine Laboratory. St. Petersburg, Florida, USA. No. 62-2. 65 pp.

Hyun, S-Y., J. H. Reynolds, and P. F. Galbreath. 2012. Accounting for tag loss and its uncertainty in a mark-recapture study with a mixture of single and double tags. Transactions of the American Fisheries Society 141: 11-25.

Iversen, E. S., and A. W. Moffett. 1962. Estimation of abundance and mortality of a spotted seatrout population. Transactions of the American Fisheries Society 91(4): 395-398.

Iversen, E. S., and D. C. Tabb. 1962. Subpopulations based on growth and tagging studies of spotted seatrout, *Cynoscion nebulosus*, in Florida. Copeia 3: 544-548.

James, J. T., G. W. Stunz, and D. A. McKee. 2007. Catch-and-release mortality of spotted seatrout in Texas: effects of tournaments, seasonality, and anatomical hooking location. North American Journal of Fisheries Management 27: 900-907.

Jensen, C. C. 2009. Stock status of spotted seatrout, *Cynoscion nebulosus*, in North Carolina, 1991-2008. North Carolina Division of Marine Fisheries. Morehead City, North Carolina, USA. 89 pp.

Jepsen, N., K. Aarestrup, F. Okland, and G. Rasmussen. 1998. Survival of radio-tagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. Hydrobiologia 371/372: 347-353.

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(2): 387-396.

Johnson, D. R., N. A. Funicelli, and J. A. Bohnsack. 1999. Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. North American Journal of Fisheries Management 19: 436-453.

Kalbfleisch, J. D., and R. L. Prentice. 2002. The Statistical Analysis of Failure Time Data. Second Edition. John Wiley & Sons, Inc., New York, New York, USA.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53: 457-481.

Kleiber, P., A. W. Argue, and R. E. Kearney. 1987. Assessment of Pacific skipjack tuna (*Katsuwanus pelamis*) resources by estimating standing stock and components of population turnover from tagging data. Canadian Journal of Fisheries and Aquatic Sciences 58: 1716-1726.

Laikre, L., S. Palm, and N. Ryman. 2005. Genetic population structure of fishes: implications for coastal zone management. AMBIO: A Journal of the Human Environment 34(2): 111-119.

Latour, R. J., K. H. Pollock, C. A. Wenner, and J. M. Hoenig. 2001*a*. Estimates of fishing and natural mortality for subadult red drum in South Carolina waters. North American Journal of Fisheries Management 21: 733-744.

Latour, R. J., J. M. Hoenig, J. E. Olney, and K. H. Pollock. 2001*b*. Diagnostics for multiyear tagging models with application to Atlantic striped bass (*Morone saxatilis*). Canadian Journal of Fisheries and Aquatic Sciences 58: 1716-1726.

Lawson, J. 1709. A new voyage to Carolina. Chapel Hill: University of North Carolina Press, 1967 (reprint of 1709 original).

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.

Lunn, D., D. Spiegelhalter, A. Thomas, and N. Best. 2009. The BUGS project: evolution, critique and future directions. Statistics in Medicine 28: 3049-3082.

Markham, A. C. 2004. The influence of salinity on diet composition, provisioning patterns, and nestling growth in bald eagles in the lower Chesapeake Bay. M.A. thesis. The College of William and Mary, Williamsburg, Virginia, USA. 127 pp.

Martin, J. H., and L. W. McEachron. 1996. Historical annotated review of winter kills of marine organisms in Texas bays. Texas Parks and Wildlife Department, Coastal Fisheries Division, Austin, Texas, USA. Management Data Series No. 118. 20 pp.

Marwitz, S. R. 1986. A summary of fish tagging in Texas bays, 1975-1982. Texas Parks and Wildlife Department, Coastal Fisheries Branch, Austin, Texas, USA. Management Data Series Number 66. 45 pp.

Matlock, G. C. 1992. Growth of five fishes in Texas bays in the 1960s. Fishery Bulletin 90: 407-411.

Matlock, G. C., L. W. McEachron, J. A. Dailey, P. A. Unger, and P. Chai. 1993. Short-term hooking mortalities of red drums and spotted seatrout caught on single-barb and treble-hooks. North American Journal of Fisheries Management 13:186-189.

