Estimating mortality rates for Albemarle Sound-Roanoke River striped bass using an integrated modeling approach

Julianne E. Harris*
North Carolina Cooperative Fisheries and Wildlife Research Unit
Department of Applied Ecology, North Carolina State University
Raleigh, North Carolina 27695-7617

Joseph E. Hightower
U. S. Geological Survey
North Carolina Cooperative Fish and Wildlife Research Unit
Department of Applied Ecology, North Carolina State University
Raleigh, North Carolina 27695-7617

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* Present address: U. S. Fish and Wildlife Service, Columbia River Fisheries Program Office, 1211 SE Cardinal Ct., Suite 100, Vancouver WA 98683

Abstract

We used a combination of sonic-telemetry, detection of PIT tags, returns of high ($100) and standard ($5 or a hat) reward tags, and catch-at-age data to identify migration patterns and mortality rates of Albemarle Sound-Roanoke River striped bass. We developed an integrated multi-state model using these multiple data sources to estimate monthly rates of fishing (all sectors) and seasonal rates of natural (M_s) mortality for striped bass 458-900 mm TL at tagging and compared calculated annual instantaneous mortality rates (Z_a) to those for individuals greater than 900 mm TL. Monthly instantaneous estimates of mortality for striped bass 458-900 mm TL from the Roanoke River recreational (Frr_t), Albemarle Sound recreational (Frs_t), and Albemarle Sound commercial ($Fcom_t$) fisheries were fairly low (all medians <0.13), seasonally appropriate, and generally precise. Monthly estimates of catch-and-release (Fcr_t), as well as Pamlico Sound (Fp_t), mortality rates were very low. Seasonal estimates of M were very low expect during the summer, when rates were 0.23-0.28 per month. Sonic-tagged anadromous females (all >900 mm TL at tagging) only stayed in the Albemarle Sound-Roanoke River system during the spawning period (~1 month) and almost all reported harvest was from the Atlantic Ocean recreational fishery. Individuals greater than 900 mm TL experienced lower rates of total annual mortality (median Z_a= 0.49), especially lower natural mortality (median M_a= 0.18), than did striped bass 458-900 mm TL at tagging (median Z_a= 1.32). Returns of standard reward tags were valuable for estimating seasonal patterns in fishing mortality rates. Detections of PIT tags in fish houses and creel surveys helped identify seasonal patterns in fishing mortality, but also allowed for estimation of standard reward reporting rates. Estimated reporting rates were generally higher for the recreational fisheries (Roanoke median: 0.30; Other combined median: 0.33) than for the commercial fishery (median: 0.17), although 95% credible intervals overlapped for all estimates. Our results suggest that striped bass 458-900 mm TL experience higher rates of mortality, especially natural mortality in the summer, than identified in the current stock assessment.

Introduction

Striped bass, *Morone saxatilis,* is an economically and ecologically important migratory fish in freshwater and marine systems (Hartman and Brandt 1995; Hartman 2003; Patrick et al. 2006; Davis et al. 2012). Spawning populations are native to the Atlantic Coast from the St. Lawrence River in Canada to the St. Johns River, Florida. Most populations north of and including the Albemarle Sound, North Carolina, are anadromous, with some larger individuals

seasonally migrating into the Atlantic Ocean and residing in coastal and non-natal estuaries from Massachusetts to North Carolina during non-spawning periods (Chapoton and Sykes 1961; Dorazio et al. 1994; Waldman et al. 2012; Gauthier et al. 2013; Kneebone et al. 2014). In the Albemarle Sound-Roanoke River (AS-RR) system in North Carolina, most striped bass spawn in the Roanoke River from March to May (Hassler et al. 1981; Rulifson 1992; Carmichael et al. 1998). Although, most juvenile and small mature striped bass spend the remainder of the year in Albemarle Sound, larger individuals leave after spawning for marine habitats (Chapoton and Sykes 1961; Haeseker et al. 1996; Callihan et al. 2014). Some individuals become anadromous at ~600 mm total length (TL), but most do not appear to leave the AS-RR system until they are much larger (Callihan et al. 2014). Although there is spatial overlap during non-spawning periods, the AS-RR population is considered a distinct stock (ASMFC 1981; Waldman et al. 2012; Gauthier et al. 2013; Kneebone et al. 2014).

