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**An integrated tagging model to estimate mortality rates of Albemarle Sound-Roanoke
River striped bass**

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Abstract

We developed an integrated tagging model to estimate mortality rates and run sizes of Albemarle Sound-Roanoke River striped bass (*Morone saxatilis*) including: 1) a multistate component for telemetered fish with a high reward external tag; 2) tag return components for fish with a low reward external or PIT tag; and 3) catch-at-age data. Total annual instantaneous mortality was 1.08 for resident (458-899 mm TL) and 0.45 for anadromous (≥ 900 mm TL) individuals. Annual instantaneous natural mortality was higher for resident (0.70) than anadromous (0.21) fish due to high summer mortality in Albemarle Sound. Natural mortality for residents was substantially higher than currently assumed for stock assessment. Monthly fishing mortality from multiple sectors (including catch and release) corresponded to seasonal periods of legal harvest. Run size estimates were 499-715 thousand. Results and simulation suggest increasing sample size for the multistate component increases accuracy and precision of annual estimates and low reward tags are valuable for estimating monthly fishing mortality rates among sectors. Our results suggest that integrated tagging models can produce seasonal and annual mortality estimates needed for stock assessment and management.

Introduction

Accurate and precise estimates of fishing and natural mortality are essential for fisheries management, but can be challenging to obtain, especially for migratory species that support multiple fisheries. Rates have effectively been estimated by external and internal tag studies (Pollock et al. 2004; Bacheler et al. 2009; Hightower and Pollock 2013; Kerns et al. 2016). Typically, tag studies use a fisheries-dependent approach, in which an externally-visible tag can be reported when the fish is caught. With data on tag reporting rate, reported tags directly inform on fishing mortality rates; however, tag returns are less informative for estimating natural mortality rates since both natural deaths and live fish are not observed. Changes in reporting rate and periods without harvest make examining seasonal patterns in natural mortality difficult or impossible. In contrast, internal tags such as passive integrated transponder (PIT) and acoustic tags are often only detected by scientists and mortality is assessed by the pattern of tag detection. Natural mortality can be detected in small, searchable systems, by repeatedly detecting a non-moving acoustic tag, but fishing mortality is usually only assessed indirectly by the disappearance of a tagged fish (Hightower et al. 2001; Hightower and Pollock 2013). With only internal tags, mortality rates from multiple fisheries cannot be differentiated and natural mortality cannot be differentiated from catch and release mortality. Thus, a study incorporating a single approach may not directly produce all needed information for a stock that supports multiple fisheries over an extensive and unsearchable geographic area, such as Albemarle Sound-Roanoke River (AS-RR) striped bass, *Morone saxatilis*.

Striped bass support intensive and economically valuable fisheries in many rivers and coastal areas along the Atlantic Coast in Canada and the USA (Patrick et al. 2006). Fisheries for the AS-RR stock are managed in North Carolina by a total allowable catch, seasonal open periods, length limits, bag limits, and gear limits. Legally, striped bass can be harvested (commercially and recreationally) in Albemarle and Pamlico sounds October 1 to April 30 if they are 458 mm TL (i.e., 18 inches) or larger. Spawning occurs in the Roanoke River in March-May

(Hassler et al. 1981; Carmichael et al. 1998) and striped bass can be recreationally harvested in the Roanoke River in March-April. In the Roanoke River, the minimum size limit is 458 mm TL and there is an exclusive slot of 559-686 mm TL (i.e., 22-27 inches). Despite extensive research on this stock, an assumed rate for annual natural mortality is currently used for stock assessment; information on natural and fishing mortality rates would improve management of this valuable species and stock (Takade-Heumacher 2010; Mroch and Godwin 2014).

In many populations, the probability that an individual striped bass is anadromous increases with fish size (Callihan et al. 2014). For the AS-RR stock, most juvenile and small mature striped bass remain in the AS-RR throughout the year. Individuals can become anadromous at 600 mm total length (TL), although most do not conduct coastal migrations until 800-900 mm TL (Haeseker et al. 1996; Callihan et al. 2014; Callihan et al. 2015). Anadromous individuals migrate in the Atlantic Ocean as far north as Massachusetts during non-spawning periods, only returning to the AS-RR for about a month during the spawning run (Callihan et al. 2014; Callihan et al. 2015). Despite spatial overlap with other Atlantic coast striped bass populations during non-spawning periods, the AS-RR population is considered a distinct stock (Waldman et al. 2012; Gauthier et al. 2013; Kneebone et al. 2014) and anadromous individuals from the AS-RR stock return annually to spawn in the Roanoke River (Callihan et al. 2015). Considering vast differences in behavior, it is unclear if anadromous individuals experience mortality rates similar to AS-RR residents.

We developed integrated tagging models to estimate mortality rates and run sizes of resident and anadromous AS-RR striped bass to aid assessment and management of this important stock. Integrated models jointly analyze multiple independent datasets to estimate a variety of demographic parameters. Using an integrated model to estimate common parameters can increase estimate precision; however, integrated models can also estimate parameters inestimable by only one likelihood component (Abadi et al. 2010; Maunder and Punt 2013). We developed the first integrated tagging model to combine: 1) passive sonic detections

on stationary receivers with returns of high reward external tags evaluated by a multistate submodel; 2) low reward external tags and passive integrated transponder (PIT) tags with harvest data, evaluated using tag return submodels; and 3) catch-at-age data evaluated by a catch curve submodel (Fig. 1). We also used simulation to evaluate accuracy and precision of an integrated tagging model including passive detections of fish with sonic tags and high reward external tags and other fish with low reward external tags. Specific objectives were to: 1) estimate seasonal natural mortality and monthly fishing mortality rates for AS-RR striped bass; 2) produce run-size estimates for striped bass in the Roanoke River; 3) compare mortality rates of resident AS-RR striped bass to those of anadromous individuals in the stock; and 4) evaluate accuracy and precision of an integrated tagging model to estimate seasonal (i.e., to understand mortality biologically) and annual (i.e., to aid stock assessment) mortality rates. Our study is the first to evaluate how this type of integrated model including a combination of passive detections of sonic tags and returns of high and low reward tags can be used to estimate seasonal natural mortality rates, fishing mortality rates from multiple sectors, and run sizes. Our approach was very useful for estimating mortality rates and stock status for AS-RR striped bass and would similarly be useful for other fish populations that are migratory, have an extensive (i.e., manually unsearchable) range, or support multiple fisheries.

Methods

Field sampling

For sonic and high (\$100) reward tagging, 143 striped bass (445-695 mm TL) were caught by hook and line and commercial pound net in western Albemarle Sound February-April, 2011 and 2012 (Table 1; Fig. 2). In addition, two males (750 and 873 mm TL) and 14 females (939-1146 mm TL) were collected by electrofishing in April and May of 2011 and 2012 on the spawning grounds in Weldon for sonic and high reward tagging (Fig. 2). To implant a Vemco V13-L sonic tag (13 mm diameter, 36 mm length, and 11 g in air) and a 23 mm half duplex PIT

tag, each striped bass was anaesthetized with buffered MS-222, measured for TL, and placed in a cradle with its gills submerged in water. In 2011, sonic tags had a random delay (i.e., time between signal submissions or “pings”) of 30-90 seconds and an expected battery life of 622 days; in 2012, the random delay was 60-120 seconds and the battery life was 880 days. To implant the internal tags (i.e., sonic and PIT), a small incision (~2 cm) was made on the fish’s ventral side between the pelvic and pectoral fins. After implantation, this incision was closed by 2-3 interrupted sutures with two wraps on each throw (Deters et al. 2012). Another small incision (<1 cm) was made on the left side below the musculature for a high (\$100) reward internal anchor tag.

Returns and detections of sonic and high reward tagged striped bass contributed to estimates of mortality. External high reward tags had instructions to cut the tag and call North Carolina State University (NCSU) for the reward, then keep or release the fish, as planned. We assumed that each captured striped bass with a high reward tag was reported and that the information reported regarding capture was without error. Specifically, we assumed that a reward of \$100 was sufficient to ensure a reporting rate of 100%, as assumed by tag return studies of similar fisheries (Latour et al. 2001; Bacheler et al. 2009). When called by an angler or fisher, we asked if the striped bass was commercially or recreationally caught, kept or released, as well as the location and date of capture. Anglers and fishers were required to send the cut tag to NCSU to receive the \$100 reward and were sent any tagging and migration information about the reported striped bass.