Maunder, M. N., and R. A. Wong. 2011. Approaches for estimating natural mortality: application to summer flounder (*Paralichthys dentatus*) in the U.S. mid-Atlantic. Fisheries Research 111: 92-99.

McCarthy, M. A. 2007. Bayesian methods for ecology. Cambridge University Press, Cambridge, UK. 296 pp.

McEachron, L. W., G. C. Matlock, C. E. Bryan, P. Unger, T. J. Cody, and J. H. Martin. 1994. Winter mass mortality of animals in Texas bays. Northeast Gulf Science 13(2): 121-138.

Miller, J. M., J. S. Burke, and G. R. Fitzhugh. 1991. Early life history patterns of Atlantic North American flatfish: likely (and unlikely) factors controlling recruitment. Netherlands Journal of Sea Research 27(3/4): 261-275.

Miranda, L. E., R. E. Brock, and B. S. Dorr. 2002. Uncertainty of exploitation estimates made from tag returns. North American Journal of Fisheries Management 22: 1358-1363.

Moffett, A. W. 1961. Movements and growth of spotted seatrout, *Cynoscion nebulosus* (Cuvier), in West Florida. Florida Board of Conservation, Tallahassee, Florida, USA. Technical Series No. 36. 35 pp.

Moore, R. H. 1976. Observations on fishes killed by cold at Port Aransas, Texas, 11-12 January 1973. The Southwestern Naturalist 20(4): 461-466.

Murphy, M. D., and R. G. Taylor. 1994. Age, growth, and mortality of spotted seatrout in Florida waters. Transactions of the American Fisheries Society 123: 482-497.

Murphy, M. D., R. F. Heagey, V. H. Neugebauer, M. D. Gordon, and J. L. Hintz. 1995. Mortality of spotted seatrout released from gill-net or hook-and-line gear in Florida. North American Journal of Fisheries Management 15: 748-753.

Murphy, M. D., D. Chagaris, and D. Addis. 2011. An assessment of the status of spotted seatrout in Florida waters through 2009. Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institue, St. Petersburg, Florida, USA. 53 pp.

Music, J. L., and J. M. Pafford. 1984. Population dynamics and life history aspects of major marine sportfishes in Georgia's coastal waters. Georgia Department of Natural Resources, Coastal Resources Division, Brunswick, Georgia, USA. Contribution Series No. 38. 382 pp.

Musick, S., and L. Gillingham. 2013. Virginia Game Fish Tagging Program Annual Report. Virginia Institute of Marine Science Marine Resource Report No. 2013-3, VSG-13-12, Gloucester Point, Virginia, USA. 94 pp.

Nichols, J. D., R. J. Blohm, R. E. Reynolds, R. E. Trost, J. E. Hines, and J. P. Bladen. 1991. Band reporting rates for mallards with reward bands of different dollar values. Journal of Wildlife Management 55: 119-126.

Nieland, D. L., R. G. Thomas, and C. A. Wilson. 2002. Age, growth, and reproduction of spotted seatrout in Barataria Bay, Louisiana. Transactions of the American Fisheries Society 131: 245-259.

North Carolina Division of Marine Fisheries (NCDMF). 2011*a*. Proclamation FF-7-2011. NCDMF, Morehead City, North Carolina, USA. 1 pp.

North Carolina Division of Marine Fisheries (NCDMF). 2011*b*. Proclamation FF-30-2011. NCDMF, Morehead City, North Carolina, USA. 1 pp.

North Carolina Division of Marine Fisheries (NCDMF). 2012. North Carolina Spotted Seatrout Fishery Management Plan. Morehead City, North Carolina, USA. 344 pp.

O'Donnell, T. 2013. Characterizing the genetic population structure of and genetic effects of cold winters on spotted seatrout (*Cynoscion nebulosus*) in the southeastern United States. M.S. Thesis. College of Charleston, Charleston, South Carolina, USA. 79 pp.

Overstreet, R. M. 1983. Aspects of the biology of the spotted seatrout, *Cynoscion nebulosus*, in Mississippi. Gulf Research Reports, Supplement 1: 1-43.