Striped bass in the AS-RR compose an economically valuable stock in North Carolina, supporting intensive commercial and recreational fisheries in the region, as well as contributing to Atlantic Coast fisheries (Richards and Rago 1999; Patrick et al. 2006; Callihan et al. 2014). Since they migrate and are harvested in multiple locations, the stock is managed jointly by the North Carolina Division of Marine Fisheries (NCDMF), the North Carolina Wildlife Resources Commission (NCWRC), and the U.S. Fish and Wildlife Service's South Atlantic Fisheries Coordination Office (Takade-Heumacher 2010). The stock is managed through a total allowable catch, seasonal open periods, length limits, bag limits, and gear limits. Striped bass can be commercially and recreationally harvested in Albemarle and Pamlico Sounds from October 1 to April 30 and can be recreationally harvested in the Roanoke River during spawning runs in March-April. In the estuaries, striped bass may be harvested when they are 18 inches (~458 mm TL) or larger, whereas in the Roanoke River, the minimum size is 18 inches, but there is also an exclusive slot of 22-27 inches.

The AS-RR striped bass stock has received extensive management since habitat loss, altered flow, and overfishing caused large population declines in the 1970s and 1980s (Hassler et al 1981; Olsen and Rulifson 1992; Patrick et al 2006). As a result of management, the stock was considered fully recovered by the Atlantic States Marine Fisheries Commission in 1997 (NCDMF and NCWRC 2004). Although this stock has received considerable research and management attention, harvest in recent years has been below the total allowable catch for all fisheries and there is still uncertainty regarding rates of fishing and natural mortality.

Accurate and precise estimation of mortality rates is essential for appropriate management of harvested species, but can be challenging especially for highly migratory

species that support multiple fisheries (including catch and release) in different geographic areas, such as the AS-RR stock of striped bass. Rates of fishing and natural mortality can be simultaneously estimated using fisheries dependent and independent tagging studies (Pine et al. 2003; Pollock et al. 2004; Bacheler et al. 2009; Hightower and Pollock 2013). Dependent methods involve an externally-visible tag attained by an angler or fisher when a tagged fish is captured. With information on reporting rate, reported tags directly inform on fishing mortality rates; however, natural mortality is often only indirectly assessed and can be imprecise with little information on seasonality and appropriately estimating reporting rate can be difficult. In contrast, internal tags, such as passive integrated transponder tags (PIT), sonic tags, and radio tags, are often detected only by scientists and mortality is assessed by the pattern of tag detection. Natural mortality can be detected directly in searchable systems, by repeatedly detecting a non-moving acoustic tag, but fishing mortality is usually assessed indirectly by the disappearance of tagged fish from the study area, since anglers do not always find internal tags (Hightower et al. 2001; Hightower and Pollock 2013). Estimating mortality rates using an entirely fishery independent approach may be unfeasible for species with geographically extensive movement patterns and fisheries.

The purpose of this study was to estimate mortality rates for AS-RR striped bass to aid in assessment and management of the stock. To estimate these rates, we combined data from telemetry, PIT tag detection, tag return, and catch-at-age using an integrated modelling approach. A combined approach can take advantage of the benefits of fishery dependent and independent sources to estimate parameters that cannot be estimated with one data source alone and to produce more accurate and precise estimates (Pollock et al. 2004; Kendall et al. 2006; Bacheler et al. 2009; Hightower and Pollock 2013). Our specific objectives were to: 1) produce seasonal estimates of natural mortality and monthly estimates of fishing mortality for all fisheries, including catch-and-release; 2) estimate patterns and behavioral impacts of catch-and-release fishing; 3) estimate tag reporting rates for low reward internal anchor tags; and 4) compare mortality rates for smaller striped bass, that appear to reside entirely within the AS-RR system, to those of larger anadromous individuals, that spend considerable time in coastal areas of the Atlantic Ocean.