Sonic tags were continuously monitored throughout the study period by stationary receivers (Vemco VR2s) in the AS-RR system (Fig. 2). In addition, four of our striped bass (558-609 mm TL) were detected in the Pamlico Sound system (Tim Ellis, NCSU) and all large females (i.e., ≥900 mm TL) were detected by VR2s along the Atlantic Coast as far north as Massachusetts (i.e., Virginia, Delaware, New York and Massachusetts; Keith Dunton, Stony Brook University; Dewayne Fox, Delaware State University; Benjamin Gahagan and William

Hoffman, Massachusetts Division of Marine Fisheries; Mary-Jane James-Pirri, University of Rhode Island; and Carter Watterson, U.S. Department of the Navy). We also conducted manual tracking (i.e., actively searching an area for an acoustically tagged fish) in the AS-RR system to identify mortality associated with tagging and natural mortality. Mortality from tag implantation surgery was assumed when an individual was continuously detected by manual tracking in the same location within the month of tagging; these fish were removed from analysis. Natural mortality was assumed when an individual was continuously found in one area, but after the month of tagging and in a new location, suggesting active movement before dying (Hightower et al. 2001).

For low reward (\$5 or a hat) and PIT tagging, striped bass were collected by boat electrofishing at Weldon (Fig. 2), March-May, 2011-2013, measured for TL, examined for an external tag and scanned for a PIT tag. Detected PIT tags were recorded. If an internal anchor tag was observed, we recorded if it was readable, unreadable, or cut (due to catch and release fishing). This information was used to assess tag loss for both PIT and internal anchor tags. If no tag was present, a small incision (<1 cm) was made on the left side below the musculature and a PIT tag was inserted into the body cavity followed by a low reward internal anchor tag. Additional striped bass were tagged in 2011 in the Roanoke River at river kilometer 64 with only a PIT tag (Hughes and Hightower 2015). In total, we incorporated 3 752 PIT-tagged individuals and 3 933 low reward-tagged individuals into analysis (122 of each tag type were ≥ 900 mm TL at tagging). Scales were also collected from striped bass on the spawning grounds, 2011-2013, and assigned an age by McCargo and Dockendorf (2012; 2013; 2014); these data were used in the catch-at-age submodel.

Biologists scanned for PIT tags with a hand held detector while sampling harvest in the Roanoke River recreational fishery, March to April 2012-2013, and in the Albemarle Sound recreational and commercial fisheries, October to April 2011-2013; these months corresponded to seasonal periods of legal harvest for striped bass in the AS-RR system. Scanning for PIT

tags was conducted at least four times per week during creel surveys (for recreational harvest) and fish house sampling (for commercial harvest). The total number of striped bass scanned each month and any PIT tag numbers detected were recorded. Low reward internal anchor tags could be returned from any fishery and included information on date, location, and capture type (i.e., commercial or recreational) and whether the striped bass was harvested or released.

Integrated survival and run size abundance model for resident striped bass

We developed separate integrated models for legal but small (i.e., 458-899 mm TL) and large (i.e., ≥ 900 mm TL) striped bass due to drastic differences in life history and harvest patterns. Specifically, all large females tagged with an acoustic tag (939-1146 mm TL) spent approximately 11 months in the Atlantic Ocean, returning to the AS-RR only during the spawning run (Callihan et al. 2015). In contrast, smaller (445-873 mm TL) telemetered striped bass in the AS-RR stock were not detected in oceanic waters. Also, small striped bass were not reported as harvest from the Atlantic Ocean, whereas those 900 mm TL or larger at tagging were almost exclusively harvested from marine waters. Individuals 458-899 mm TL at tagging are referred to as “resident” and those ≥ 900 mm TL and larger are referred to as “anadromous”.

Multistate submodel for resident striped bass

To estimate mortality rates, a capture history ($Y_{i,t}$) for each included resident striped bass ($i = 1, 2, \dots, 103$) tagged with an acoustic and high reward tag in each month ($t = 1, 2, \dots, 33$; March 2011 to October 2013) was produced using information from detections on VR2s, detections by manual tracking, and returns of high reward external tags. Capture histories ($Y_{i,t}$) were analyzed using a state-space multistate capture-recapture (“Multistate”) model (Fig.1). Similar multistate models with live detections and dead recoveries have been used for multiple species (Kendall et al. 2006; Bischof et al. 2009; Duriez et al. 2009; Kerns et

al. 2016). State-space models have two processes, the state process (i.e., an individual's estimated "true" state) and the observation process (i.e., what was actually observed), modeled by separate categorical distributions in the integrated likelihood.

State process

For our multistate model, individuals were estimated to be in one of nine true states as a function of survival status (e.g., alive or dead by a specific fishery) and status of the high reward tag (i.e., intact or cut/lost). The true state ($Q_{i,t}$) of individual i in month t was estimated using a categorical distribution based on the individual's estimated true state in month $t - 1$ ($Q_{i,t-1}$) and the probability of transition (Ω) to other true states (Kéry and Schaub 2012; equations for transition probabilities are on Fig. 1 Inset):

$$(1) \quad Q_{i,t} \sim \text{Categorical}(\Omega_{Q_{i,t-1}, 1, 2, \dots, 9})$$

The nine estimated true states are (Fig. 1 Inset): 1) alive with a high reward tag; 2) reported harvest by the Albemarle Sound commercial fishery sector; 3) reported harvest by the Roanoke River recreational fishery sector; 4) reported harvest by the Albemarle Sound recreational fishery sector; 5) reported harvest by combined recreational and commercial fishing in the Pamlico fishery sector; 6) reported catch in the catch-and-release (removal of the high reward tag, but release of the fish) fishery sector; 7) natural mortality; 8) alive without a high reward tag (i.e., tag was cut or lost); and 9) undetermined death (i.e., mortality without a high reward tag). Striped bass could be alive and detected on a VR2 with or without a high reward external tag.

To estimate rates of fishing mortality, natural mortality, and catch and release, Jiang et al. (2007) developed a tag return model that assessed tag removal as distinguished from fish death, which is calculated indirectly. Since we also have removal of high reward tags via harvest, catch and release, and tag loss (as opposed to just harvest), we used the Jiang et al. (2007) model to estimate transition probabilities and mortality rates. Total monthly instantaneous removal of high reward tags (T_t) was calculated as a function of monthly fishing

213 rates ($F_{t,s=1,2,\dots,5}$) from five fishery sectors ($s = 1, 2, \dots, 5$), monthly natural mortality (M_q) estimated
 214 quarterly ($q = 1, 2, 3, 4$), and a monthly rate of internal anchor tag retention (I):

$$(2) \quad T_t = \sum_{s=1}^5 F_{t,s} + M_q + \text{Log}(I)$$

215 We estimated instantaneous monthly tag removal rates for five fishery sectors: commercial
 216 fishing in Albemarle Sound ($F_{t,s=1}$); recreational fishing in the Roanoke River ($F_{t,s=2}$);
 217 recreational fishing in the Albemarle Sound ($F_{t,s=3}$); fishing in the Pamlico system ($F_{t,s=4}$); and
 218 catch and release fishing ($F_{t,s=5}$). Monthly natural mortality (M_q) was estimated quarterly
 219 (March-May, June-August, September-November, and December-February) since unique
 220 monthly estimates were imprecise and quarterly estimates appeared to capture seasonal
 221 variability (See Results). A monthly internal anchor tag retention rate (I) was estimated by the
 222 recapture of striped bass tagged with both a PIT and an internal anchor tag after time at large
 223 using a binomial likelihood:

$$(3) \quad C^{IA}_g \sim \text{Binomial}(I^G, N^{IA}_g)$$

225 C^{IA}_g was the number of striped bass recaptured with a readable internal anchor tag after being
 226 at large for G months ($G = 1, 2, 12, 13, 14, 24, 25$), indexed as, $g = 1, 2, \dots, 7$) and N^{IA}_g was the total
 227 number of striped bass known to previously have had an internal anchor tag (i.e., known from its
 228 PIT tag) recaptured after being at large for G months. Internal anchor tag loss was considered
 229 independent of PIT tag loss and loss of both tags was not addressed, but would be minimal.