Pascual, M. A., and O. O. Iribarne. 1993. How good are empirical predictions of natural mortality? Fisheries Research 16(1): 17-24.

Patterson, H. M., R. S. McBride, and N. Julien. 2004. Population structure of red drum (*Sciaenops ocellatus*) as determine by otolith chemistry. Marine Biology 144: 855-862.

Pattillo, M. E., T. E. Czapla, D. M. Nelson, and M. E. Monaco. 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life histories summaries. Estuarine Living Marine Resources Report No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, Maryland, USA. 377 pp.

Pine, W. E., J. E. Hightower, L. G. Coggins, M. V. Lauretta, and K. H. Pollock. 2012. Design and analysis of tagging studies. I*n* A. V. Zale, D. L. Parrish, and T. M. Sutton (Eds.). Fisheries Techniques, Third Edition. American Fisheries Society, Bethesda, Maryland, USA. pp 521-572.

Polacheck, T., J. P. Eveson, G. M. Laslett, K. H. Pollock, and W. S. Hearn. 2006. Integrating catch-at-age and multiyear tagging data: a combined Brownie and Petersen estimation approach in a fishery context. Canadian Journal of Fisheries and Aquatic Sciences 63(3): 534-548.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53(1): 7-15.

Pollock, K. H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. Journal of the American Statistical Association 86: 225-238.

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. American Fisheries Society, Bethesda, Maryland, USA. Symposium 12: 423-434.

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., 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(3): 639-648.

Pollock, K. H., and W. E. Pine. 2007. The design and analysis of field studies to estimate catch-and-release mortality. Fisheries Management and Ecology 14(2): 123-130.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press, Inc., New York, New York, USA. 542 pp.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191. 382 pp.

Rogillio, H. E. 1980. Movement and migration of the spotted seatrout in southeast Louisiana. Louisiana Department of Wildlife and Fisheries, New Orleans, Louisiana, USA. Completion Report D-J Project F-33. 19 pp.

Rogillio, H. E. 1985. Movement study of estuarine sportfish. Louisiana Department of Wildlife and Fisheries, New Orleans, LA, USA. Completion Report D-J Project F-41. 40 pp.

Rooker, J. R., G. W. Stunz, S. A. Holt, and T. J. Minello. 2010. Population connectivity of red drum in the northern Gulf of Mexico. Marine Ecology Progress Series 407: 187-196.

Rutherford, E. S., J. T. Tilmant, E. B. Thue, and T. W. Schmidt. 1989. Fishery harvest and population dynamics of spotted seatrout, *Cynoscion nebulosus*, in Florida Bay and adjacent waters. Bulletin of Marine Science 44(1): 108-125.

Schwartz, M. K., G. Luikart, and R. S. Waples. 2006. Genetic monitoring as a promising tool for conservation and management. Trends in Ecology and Evolution 22: 25-33.

Simmons, E. G. 1957. An ecological survey of the Upper Laguna Madre of Texas. Publications of the Institute of Marine Science, University of Texas 4(2): 156-200.

Smith, H. M. 1907. The Fishes of North Carolina (Vol. 2). EM Uzzell & Co. 453 pp.

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(5): 886-897.

Smith, W. E., F. S. Scharf, and J. E. Hightower. 2009. Fishing mortality in North Carolina's southern flounder fishery: direct estimates of instantaneous fishing mortality from a tag return experiment. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 1(1): 283-299.

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(2): 461-464.

Stevens, P. W., and K. J. Sulak. 2001. Egress of adult sport fish from an estuarine fish replenishment zone within Merritt Island National Wildlife Refuge, Florida. Gulf of Mexico Science 2: 77-89.

Storey, M., and E. W. Gudger. 1936. Mortality of fishes due to cold at Sanibel Island, Florida, 1886-1936. Ecology 17(4): 640-648.

Stunz, G. W., and D. A. McKee. 2006. Catch-and-release mortality of spotted seatrout in Texas. North American Journal of Fisheries Management 26: 843-848.