Methods

We included two tagging approaches to estimate mortality rates using an integrated model: 1) a small number of striped bass were tagged with both a sonic and a high ($100) reward internal anchor tag with movement, mortality, and behavior after catch-and-release

assessed by detection on sonic receivers and return of high reward tags and mortality modeled using a multistate capture-recapture model (MSCR); and 2) many striped bass were tagged with a PIT and a standard ($5 or a hat) reward internal anchor tag, with PIT tags detected by biologists sampling a known or estimated proportion of the harvest and internal anchor tags returned by anglers and fishers, with mortality modeled using instantaneous rates formulations of tag return models (Brownie et al. 1985; Hoenig et al. 1998a). In addition, catch-at-age data were included in a catch-curve analysis. Likelihoods from all approaches, as well as those for other required parameters (such as tag retention rates) were evaluated together in one integrated model using Bayesian analysis methods with either JAGS or OpenBUGS software (Plummer 2003; Spiegelhalter et al. 2010). With the exception of standard reward reporting rate for the Atlantic Ocean recreational fishery (see methods), all priors were selected to be vague and are listed in Table 1. The joint likelihood of independent datasets is the product of all individual likelihoods which can be defined implicitly from the individual likelihood components in a Bayesian analysis, making it a fairly simple to integrate multiple data sources to estimate common parameters with appropriate variance (Rhodes et al. 2011; Kéry and Schaub 2012).

Field Methods

For tagging approach 1, striped bass (n=143, 445-695 mm TL) were collected by hook and line and by commercial pound net in the western side of Albemarle Sound (all <10 km from the mouth of the Roanoke River) between February and April in 2011 and 2012 (Figure 1). The objective was to tag striped bass that were or would soon be legal to harvest in the Albemarle Sound (i.e., 458 mm TL, n=138). In addition, larger striped bass were targeted for tagging by electrofishing on the spawning grounds at Weldon in late April in 2011 and early May in 2012 (Figure 1). Of the 19 collected individuals, 17 were females (939-1146 mm TL) and 2 were males (750 and 873 mm TL). Larger, older, striped bass are comparatively rare in the population and large females are likely highly fecund and thus can contribute comparatively more to population growth than smaller individuals (Boyd 2011). For surgical implantation of a Vemco V13-L (13 mm in diameter, 36 mm in length, and 11 g in air) sonic tag and a 23 mm half duplex PIT tag, each striped bass was anaesthetized with MS-222 (buffered with sodium bicarbonate to a pH of 7), measured for TL, and placed into a tagging cradle with its gills submerged in circulating water. In 2011, sonic tags had a random delay period of 30-90 seconds and an expected battery life of 622 days, whereas in 2012, the random delay was extended to 60-120 seconds and the battery life was extended to 880 days. A small incision (~2 cm) was made on the ventral side of the fish between the pelvic and pectoral fins. After placing

the sonic and PIT tag inside the body cavity, the incision was closed by 2-3 interrupted sutures with two wraps on each throw (Deters et al. 2012). After that, a small incision (<1 cm) was made on the left side of the striped bass below the musculature and a red high ($100) reward internal anchor tag was placed into the incision. Internal anchor tags gave basic instructions that if caught, the angler or fisher should cut the tag and call a North Carolina State University phone number for a $100 reward, then keep or release the fish, as planned. Striped bass were held in a tank until fully recovered from anesthesia and then, immediately released.