230 To estimate monthly instantaneous mortality (Z_t) for resident striped bass (as opposed
 231 to removal of tags), we needed to account for the monthly instantaneous rate of mortality
 232 associated with catch and release (Kerns et al. 2012) or the catch and release mortality rate
 233 (F^{CR}_t):

$$(4) \quad Z_t = \sum_{s=1}^4 F_{t,s} + F^{CR}_t + M_q$$

For striped bass, the probability of death associated with catch and release increases with increasing water temperature (Nelson 1998; Bettinger et al. 2005; Millard et al. 2005). Due to the small sample size in our study (only 1 of 12 fish caught and released died), we did not use our data to directly estimate F^{CR}_t . Instead, we used data in Nelson's (1998) hooking mortality study of striped bass in the Roanoke River to estimate the probability of death associated with a catch and release event as a function of water temperature using logistic regression:

$$(5) \quad C^{CRD}_k \sim \text{Binomial}(\psi_k, N^{CRD}_k)$$

The number of individuals that died (C^{CRD}_k) in each experimental sample ($k = 1, 2, \dots, 5$) in the Nelson (1998) study was a function of the total number of striped bass caught for that specific experimental sample (N^{CRD}_k) and the probability of death due to catch and release (ψ_k) during the sample, which was evaluated as a function of water temperature. Water temperature during samples in the Nelson (1998) study was recorded to range from 16.0 to 23.5 °C. The logit link was used to evaluate ψ_k as a function of water temperature during the sample (W_k):

$$(6) \quad \text{Logit}(\psi_k) = \beta_1 + \beta_2 W_k$$

where $\beta_1 + \beta_2$ are the intercept and slope coefficients, respectively. Thus, the mortality rate associated with catch and release fishing (i.e., F^{CR}_t) was estimated by the rate of catch and fishing (i.e., $F_{t,s=5}$) and the logistic function for catch and release mortality as a function of temperature using average monthly water temperature (W_t) at the USGS gauging station at Halifax in the Roanoke River (range from 8.3 to 30.0 °C during the study):

$$(7) \quad F^{CR}_t = F_{t,s=5} \exp(\beta_1 + \beta_2 W_t) / (1 + \exp(\beta_1 + \beta_2 W_t))$$

To aid stock assessment, study-wide annual rates of total instantaneous mortality (Z) and total instantaneous natural mortality (M) were calculated. Two annual rates of fishing (all fisheries combined), natural, and total mortality were calculated (May 2011 - April 2012 and May 2012 - April 2013). Estimates from both years were used to calculate study-wide rates for Z and M :

$$(8) \quad Z = \sum_{May\ 2011}^{April\ 2012} \frac{Z_t}{2} + \sum_{May\ 2012}^{April\ 2013} \frac{Z_t}{2}$$

$$(9) \quad M = \sum_{May\ 2011}^{April\ 2012} \frac{M_q}{2} + \sum_{May\ 2012}^{April\ 2013} \frac{M_q}{2}$$

258 Observation process

259 The observation process in the multistate model (Fig. 1) links an individual's true state to
 260 what is observed, accounting for less than 100% detection of live individuals or deaths. What is
 261 observed ($Y_{i,t}$) for individual i in month t is based on observation probabilities (θ) for the
 262 individual's estimated true state ($Q_{i,t}$) in month t (Kéry and Schaub 2012):

$$(10) \quad Y_{i,t} \sim \text{Categorical}(\theta_{Q_{i,t},1,2,\dots,8})$$

264 We had eight observed states: 1) detected alive on a stationary receiver; 2) reported harvest by
 265 commercial fishing in the Albemarle Sound; 3) reported harvest by recreational fishing in the
 266 Roanoke River; 4) reported harvest by recreational fishing in the Albemarle Sound; 5) reported
 267 harvest in the Pamlico system; 6) reported catch-and-release; 7) detected natural mortality; and
 268 8) undetected. We assumed all intact high reward tags on caught striped bass were returned
 269 and information was reported without error; thus, all fishery deaths for individuals with an intact
 270 high reward internal anchor tag in the previous month (i.e., true states #2,3,4,5,6) were detected
 271 with a probability of 1 as observed states #2,3,4,5,6, respectively (Fig. 1 Inset). A reported
 272 harvest would also indicate that the fish's true state was #1 in all previous months (Fig. 1 Inset).
 273 In contrast, after removal (i.e., cut or loss) of the internal anchor tag, any death was considered
 274 undetectable (i.e., true state #9 has observed state #8 with a probability of 1; Fig. 1 Inset). The
 275 remaining true states (#1,7,8) could either be detected or undetected. Monthly detection
 276 probabilities (p_t^{LIVE}) for live fish with (true state #1) or without (true state #8) an internal anchor
 277 tag were estimated in the model by the pattern of detections on stationary receivers (Fig. 1 Inset
 278 and Fig. 2). Detection of natural mortality (true state #7) was rare; thus, we only estimated an

overall mean detection probability (p^{NM}). As described by Hightower et al. (2001), we assumed that an individual found in the same location on multiple events without report from an angler or fisher died of natural mortality and still possessed an intact high reward internal anchor tag at the time of death (i.e., the true state in the month before death was #1; Fig. 1 Inset). We assumed no sonic-tag loss.

Tag detection submodel for resident striped bass with an internal PIT tag

We constructed matrices of detections of PIT tags ($X^{PIT}_{c,t,s}$) by release cohort ($c = 1, 2, \dots, 5$), month ($t = 1, 2, \dots, 33$), and scanned fishery sector ($s = 1, 2, 3$). Although tagging was completed weekly in April 2011, May 2011, April 2012, May 2012, and April 2013, tags were collapsed into monthly intervals (i.e., five monthly cohorts) for analysis. Detections of PIT tags were analyzed by an instantaneous rates formulation of the Brownie tag return model (Brownie et al. 1985; Hoenig et al. 1998a). PIT tags were detected by scanning a known or estimated fraction of harvest from three of the five fishery sectors (s): commercial harvest in Albemarle Sound ($s = 1$); recreational harvest in the Roanoke River ($s = 2$); and recreational harvest in Albemarle Sound ($s = 3$). We accounted for the fraction of harvest scanned for PIT tags and assumed all PIT tags scanned were detected. Detected PIT tags (i.e., $X^{PIT}_{c,t,s}$) were assumed to be from a multinomial distribution with an expected detection probability matrix ($P^{PIT}_{c,t,s}$) based on the number of individuals released in each cohort (R^{PIT}_c ; Fig. 1):

$$(11) \quad X^{PIT}_{c,t,s} \sim \text{Multinomial}(P^{PIT}_{c,t,s}, R^{PIT}_c)$$

The probability of detecting a PIT tag (i.e., $P^{PIT}_{c,t,s}$) was a function of mortality rates and multiple nuisance parameters:

$$(12) \quad P^{PIT}_{c,t,s} = S_{t,s} \delta \phi^{PIT}_{c,t} \frac{F_{t,s}}{Z_t} (1 - \exp(-Z_t))$$

where $S_{t,s}$ is the proportion of harvested PIT tags scanned during month t from sector s , δ is the proportion of PIT tags retained, $\phi^{PIT}_{c,t}$ is cumulative survival for individuals within cohort c from tagging until month t , $\frac{F_{t,s}}{Z_t}$ is the proportion of total instantaneous mortality (Z_t) during month t attributed to fishery sector s , and $(1 - \exp(-Z_t))$ is total proportion of mortality for month t . The sampling process for the proportion of harvested PIT tags scanned, by sector and month ($S_{t,s}$), was represented using a binomial likelihood, with the total number of striped bass examined for PIT tags ($E_{t,s}$) and total harvest ($H_{t,s}$):

$$(13) \quad E_{t,s} \sim \text{Binomial}(S_{t,s}, H_{t,s})$$

Harvest for the Albemarle commercial striped bass fishery must be reported daily to the North Carolina Division of Marine Fisheries; harvest in the Albemarle Sound recreational fishery and the Roanoke River recreational fishery are estimated by creel surveys conducted by the North Carolina Division of Marine Fisheries and the North Carolina Wildlife Resources Commission. Unlike for internal anchor tags, PIT tag loss did not appear to increase over time; thus, it was assumed that an initial tag loss value was appropriate; the PIT tag retention probability (δ) was estimated by a binomial likelihood, with the number of fish with PIT tags (C^{PIT}) and the number of fish known to have previously had a PIT tag from a present internal anchor tag (N^{PIT}):

$$(14) \quad C^{PIT} \sim \text{Binomial}(\delta, N^{PIT})$$

For the month of release, an additional parameter was included to account for multiple releases within the month. The proportion of the newly released cohort available to the Roanoke River recreational fishery (μ^{PIT}_c) was estimated using a normal distribution (with standard deviation σ^{PIT}_c) based on the proportion of the month available ($V^{PIT}_{n,c}$) for all individuals in that cohort:

$$(15) \quad V^{PIT}_{n,c} \sim \text{Normal}(\mu^{PIT}_c, \sigma^{PIT}_c)$$

Also, while individuals could be (and sometimes were) caught in the Roanoke River on the day they were tagged, they were not immediately available to fisheries elsewhere (i.e., Albemarle

Sound and the Pamlico system) due to physical distance, so a parameter was included (γ) to account for spatial non-mixing during the month of release for fisheries outside the Roanoke River (Hoenig et al. 1998b; Waterhouse and Hoenig 2011).