Tabb, D. C. 1958. Differences in the estuarine ecology of Florida waters and their effect on populations of the spotted weakfish, *Cynoscion nebulosis* (Cuvier and Valenciennes). Transactions of the 23rd North American Wildlife Conference. Wildlife Management Institute, Washington, D.C., USA. pp. 392-401.

Tabb, D. C., and R. B. Manning. 1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July, 1957 through September, 1960. Bulletin of Marine Science 11(1): 552-649.

Taylor, R. G., J. A. Whittington, W. E. Pine, III, and K. H. Pollock. 2006. Effect of different reward levels on tag reporting rates and behavior of common snook anglers in Southeast Florida. North American Journal of Fisheries Management 26: 645-651.

Therneau, T. 2012. A package for survival analysis in S. R package version 2.36-14.

Thompson, J. S., D. S. Waters, J. A. Rice, and J. E. Hightower. 2007. Seasonal natural and fishing mortality of striped bass in a southeastern reservoir. North American Journal of Fisheries Management 27: 681-694.

Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal homing in a marine fish metapopulation. Science 291(5502): 297-299.

Tremain, D. M., C. W. Harnden, and D. H. Adams. 2004. Multidirectional movements of sportfish species between an estuarine no-take zone and surrounding waters of the Indian River Lagoon, Florida. Fisheries Bulletin 102: 533-544.

VanderKooy, S. J. (Ed.). 2001. The spotted seatrout fishery of the Gulf of Mexico, United States: a regional management plan. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi, USA. Publication No. 87. 204 pp.

VanderKooy, S. J., and R. G. Muller. 2003. Management of spotted seatrout and fishery participants in the U.S.. *In*: Biology of the spotted seatrout, S. A. Bortone (Ed.). CRC Press, Boca Raton, Florida, USA. pp. 227-245.

Vetter, E. F. 1988. Estimation of natural mortality if fish stocks: a review. Fishery Bulletin 86: 25-43.

Vogelbein, W. K., and R. M. Overstreet. 1987. Histopathology of the internal anchor tag in spot and spotted seatrout. Transactions of the American Fisheries Society 116: 745-756.

Wakeman, J. M., and P. R. Ramsey. 1985. A survey of population characteristics for red drum and spotted seatrout in Louisiana. Gulf Research Reports 8(1): 1-8.

Ward, R. D. 2000. Genetics in fisheries management. Hydrobiologia 420: 191-201.

Ward, R., K. Bowers, R. Hensley, B. Mobley, and E. Belouski. 2007. Genetic variability in spotted seatrout (*Cynoscion nebulosus*), determined with microsatellite DNA markers. Fishery Bulletin 105: 197-206.

Waters, D. S., R. L. Noble, and J. E. Hightower. 2005. Fishing and natural mortality of adult largemouth bass in a tropical reservoir. Transactions of the American Fisheries Society 134(3): 563-571.

Watts, B. D., and B. J. Paxton. 2007. Ospreys of the Chesapeake Bay: population recovery, ecological requirements, and current threats. Waterbirds 30(Special Publication 1): 39-49.

Welsch, W. W., and C. M. Breder, Jr. 1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bulletin of the U.S. Bureau of Fisheries 39: 141-201.

Wenner, C. A., W. A. Roumillat, J. E. Moran, Jr., M. B. Maddox, L. B. Daniel, III, and J. W. Smith. 1990. Investigations on the life history and population dynamics of marine recreational fishes in South Carolina: Part 1. South Carolina Wildlife and Marine Resources Department, Charleston, South Carolina, USA. Final Report for Federal Aid in Fish Restoration Act Project F-37. 177 pp.

Wenner, C., and J. Archambault. 1996. Spotted seatrout: natural history and fishing techniques in South Carolina. South Carolina Department of Natural Resources, Marine Resources Division, Charleston, South Carolina, USA. Educational Report No. 18. 52 pp.

Wetherall, J. A. 1982. Analysis of double-tagging experiments. Fishery Bulletin 80(4): 687-701.

Wiggers, R. K. 2010. South Carolina marine game fish tagging program: 1978-2009. South Carolina Department of Natural Resources, Marine Resources Division, Charleston, South Carolina, USA. 60 pp.