Tag return submodel for resident striped bass with a low reward external tag

Similar to PIT tags, the number of returns of low reward tags from each cohort ($c = 1, 2, \dots, 6$), in each month ($t = 1, 2, \dots, 33$) from each fishery sector ($s = 1, 2, \dots, 5$) was recorded in a matrix ($\mathbf{X}^{LRT}_{c,t,s}$); however, unlike for PIT tags, low reward tags could be and were returned from all five fishery sectors: commercial harvest in Albemarle Sound ($s = 1$); recreational harvest in the Roanoke River ($s = 2$); recreational harvest in Albemarle Sound ($s = 3$); harvest in the Pamlico system ($s = 4$); and catch and release fishing ($s = 5$). Similar to PIT tags, low reward tags put out weekly were collapsed into monthly cohorts for the months of April 2011, May 2011, April 2012, May 2012, April 2013, but also May 2013 (i.e., 6 cohorts). Parameter estimates were obtained using a multinomial likelihood:

$$(16) \quad \mathbf{X}^{LRT}_{c,t,s} \sim \text{Multinomial}(\mathbf{P}^{LRT}_{c,t,s}, R^{LRT}_c)$$

The expected number in each matrix cell for each cohort (c), month (t), and fishery sector (s) was the product of the total number of individuals released in each cohort (R^{LRT}_c) and return probability ($\mathbf{P}^{LRT}_{c,t,s}$) which are a function of mortality rates and nuisance parameters (Fig. 1):

$$(17) \quad \mathbf{P}^{LRT}_{c,t,s} = I_t \lambda_* \phi^{LRT}_{c,t} \frac{F_{t,s}}{T_t} (1 - \exp(-T_t))$$

I_t is the cumulative internal anchor tag retention from tagging to month t , λ_* is the reporting rate of low reward internal anchor tags, $\phi^{LRT}_{c,t}$ is cumulative survival for cohort c from tagging to month t , $\frac{F_{t,s}}{T_t}$ is the proportion of total instantaneous removal of internal anchor tags (T_t) in month t attributed to fishery sector s , and $(1 - \exp(-T_t))$ is total proportion of low reward tags removed in month t . Unlike for high reward tags which we assumed were always reported, we estimated

two reporting rates for low reward internal anchor tags, one for the commercial fishery in Albemarle Sound (λ_1) and one for all other fisheries (λ_2), which were predominantly recreational. Similar to PIT matrices, nuisance parameters were included to account for release timing and spatial non-mixing during the month of release for each cohort (Fig 1).

Catch-at-age submodel for resident striped bass

Catch-at-age data ($N^{AGE}_{a,y}$) from scales assigned an age by McCargo and Dockendorf (2012; 2013; 2014) were used in a catch curve likelihood model (i.e., linear regression of the natural log of catch by estimated age) to contribute to the estimate of study-wide annual instantaneous total mortality (i.e., Z) in the integrated model (i.e., equation (8); Fig. 1). We assumed a linear decline in catch-at-age for striped bass ages 3-9 (Fig. 3). These age classes generally correspond to the sizes of striped bass we considered resident (i.e., ages 3-9 were generally 458-900 mm TL; McCargo and Dockendorf 2012; 2013; 2014). Expected values ($\mu^{AGE}_{a,y}$) for each included age ($a = 3, 4, \dots, 9$) and spawning run ($y = 1, 2, 3$) were estimated by a normal distribution with standard deviation (σ^{AGE}):

$$(18) \quad N^{AGE}_{a,y} \sim \text{Normal}(\mu^{AGE}_{a,y}, \sigma^{AGE})$$

Thus, $\mu^{AGE}_{a,y}$ was estimated by linear regression with an intercept (α) and a slope equal to study-wide annual total instantaneous fishing mortality (i.e., Z ; equation (8)):

$$(19) \quad \mu^{AGE}_{a,y} = \alpha - Z$$

Roanoke River striped bass run size abundance estimates

We used estimates of catch ($H_{y,1}$) and exploitation ($H_{y,2}$) in the Roanoke River during three spawning runs (2011-2013, indexed as $y = 1, 2, 3$) to produce total ($A_{y,1}$) and harvestable ($A_{y,2}$) run size abundance estimates (Fig. 1). Total run sizes were estimated by evaluating total catch (i.e., harvest and catch and release), whereas harvestable run size estimates were

evaluated using information on harvest only. Total run size estimates for each spawning run were produced by dividing total catch in the Roanoke River during that spawning run (i.e., estimated harvest and catch and release in the Roanoke River) by exploitation of tags in the Roanoke River during that spawning run (i.e., estimated fraction of total tag removal due to harvest in the Roanoke River and catch and release, in March to May of that year). Expected total catch was estimated for each spawning run from a normal distribution with expected values ($H_{y,1}$) and error ($\sigma^{HAR}_{y,1}$) from McCargo and Dockendorf (2012; 2013; 2014). Exploitation of tags in the Roanoke River during the spawning run was estimated as:

$$(20) \quad (1 - \exp(-T_y))(F_{y,s=2} + F_{y,s=5}) / T_y$$

where $F_{y,s=2}$ is the sum of recreational fishing mortality in the Roanoke River during the run, $F_{y,s=5}$ is the sum of the catch and release fishing rate during the spawning run, and T_y is instantaneous removal of tags (described above) during the spawning run in each year. We similarly estimated the harvestable run size by dividing a similar estimate of total harvest with error (i.e., $H_{y,2}$ and $\sigma^{HAR}_{y,2}$) in the Roanoke River by exploitation due only to harvest:

$$(21) \quad (1 - \exp(-T_y))F_{y,s=2} / T_y$$

Model analyses

All models in this study were evaluated by Bayesian methods with JAGS software (Plummer 2003) called from R statistical analysis software (R Core Team 2013). Prior distributions for the integrated model for resident striped bass are in Table 2. For integrated models (i.e., resident and anadromous), posterior distributions were from three chains and 500 000 iterations after a burn-in of 100 000, which resulted in Rhat scores of less than 1.03 for all parameters. Model convergence is often assumed when Rhat scores for all parameters are less than 1.1 (Gelman and Hill 2007; Kéry and Schaub 2012). The joint likelihood in an integrated model is the product of all individual likelihoods (Fig. 1). In JAGS, the joint likelihood

is defined implicitly; thus, multiple data sources can be included to estimate common parameters with appropriate variance (Rhodes et al. 2011; Kéry and Schaub 2012). To evaluate the relative contribution of tag returns to the overall analysis for resident striped bass, we compared mortality rate estimates from the integrated model to those from a multistate telemetry model alone (Fig.1). For all models, we report the median of the posterior distribution as a measure of central tendency (i.e., as the “estimate”) and 2.5% and 97.5% values in the posterior distribution as 95% credible intervals.

Integrated survival model and analysis for anadromous striped bass

Given small sample sizes of tagged striped bass at least 900 mm TL at tagging (14 sonic and high reward tagged females and 122 low and PIT tagged males and females), we only estimated fishing and natural mortality for the AS-RR system and for the Atlantic Ocean. Similar to Rudd et al. (2014), periods were based on area (i.e., rather than month); the first period in a year represented the approximately month-long spawning migration in the AS-RR system, whereas the second period represented 11 months in the Atlantic Ocean, as described by Callihan et al. (2015). Since we did not sample any ocean fishery for PIT tags and only one high reward tag was returned from the ocean, we used a stochastic variable (a uniform from 0.3 to 0.5) to estimate reporting rate for low reward tags in the tag return matrix. This range for reporting rate would be generally expected given estimated reporting rates for resident striped bass (See Results). We assumed internal anchor tag retention was not impacted by fish size; thus, we used the same data and likelihood model to estimate the rate for anadromous fish as used for residents (equation (3)). We did not include a non-mixing parameter. Since stationary receiver coverage was very high in the Roanoke River and few fish appeared to be missed during the Atlantic Ocean residence (i.e. 11 months), we estimated one mean detection probability for all periods using the same prior distribution as used for resident striped bass (i.e., a uniform from 0 to 1). We did not detect any natural mortality; thus, all natural mortality was

assessed within the model by the cessation of detections on stationary receivers. We had no indication of catch and release; thus, any mortality from it was assumed to be negligible. We estimated average monthly rates of fishing and natural mortality for anadromous striped bass in the Atlantic Ocean (f^{OCEAN} and m^{OCEAN}) and the AS-RR system (f^{ASRR} and m^{ASRR}) using the same prior distributions as used for monthly fishing mortality rates for resident striped bass (i.e., a uniform from -10 to 1 on a natural log scale). We calculated average annual rates of fishing (F^{ANA}) natural (M^{ANA}), and total (Z^{ANA}) instantaneous mortality for anadromous striped bass based on the amount of time spent in each area (i.e., 11 months in the Atlantic Ocean and 1 month in the AS-RR system; Callihan et al. 2015):

$$(22) \quad F^{ANA} = 11(f^{OCEAN}) + f^{ASRR}$$

$$(23) \quad M^{ANA} = 11(m^{OCEAN}) + m^{ASRR}$$

$$(24) \quad Z^{ANA} = F^{ANA} + M^{ANA}$$

Simulation to evaluate an integrated tagging model

By simulation (n=500 replicates), we examined monthly and annual fishing and natural mortality rates estimated by a multistate model of passive detections of sonic-tags with return of high reward tags ("Multistate"), as compared to an integrated model that also included returns of low reward tags ("Integrated"). Monthly estimates identify seasonal patterns in mortality to inform biology and improve management, whereas annual estimates are used directly for stock assessment. Capture histories and tag return matrices were simulated using median posterior estimates of F_t , M_e , and p^{LIVE}_t from our final integrated model for resident AS-RR striped bass (Table 3). F_t was equal to the sum of all fishing mortality rates (i.e., $F_{t,s=1,2,3,4}$ and F^{CR}_t). An average reporting rate (from our posterior estimates) for commercial and recreational fisheries in the AS-RR system was used in integrated model simulations (i.e., 0.40). There were 15 simulated periods (i.e., months) corresponding to April 2011 to June 2012. Datasets were

simulated in Program R and mortality rates for simulated datasets were estimated in JAGS. Prior distributions for parameters in the simulated models were the same as those used in the integrated model for resident striped bass (Table 2). Simulated datasets were evaluated with a burn-in of 1 000 and iteration increments of 1 000 until convergence was reached, as assumed when Rhat scores for all estimated parameters were less than 1.1 (Gelman and Hill 2007; Kéry and Schaub 2012).

The multistate and integrated models evaluated by simulation were simplified as compared to the resident striped models to be generally practical for other fish populations and studies. Simplifications included estimating only one rate of fishing mortality (as opposed to fishing mortality by sector), and assuming no tag loss, no non-mixing, no catch and release fishing and no manual searches. A multistate model was used to analyze simulated capture histories of striped bass each tagged with a sonic and a high reward tag released before the start of month one. There were three true states: 1) alive with both tags; 2) harvested; and 3) natural death. There were three observed states: 1) detected alive; 2) returned high reward tag indicating harvest; and 3) not detected. High reward tags were assumed to be returned with a probability of 1. Live fish were detected with a probability of p^{LIVE}_t , but we assumed no manual searching so there was no detection of natural mortality. For the integrated model, an instantaneous rates formulation of a Brownie tag return model was used to analyze simulated low reward tag return matrices (Brownie et al. 1985; Hoenig et al. 1998a).

To examine if multistate and integrated models appropriately assess monthly and seasonal patterns in mortality rates, we evaluated 100 fish tagged with both a sonic and a high reward tag and 1 000 fish tagged with a low reward tag. These are similar to the sample sizes we had for our striped bass study and thus help evaluate the expected value of our results, but are also potentially reasonable sample sizes for similar studies on other species. Tagged fish were released before the start of the simulation. Although unlikely to affect model results, one low reward tagged individual was released in all other months for coding purposes. We

estimated monthly rates of fishing mortality, and both monthly and seasonal patterns for natural mortality rates. Estimates from the final month (i.e., simulated period 15) were not examined due to confounding between the final estimate of natural mortality and detection probability. We visually assessed seasonal patterns in fishing and natural mortality rates identified by the multistate and integrated models.

Since annual rates are used in stock assessment, we also examined impacts of sample size on bias, accuracy, and precision of annual fishing (F^{SIM}) and natural (M^{SIM}) mortality rates. Estimates of F^{SIM} and M^{SIM} were calculated in JAGS as the sum of rates from months 1-12:

$$(25) \quad M^{SIM} = \sum_{t=1}^{12} M^{SIM}_t$$

$$(26) \quad F^{SIM} = \sum_{t=1}^{12} F^{SIM}_t$$

We ran simulations assuming 50, 100, or 200 sonic and high reward tagged fish in the multistate component and 0, 1 000, or 2 000 fish in the low reward tag return component. These sample sizes correspond generally to what may be practical in future studies and illustrate the potential value of results from our study of striped bass. Simulations with 0 fish tagged for the low reward tag return component are an evaluation of a multistate only model.

We assessed annual estimates for different simulated sample sizes visually and by calculations. We quantified percent bias for each simulation by relative error (RE; calculated as $((\text{estimate} - \text{True}) / \text{True}) * 100$; Vandergrout and Brendan 2015). We quantified percent accuracy of each simulation by absolute relative error (ARE; calculated as absolute value of $((\text{estimate} - \text{True}) / \text{True}) * 100$; Wilberg and Bence 2006). We plotted the medians (i.e., MRE and MARE) and the 1st and 3rd quantiles from our simulations to evaluate percent bias (MRE close to zero suggests lack of bias) and percent accuracy (i.e., MARE close to zero suggests accuracy) for different sample sizes. Finally, we also assessed precision by the percent coefficient of variation ($CV = (\text{standard deviation of all estimates}) / (\text{mean of all estimates}) * 100$).

Results

Integrated survival and run size abundance model for resident striped bass

Of the 103 sonic and high reward tagged residents included in analysis, seven (6.8%) were reported as harvest in the commercial fishery in Albemarle Sound, two (1.9%) were reported as recreational harvest in the Albemarle Sound, two (1.9%) were reported as recreational harvest in the Pamlico system, five (4.9%) were reported as recreational harvest in the Roanoke River, and 12 (11.7%) were reported as catch and release (Table 1). No striped bass less than 900 mm TL were reported as caught in any other area. Detection patterns on stationary receivers corroborated angler and fisher reports both spatially and temporally. We detected one instance of mortality after catch and release; it occurred in mid-June at the mouth of the Roanoke River. Within the integrated model, mortality due to catch and release was estimated by logistic regression as a function of temperature with an intercept (i.e., β_1) estimated at -8.60 (95%: -13.27 – -4.67) and a slope (i.e., β_2) estimated at 0.31 (95%: 0.12 – 0.52), illustrating an increase in catch and release mortality, as temperature increased.

We scanned 24.5% of the commercial harvest in Albemarle Sound and detected 41 PIT tags (Table 1). Lower percentages of the recreational harvest were estimated to have been scanned (8.2% in the Roanoke River and 5.3% in the Albemarle Sound) due to the dispersed nature of those fisheries in time and space. We detected 10 PIT tags in the Roanoke River recreational fishery and only one in the Albemarle Sound recreational fishery. Low reward tags were returned from commercial (n=37) and recreational (n=45) fisheries in the Albemarle Sound, the recreational fishery in the Roanoke River (n=65), fisheries in the Pamlico Sound system (n=4), and as a result of catch and release (n=144). Low reward tags from striped bass 458-899 mm TL were not returned from any other locations. Non-mixing (i.e., γ) outside of the Roanoke River during the month of release was estimated in the integrated model as 0.11 (95%: 0.014 – 0.40).

PIT tags were retained in 71 of 74 striped bass ($\delta = 0.94$, 95%: 0.86 – 0.98). Internal anchor tags were retained and readable for at least 25 months in 52 of 61 recaptured individuals ($I = 0.94$, 95%: 0.93 – 0.96). Reporting rate was slightly lower for the Albemarle Sound commercial fishery ($\lambda_1 = 0.36$, 95%: 0.23 – 0.58) than for the combined recreational fisheries ($\lambda_2 = 0.43$, 95%: 0.32 – 0.59), although 95% credible intervals overlapped.

Monthly detection probability estimates (i.e., p^{LIVE}_t) for resident striped bass were 0.38 to 0.99. Detection was highest in the spring when most sonic-tagged striped bass were in the Roanoke River, since few detected striped bass were missed at even one receiver during the spawning run (Fig. 2). Detection probability was lowest during fall, when individuals were dispersed throughout the Albemarle Sound. Detection probability for natural mortality (i.e., p^{NM}) was 0.11 (95%: 0.08 – 0.13).

Survival for resident striped bass

The natural log of the average number of striped bass age 3 – 9 caught in the Roanoke River during spring spawning surveys generally showed a linear pattern of decline with age (Fig. 3). The pattern of decline in catch-at-age expected by the estimated intercept of the catch-at-age submodel ($\alpha = 11.11$, 95%, 10.17 – 12.43) and estimated study-wide total instantaneous mortality for resident striped bass (i.e., Z , see below for estimate) was similar to the pattern of decline observed from scales of striped bass catch ages 3 – 9. The pattern of decline was not linear (and not well represented by the integrated model expected values for residents) for striped bass below age-3 or above age-9. Within the integrated model, the standard deviation for the catch-at-age submodel (i.e., σ^{AGE}) was 0.87 (95%: 0.60 – 1.38).