Wilcox, J. 1887. Fish killed by cold along the Gulf of Mexico and coast of Florida. Bulletin of the United States Fish Commission 6: 123.

Wiley, B. A., and R. W. Chapman. 2003. Population structure of spotted seatrout, *Cynoscion nebulosus*, along the Atlantic Coast of the U.S. *In*: Biology of the spotted seatrout, S. A. Bartone (Ed.), CRC Press. Boca Raton, Florida, USA. pp. 31-40.

Williams, E. H. 2002. The effects of unaccounted discards and mis-specified natural mortality on harvest policies based on estimates of spawner per recruit. North American Journal of Fisheries Management 22(1): 311-325.

Wilson, M. M., T. M. Bert, and S. Seyoum. 2002. Genetic stock structure of the spotted seatrout, *Cynoscion nebulosus*, in Florida. Florida Marine Research Institute Report No. IHR2002-005. St. Petersburg, Florida, USA. 15 pp.

Woodward, A. G., J. M. Pafford, and N. Nicholson. 1990. Exploitation, movement, and growth of spotted seatrout in coastal Georgia. Georgia Department of Natural Resources, Coastal Resources Division, Recreational Fisheries Program. Brunswick, Georgia, USA. Contribution Series 52. 38 pp.

Woodward, A. G., and D. J. Mericle. 1995. Exploitation and stock structure of spotted seatrout in coastal Georgia. Georgia Department of Natural Resources, Coastal Resources Division, Brunswick, Georgia, USA. Final Report for Federal Aid in Fish Restoration Act Project F-31. 43 pp.

Wuenschel, M. J., J. A. Hare, M. E. Kimball, and K. W. Able. 2012. Evaluating juvenile thermal tolerance as a constraint on adult range of gray snapper (*Lutjanus griseus*): A combined laboratory, field and modeling approach. Journal of Experimental Marine Biology and Ecology 436-437: 19-27.

Youngs, W. D., and D. S. Robson. 1975. Estimating survival rates from tag returns: model tests and sample size determination. Journal of the Fisheries Research Board of Canada 32: 2365-2371.

ACKNOWLEDGEMENTS

This study required extensive collaboration between academic researchers, managers, and fishery participants. Most importantly was the assistance with tagging received from the following professional fishing guides and accomplished anglers: Capt. Donnie Davis, Capt. Gary Dubiel, Capt. Brian Horsley, Capt. Ricky Kellum, Capt. Ed Lawrence, Jon Lucy, Capt. David Mason, Capt. Dave Stewart, Brad Tayloe, and Capt. Dave Watkins. Tyler Averett and Stephen Poland provided essential technical assistance with all field and lab duties throughout this study. David Mason graciously provided housing, field assistance, and other logistical support in the Pungo River. Ricky Kellum assisted with collecting fish for laboratory experiments. Dr. Eric Anderson, Dr. Craig Harms, Skip Kemp, and Dana Schmidt provided expertise and guidance on fish husbandry and surgical procedures. Greg Bolton, Brian Efland, Anthony Frost, Ben Kornegay, Jeffrey Merrell, Dr. John Miller (deceased), Rick Patterson, and Paul Rudershausen also provided field, laboratory, or logistical support. Numerous NCDMF personnel collected survey and aging data, and in particular, Beth Burns (retired), Chip Collier, Carol Etheridge, Marc Hamric, Christine Jensen, Greg Judy (retired), Lele Judy (retired), Mike Loeffler, Lee Paramore, Jason Rock, and David Skinner directly assisted NCSU researchers during this tagging study. In addition to proceeds from sales of the NC Coastal Recreational Fishing License, NC Sea Grant (No. 08-FEG-06) provided funding for early data used in this report (i.e., 2008-2009 tagging). NCSU, the Raleigh Saltwater Sportfishing Club, the NC Wildlife Federation, and the NC Chapter of the Coastal Conservation Association provided additional scholarship support for Tim Ellis. Baits used by NCSU researchers to collect spotted seatrout by hook-and-line for tagging were generously donated by the following: Berkley® (Gulp!®), Betts®, D.O.A.™, Sea Striker (Got-cha®), MirrOlure®, Smithwick®, and Storm®.