Fishing mortality rates estimated by the integrated model for resident striped bass, March 2011 to May 2013, were consistent with monthly periods of legal harvest (Fig. 4). Monthly rates of fishing mortality were highest in March and April during the spawning run when

all fisheries were open. Catch and release was highest during the spawning period, but was reported during almost all months. Catch and release mortality was low (Fig. 4). Total annual instantaneous fishing mortality was 0.45 (95%: 0.34 – 0.58) in the first year and 0.31 (95%: 0.23 – 0.43) in the second year. Natural mortality was highest in the summer and almost non-existent during the rest of the year (Fig. 4). Annual instantaneous natural mortality was 0.62 (95%: 0.46 – 0.80) in the first year and 0.79 (95%: 0.57 – 1.05) in the second year, for a study-wide rate (i.e., M) of 0.70 (95%: 0.58 – 0.86). The study-wide total annual instantaneous mortality rate for resident striped bass (i.e., Z) was 1.08 (95%: 0.94 – 1.28).

Seasonal estimates of natural mortality for striped bass 458-899 mm TL at tagging produced by telemetry and high reward tag returns alone (i.e., “Multistate”) were very similar in pattern, magnitude, and precision to those from the integrated model (Fig. 4). Monthly estimates of fishing mortality rates were also generally similar to those from the integrated model, although they were dramatically less precise (Fig. 4). Imprecision in fishing mortality rates for the multistate only model was most evident in late 2012 and 2013 when the number of sonic and high reward tagged fish was lower as compared to earlier in the study (Table 1; Fig. 4). The multistate only model produced a similar estimate of study-wide annual instantaneous natural mortality (0.74, 95%: 0.53 – 0.99), but a higher estimate of study-wide total annual instantaneous mortality (1.52, 95%: 1.22 – 1.90) than the integrated model.

Roanoke River striped bass run size abundance estimates

Roanoke River run size estimates during the study period ranged from approximately 499 000 to 715 000 individuals. Harvestable-size striped bass were estimated to comprise 20% (2013) to 56% (2012) of the total run in each year (Table 4).

Integrated survival model for anadromous striped bass

For striped bass at least 900 mm TL at tagging, two sonic and high reward-tagged individuals were known to be harvested, one recreationally in the Atlantic Ocean off the coast of Massachusetts and the other in the Albemarle Sound commercial fishery upon entry in the AS-RR system during the spawning run. Detection probability on stationary receivers in the AS-RR system and Atlantic Ocean within a period was estimated by the integrated model at 0.95 (95%: 0.83 – 0.99). Of the 122 low reward tagged individuals, nine were reported as recreational harvest in the Atlantic Ocean off the coasts of Massachusetts, New York, and New Jersey and none were reported from any other areas. Annual instantaneous natural mortality (i.e., M^{ANA}) was estimated at 0.21 (95%: 0.03 – 0.52), annual instantaneous fishing mortality (i.e., F^{ANA}) was estimated to be 0.23 (95%: 0.01 – 0.48), and annual total instantaneous mortality (i.e., Z^{ANA}) was estimated at 0.45 (95%: 0.21 – 0.86). For these larger striped bass, the median estimate of monthly fishing mortality was higher in the Atlantic Ocean ($f^{OCEAN} = 0.019$, 95%: 0.008 – 0.041) than Albemarle Sound ($f^{ASRR} = 0.011$, 95%: 0.000 – 0.059), whereas average monthly natural mortality was higher in Albemarle Sound ($m^{ASRR} = 0.147$, 95%: 0.001 – 0.380), as compared to the Atlantic Ocean ($m^{OCEAN} = 0.003$, 95%: 0.000 – 0.032), although 95% credible intervals were sometimes large and overlapped. For anadromous striped bass, the most substantial mortality component was natural mortality in Albemarle Sound during emigration after spawning.

Simulation to evaluate an integrated tagging model

Simulation showed that both the multistate only model and the integrated model produced estimates of monthly and annual fishing and natural mortality rates that would increase understanding of biology and be valuable for stock assessment (Figs. 5 and 6). Monthly rates estimated by both the multistate and the integrated model identified seasonal patterns in fishing and natural mortality rates; however, the integrated model produced more

accurate and precise estimates of monthly fishing mortality rates than the multistate only model (Fig. 5). In addition, estimating a seasonal pattern for natural mortality produced higher accuracy and precision for natural mortality than estimating it as a monthly rate (Fig. 5).

With adequate sample size, multistate and integrated tagging models produced unbiased, accurate, and precise estimates of annual fishing and natural mortality rates useful for stock assessment (Fig. 6). Regardless of sample size, the interquartile range for estimated mortality rates and RE values overlapped zero (Fig. 6). For all sample sizes examined, MRE values for natural mortality were slightly positive. Values of MRE for fishing mortality were slightly positive for the multistate only model, but slightly negative for the integrated model. Bias decreased and accuracy and precision increased with increasing sample size of sonic and high reward tags in the multistate component, whereas increasing the number of low reward tags in the tag return component had barely perceivable effects (Fig. 6). The MRE was below 10% for all sample sizes examined, but was only below 5% when at least 100 individuals were tagged with a sonic and high reward tag. The MARE was below 20% for all sample sizes, but was only below 10% when at least 200 individuals were tagged with a sonic and high reward tag. The CV was below 30% for all sample sizes examined, and was below 20% if at least 100 individuals were tagged with a sonic and high reward tag (Fig. 6).

Discussion

Our results show that the combination of live detections of sonic-tagged individuals on stationary receivers with reported harvest of external tags evaluated by a multistate or integrated model can provide extensive, fine-scale, high quality data on mortality rates. When fishing mortality is assumed to always be reported, the state space portion of the multistate model uses detection patterns to effectively differentiate living, but undetected fish, from natural mortality. Since state space multistate models are flexible in design and provide unbiased, accurate, and precise estimates of annual fishing and natural mortality, they could be used to

improve stock assessment for multiple species (Hightower and Harris *In Press*). However, our striped bass example illustrates how small sample sizes can result in imprecise monthly estimates of mortality rates from multiple fishery sectors when a multistate only model is evaluated. Low precision in monthly estimates for multiple fishery sectors is likely because few individuals were caught in any one fishery sector within a month. The number of sonic-tags used is limited by expense and the potential for tag transmissions to collide (i.e., multiple tags transmitting at same time can result in none being detected by a stationary receiver) in areas of high density. The addition of low reward tag return and PIT detection data through analysis of an integrated model clarified monthly patterns in fishing mortality by sector. Tag return models alone can also produce valid estimates of fishing mortality rates, as long as reporting rate is effectively estimated (see Pollock et al. 1991; 2001; 2002). However, natural mortality is estimated only indirectly in tag return models and seasonal patterns cannot be assessed during periods without harvest (i.e., April-October in this study). In our study, low reward tags likely contributed more to estimates for recreational fisheries since reporting rate was slightly higher as compared to the commercial sector. In contrast, PIT tags were more helpful for estimating commercial fishing mortality rates, since commercial harvest must be reported and scanning harvest in fishhouses was much more efficient than scanning dispersed (both spatially and temporally) recreational fisheries; thus, more commercial harvest was scanned and more PIT tags were detected in the commercial fishery (Table 1).

The integrated tagging model helped us identify spatial and temporal patterns in striped bass fishing and natural mortality rates. As expected, Roanoke River recreational fishing was concentrated in the early part of the spawning run. Albemarle Sound fisheries were temporally dispersed, but peaked during or just before the spawning run. Catch and release did not contribute substantially to mortality because water temperature during periods of high catch and release rates were low (Nelson 1998; Bettinger et al. 2005; Millard et al. 2005). However, catch and release may also impact population growth by altering spawning behavior. Movement

patterns and spawning behavior can be evaluated by examining detection patterns on stationary receivers in response to reported catch and release. Impacts of repeated catch and release of a single striped bass were not evaluated, but could be important (Kerns et al. 2012).

Although natural mortality was low during most of the year, it was substantial during summer months, when water temperatures peaked in Albemarle Sound. Striped bass in poor physical condition (i.e., low relative weight and high occurrence of lesions) have been observed in Albemarle Sound during summer; poor condition during this period may be a result of thermal stress and may be more prevalent for individuals larger than 325 mm TL (Haeseker et al. 1996). It may be possible to use summer water temperature to predict annual natural mortality and thus the status of the stock on an annual basis. A better understanding of the impacts of estuarine water temperature on striped bass natural mortality would help evaluate potential impacts of climate change on fish populations.

Our study suggests that larger anadromous striped bass had substantially different mortality rates than residents. Annual instantaneous natural mortality for striped bass 458-899 mm TL was estimated at 0.70 (95%: 0.58 – 0.86) as compared to 0.21 (95%: 0.03 – 0.52) for larger striped bass in the population. These differences may be attributed to fish behavior. Anadromous females spent little time in Albemarle Sound, appearing to use it only as a corridor to reach spawning grounds in the Roanoke River in the spring (Callihan et al. 2015). However, these anadromous fish were estimated to experience the highest natural mortality rates in the AS-RR during emigration after spawning. Higher natural mortality in the AS-RR, compared to the Atlantic Ocean, may be a function of spawning stress, warmer water temperatures, reduced feeding, or a combination. Larger individuals may reduce thermal stress and increase food availability by migrating to northern areas of the Atlantic Ocean during non-spawning periods, especially during warm periods in their natal estuaries (Secor and Piccoli 2007; Mather et al. 2009; Callihan et al. 2014). After emigration, these anadromous striped bass are vulnerable to recreational fisheries along the Atlantic Coast. Understanding mortality rates for anadromous

striped bass is essential because they likely contribute more to future year classes than younger individuals due to their higher fecundity (Boyd 2011).

Although we evaluated two size classes (i.e., above and below 900 mm TL), size likely impacts mortality on a finer scale. In general, juvenile fish survival increases with size, as individuals become less available to predators (Lorenzen 1996; Sogard 1997). However, natural mortality in the summer for larger, but not yet anadromous, striped bass may be higher than for smaller resident individuals (Haeseker et al. 1996). Fishing mortality is also impacted by fish size. The Roanoke River has a protective slot of 559 to 686 mm TL (i.e., 22-27 inches), but this size class may be more prevalent in Albemarle Sound recreational and commercial fisheries. Regardless, the natural log of catch-at-age data showed a fairly linear decline ages 3 – 9, suggesting that striped bass in this range had similar total mortality, even if specific causes varied. Striped bass below age-3 were less represented in Roanoke River catch likely because they had not fully recruited to the spawning population, especially for females (Boyd 2011). Catch-at-age data and our models suggest that individuals age-10 and older (average age-10 female = 880 mm TL; average age-10 male = 809 mm TL) have lower mortality than younger fish (Fig. 3), likely as a result of a change to an anadromous life history pattern. Callihan et al. (2014) found that AS-RR striped bass 700-800 mm TL were often caught in coastal areas adjacent to North Carolina and individuals 800 mm TL and larger were frequently caught in northern coastal waters. We tagged only a few (49 PIT tags, 59 low reward tags, 2 sonic and high reward tags) striped bass 700-900 mm TL, so our mortality results may not be representative for this transitional size category.

As with all approaches, when using an integrated tagging model to estimate mortality rates it is essential to consider model assumptions. Our results suggest that natural mortality is higher than assumed in recent AS-RR striped bass stock assessments (Takade-Heumacher 2010; Mroch and Godwin 2014). Recent assessment estimates are from a forward projecting catch-at-age model, with data from fishery independent surveys and fishery dependent catch.

In these assessments, natural mortality is assumed to be 0.15, which is much lower than our average estimate of 0.70 (95%: 0.58 – 0.86). Potential biases from field sampling that could result in estimates of natural mortality being higher than true values should be considered for all tagging studies and are: 1) tag expulsion (i.e., loss); 2) delayed tagging mortality; 3) emigration to areas not covered by stationary receivers; and 4) less than 100% reporting of high reward tags. Sonic-tag expulsion has been reported for other fish (Moore et al. 1990; Daniel et al. 2009; Boone et al. 2013); however, we did not detect any evidence of sonic tag expulsion (i.e., all striped bass reported showed an expected pattern of sonic detections and sometimes we were able to retrieve the sonic tag from the angler or fisher). We accounted for expulsion of internal anchor and PIT tags by direct estimation. Delayed tagging mortality is difficult to assess and would appear as natural mortality. We would expect delayed tagging mortality to result in a less dramatic seasonal pattern than was observed for natural mortality. Emigration to areas without stationary receivers would also appear as natural mortality, since individuals would cease to be detected. We did not detect evidence of such emigration and no tags were reported from other areas, but undetected emigration north to Chesapeake Bay is possible. Random temporary emigration should be accounted for by detection probability. Collapsing live detections into bins (i.e., months) has been observed to bias survival estimation, but this bias is usually small when survival rates are high relative to the estimation period (i.e., survival within a month; Hargrove and Borland 1994; Barbour et al. 2013).

We developed an integrated tagging model to estimate monthly fishing and seasonal natural mortality rates. Our monthly mortality rate estimates inform striped bass biology and our annual estimates could be used in stock assessment to improve management of this economically valuable stock. Our study demonstrates how Bayesian methods make analysis of a complicated integrated model with multiple data sources and nuisance parameters (Fig. 1) manageable. Careful consideration must be made with regard to model assumptions and to the choice of priors. Prior selection for these types of models should receive more study in the

future. Our simulations suggest that both multistate only models and integrated models produce unbiased, accurate, and precise estimates of annual mortality rates, and increasing the number of sonic and high reward tags increases precision and accuracy of annual estimates. Multistate only models with passive or active detections of acoustically tagged individuals with or without external tags have the potential to contribute substantially to fisheries management (Hightower and Harris *In Press*). In contrast, our integrated model for striped bass demonstrated improved precision for monthly estimates of fishing mortality rates, especially for multiple fishery sectors, as compared to a multistate only model. Although not evaluated by simulation, increased tag returns in an integrated model may improve estimates for multiple fishery sectors. Thus, optimal sample sizes of telemetered fish with high reward tags and fish with low reward tags would depend on the biology of the species (i.e., potential for tag collisions), number of fishery sectors, and funding (i.e., sonic with high reward tags are expensive). This integrated tagging model could be modified to estimate components of natural and fishing mortality for a variety of migratory fish species that support recreational, commercial, and catch-and-release fisheries.

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1 **Table 1.** Detections and returns of tagged resident striped bass (excluding tagging mortalities) in the Albemarle Sound-Roanoke
2 River, North Carolina, used to estimate mortality rates by an integrated tagging model.

Tag Type	Number	Tagging period	Censored period	Number Returned			Number Detected		
				2011	2012	2013	2011	2012	2013
Sonic and high reward	17	February 2011	October 2012	5	2	1	17	11	0
Sonic and high reward	17	March 2011	November 2012	6	0	0	17	7	0
Sonic and high reward	34	April 2011	December 2012	4	2	0	34	12	0
Sonic and high reward	1	May 2011	January 2012	0	0	0	1	1	0
Sonic and high reward	25	February 2012	End of study	NA	6	0	NA	21	5
Sonic and high reward	9	March 2012	End of study	NA	1	1	NA	8	6
PIT	727	April 2011	NA	NA	NA	NA	7	4	3
PIT	1079	May 2011	NA	NA	NA	NA	1	2	2
PIT	987	April 2012	NA	NA	NA	NA	NA	5	18
PIT	760	May 2012	NA	NA	NA	NA	NA	0	12
PIT	77	April 2013	NA	NA	NA	NA	NA	NA	2
Low reward	622	April 2011	NA	40	29	3	NA	NA	NA
Low reward	981	May 2011	NA	25	49	3	NA	NA	NA
Low reward	987	April 2012	NA	NA	73	22	NA	NA	NA
Low reward	760	May 2012	NA	NA	20	13	NA	NA	NA
Low reward	77	April 2013	NA	NA	NA	7	NA	NA	NA
Low reward	384	May 2013	NA	NA	NA	11	NA	NA	NA

Table 2. Description of symbols for **(A)** indices, data, and **(B)** estimated parameters (ordered alphabetically) in the integrated model for resident striped bass in the Albemarle Sound-Roanoke River, North Carolina, with prior distribution (when applicable).

(A)

Indices	Description
a	Ages included in the catch-at-age submodel ($a = 3, 4, \dots, 9$)
c	PIT tag ($c = 1, 2, \dots, 5$) or low reward tag ($c = 1, 2, \dots, 6$) cohorts
g	Index for months at large before recapture for striped bass tagged with an internal anchor tag ($g = 1, 2, \dots, 7$)
i	Telemetered individuals ($i = 1, 2, \dots, 103$)
k	Experimental samples (Nelson 1998) to evaluate impacts of water temperature on catch and release mortality ($k = 1, 2, \dots, 5$)
n	Individuals in each cohort for PIT or low reward tagged individuals
q	Quarters based on season ($q = 1, 2, 3, 4$)
s	Fishery sectors ($s = 1, 2, \dots, 5$)
t	Months ($t = 1, 2, \dots, 33$)
y	Spawning run years ($y = 1, 2, 3$)
Data	
C^{CRD}_k	Number of N^{CRD}_k that died of catch and release mortality in each experimental temperature sample (Nelson 1998)
C^{IA}_g	Number of N^{IA}_g with an intact internal anchor tag
C^{PIT}	Number of N^{PIT} with an intact PIT tag
$E_{t,s}$	Number of $H_{t,s}$ examined for a PIT tag by month and fishery sector
$H_{t,s}$	Harvest by month and fishery sector
$H_{y,1,2}$	Total catch ($H_{y,1}$) and harvest ($H_{y,2}$) in the Roanoke River during each spawning run year
$N^{AGE}_{a,y}$	Number of individuals in each age class during each spawning run year (from scales)
N^{CRD}_k	Number sampled to estimate catch and release mortality by experimental temperature sample (Nelson 1998)
N^{IA}_g	Number recaptured to estimate monthly rate of tag retention for internal anchor tags
N^{PIT}	Number recaptured to estimate PIT tag retention
R^{LRT}_c	Number tagged with a low reward tag by cohort
R^{PIT}_c	Number tagged with a PIT tag by cohort
$V^{LRT}_{n,c}$	Proportion of the release month available for each individual in the low reward tag cohort
$V^{PIT}_{n,c}$	Proportion of the release month available for each individual in the PIT tag cohort
W_k	Water temperature in experimental samples (Nelson 1998) to evaluate impacts on catch and release mortality
W_t	Monthly water temperature at the USGS gauging station at Halifax in the Roanoke River
$X^{LRT}_{c,t,s}$	Tag return matrix for low reward tags
$X^{PIT}_{c,t,s}$	Tag return matrix for PIT tags
$Y_{i,t}$	Capture history matrix for all telemetered individuals
$\sigma^{HAR}_{y,1,2}$	Standard deviation on total catch ($\sigma^{HAR}_{y,1}$) and harvest ($\sigma^{HAR}_{y,2}$) in the Roanoke River during each spawning run year

6

7 **Table 2.** Continued

8 **(B)**

Parameters	Description	Prior (if applicable)
$A_{y,1,2}$	Total ($A_{y,1}$) and harvestable ($A_{y,2}$) run size estimates by spawning run year	
$F_{t,s=1,2,\dots,5}$	Monthly fishing mortality rates for the five (1-5) sectors (Priors on natural log scale)	Uniform (-10,1)
F^{CR}_t	Monthly fishing mortality due to catch and release	
I	Monthly tag retention rate for internal anchor tags	Uniform (0,1)
M	Study-wide annual instantaneous natural mortality of resident striped bass	
M_q	Average monthly natural mortality estimated quarterly (Prior on natural log scale)	Uniform (-10,1)
$P^{LRT}_{c,t,s}$	Return probabilities for low reward tags	
$P^{PIT}_{c,t,s}$	Detection probabilities for PIT tags	
p^{LIVE}_t	Monthly detection probability for telemetered individuals	Uniform (0,1)
p^{NM}	Detection probability for natural mortality	Uniform (0,1)
$Q_{i,t}$	Estimated “true” states for all telemetered individuals during all months	
$S_{t,s}$	Proportion of harvested PIT tags that were scanned	Uniform (0,1)
T_t	Monthly instantaneous removal of internal anchor tags	
Z	Study-wide annual instantaneous total mortality of resident striped bass	
Z_t	Monthly total instantaneous mortality of resident striped bass	
α	Intercept for the catch curve in the catch-at-age submodel	Uniform (0, 20)
$\beta_{1,2}$	Intercept β_1 and slope β_2 for the logistic likelihood model of temperature on catch and release mortality	Normal (0,0.01)
γ	Non-mixing during the month of release for low reward and PIT tagged fish	Uniform (0,1)
δ	PIT tag retention rate	Uniform (0,1)
$\lambda_{1,2}$	Reporting rates for the commercial (λ_1) and recreational (λ_2) fisheries	Uniform (0,1)
$\theta_{Q_{i,t},1,2,\dots,8}$	The eight observation probabilities for the nine true states in the multistate submodel	
$\mu^{AGE}_{a,y}$	Expected natural log of the number of fish by age and spawning run year	
μ^{LRT}_c	Mean proportion of the month remaining after release by cohort for low reward tags	Uniform (0,1)
μ^{PIT}_c	Mean proportion of the month remaining after release by cohort for PIT tags	Uniform (0,1)
σ^{AGE}	Standard deviation on $\mu^{AGE}_{a,y}$	Uniform (0,10)
σ^{LRT}_c	Standard deviation on μ^{LRT}_c	Uniform (0, 20)
σ^{PIT}_c	Standard deviation on μ^{PIT}_c	Uniform (0, 20)
$\phi^{LRT}_{c,t}$	Cumulative survival for low reward-tagged individuals in a cohort from tagging until month t	
$\phi^{PIT}_{c,t}$	Cumulative survival for PIT-tagged individuals in a cohort from tagging until month t	
ψ_k	Probability of death due to catch and release as a function of water temperature	
$\Omega_{Q_{i,t},1,2,\dots,9}$	Probabilities to transition into each of the nine true states for the multistate submodel	

Table 3. Parameter values (i.e., monthly estimates from the integrated model for resident striped bass in the Albemarle Sound-Roanoke River, North Carolina) used in simulation analyses to evaluate a multistate and an integrated model to estimate mortality rates.

Period	Fishing mortality (F_t)	Natural mortality (M_e)	Detection probability (p^{LIVE}_t)
1	0.151	0.007	0.953
2	0.007	0.007	0.989
3	0.006	0.007	0.989
4	0.008	0.185	0.755
5	0.004	0.185	0.681
6	0.003	0.185	0.633
7	0.019	0.002	0.747
8	0.018	0.002	0.779
9	0.022	0.002	0.675
10	0.024	0.001	0.854
11	0.019	0.001	0.859
12	0.144	0.001	0.874
13	0.162	0.003	0.966
14	0.011	0.003	0.824
15	0.005	0.003	0.692

Table 4. Total spawning run size and harvestable run size estimates (with 95% credible intervals) for striped bass in the Roanoke River, North Carolina, by spawning year.

Year	Total Run	Harvestable Run
2011	694 993 (399 373 – 1 195 197)	214 792 (111 118 – 411 780)
2012	498 881 (333 254 – 747 793)	281 350 (169 423 – 440 971)
2013	715 185 (397 160 – 1 204 808)	140 756 (53 540 – 288 071)

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Fig. 1. Directed acyclic graph (DAG) for the integrated model to estimate mortality rates and run sizes for resident striped bass in the Albemarle Sound-Roanoke River, North Carolina. Ovals represent estimated parameters and boxes represent datasets. Solid arrows indicate stochastic relationships and dashed arrows indicate deterministic relationships (i.e., functions). Dashed boxes indicate the portion of the integrated model described within. The inset illustrates relationships among and transition equations between all estimated true states (with numbers corresponding to descriptions in the text) in the multistate telemetry submodel, illustrated by the larger grey oval in the DAG. Datasets, estimated parameters, and indices are in Table 2.

26

27 **Fig. 2.** Locations of stationary receivers (VR2 Locations) in North Carolina from North Carolina State University (NCSU) in the
28 Roanoke River (black dots) and North Carolina Division of Marine Fisheries (DMF) in the Albemarle Sound (grey dots). The
29 Basemap for the Roanoke River and Albemarle Sound were from 1:24,000-scale detailed hydrography data located in the NC
30 OneMap Geospatial Portal originated and published by the NC Center for Geographic Information and Analysis.

Fig. 3. Natural log of average catch-at-age from scales of striped bass caught during spring spawning surveys (2011-2013) by North Carolina Wildlife Resources Commission and North Carolina Division of Marine Fisheries in the Roanoke River, North Carolina (black dots), with expected natural log of catch-at-age (black line) and 95% credible intervals (grey lines) from the integrated model for resident striped bass in the Roanoke River-Albemarle Sound, North Carolina.

38
39 **Fig. 4.** Monthly mortality rates (error bars illustrate 95% credible intervals) by fishery sector, as well as natural mortality, total fishing
40 mortality (i.e., sum of $F_{t,s=1,2,3,4}$ and F^{CR}_t) and catch and release for resident striped bass in the Albemarle Sound-Roanoke River
41 system, North Carolina, estimated by an integrated model (upper panels) and the multistate only model (lower panels). Note:
42 different y-axis ranges.

Fig 5. Boxplots of monthly fishing (“F”) and natural (“M”) mortality rate estimates from simulated models (each row is a model). Rows 1 and 3 are from multistate only models with high reward tags and telemetry (“Multistate”). Rows 2 and 4 are from integrated models with the same multistate component, but also a low reward tag return component (“Integrated”). Models estimated either monthly (rows 1 and 2) or seasonal (rows 3 and 4) values for M. Red lines indicate true simulated monthly mortality rates.

Fig 6. Boxplots of estimates (upper panels), interquartile ranges of percent relative error and percent absolute relative error (middle panels), and percent coefficients of variation (lower panels) of annual instantaneous fishing (left panels) and natural (right panels) mortality rates from simulated models with different sample sizes of fish with sonic and high reward tags, and fish with low reward tags. Each red line indicates the true simulated rate or a median relative error of zero.