Movement patterns of live sonic-tagged striped bass were continuously monitored using stationary receivers (Vemco VR2s; Figure 1). North Carolina State University maintained multiple stationary receivers in the Roanoke River and the North Carolina Division of Marine Fisheries (Michael Loeffler, North Carolina Division of Marine Fisheries) maintained multiple stationary receivers in Albemarle Sound. Stationary receivers were downloaded and checked for any problems at least every 1-2 months (more frequently during the spring spawning season) and were generally operational in the AS-RR sampling area throughout the study period, although some receivers became non-operational or went missing at random and were replaced as soon as possible. Tagged striped bass were also detected outside the AS-RR system by other researchers. Most notably, striped bass (n=4, 558-609 mm TL) were detected on stationary receivers in the Pamlico Sound (Tim Ellis, North Carolina State University) and large female striped bass (n=14, >900 mm TL) were detected on stationary receiver arrays in coastal and estuarine areas (i.e., Virginia, Delaware, New York and Massachusetts) on the Atlantic Coast (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). Detections sent by other researchers from outside the AS-RR sampling area were incredibly valuable and greatly appreciated.

Identification of fishing deaths and rates of catch and release of sonic-tagged striped bass were evaluated by returns of high reward tags. When a high reward tag was returned, we obtained information on whether the fish was caught commercially or recreationally, the location and date of the capture, and whether the fish was kept or released, and then sent out the $100 reward. Survival and behavior patterns after catch and release were evaluated using manual tracking and by examining movement patterns on stationary receivers. Additional manual tracking was completed in the Roanoke River and western Albemarle Sound, mostly during the spring, to detect striped bass that died due to the tagging process or natural mortality. Mortality associated with surgery to implant sonic-tags (i.e., sonic-tagging mortality) was assumed when

a striped bass was continuously detected in the same location within the month of tagging; long-term impacts (either survival or behavioral) of the sonic-tag were not evaluated. Natural mortality was assumed when a tagged fish was continuously found in one area, but after the month of tagging and in a new location, suggesting that the striped bass actively moved before dying (Hightower et al. 2001). Some manual tracking was done in the Albemarle Sound, but because of the area's large size and the behavior and distribution of striped bass in the system, detections could rarely be assumed as natural mortality; thus, natural mortality was more often inferred in the model by a cessation in live detections on stationary receivers.

For tagging approach 2, striped bass at least 458 mm in TL (i.e., at least 18 inches) were collected by boat electrofishing on the spawning grounds at Weldon (rkm 208; Figure 1), March-May, 2011-2013, and tagged with a PIT and standard reward ($5 or a hat) internal anchor tag, as part of the North Carolina Wildlife Resources Commission and North Carolina Division of Marine Fisheries annual striped bass spawning and tagging surveys. Collected striped bass were measured for TL, examined for the presence of an internal anchor tag and scanned for the presence of a PIT tag. If a PIT tag was detected, the number was recorded. If an internal anchor tag was detected, it was recorded if the tag was readable (and number recorded), unreadable, or cut (due to catch and release fishing). If no tag was present, a small incision (<1 cm) was made on the left side below the musculature and a PIT tag was first inserted into the body cavity and then a low reward internal anchor tag was placed into the incision. For some striped bass, scales were taken and used by North Carolina Wildlife Resources Commission to create an age-length keyto determine the proportion of the run in each age class (McCargo and Dockendorf 2012; 2013; and 2014). Additional striped bass were tagged with only a PIT tag during 2011 just upstream of Williamston (~rkm 65), as part of a hydroacoustic study to estimate run sizes of anadromous species in the Roanoke River (Hughes 2012).

Although live detections were occasionally made by recapture during spawning ground electrofishing surveys, analysis of data from tagging approach 2 only included PIT detections and returns of harvested internal anchor tags. PIT tags were detected by North Carolina Division of Marine Fisheries, North Carolina Wildlife Resources Commission, and North Carolina State University creel and fish house samplers monitoring harvest from the Roanoke River recreational fishery, Albemarle Sound Recreational fishery, and Albemarle Sound Commercial fishery. Samplers recorded the total number of striped bass scanned for a PIT tag (sometimes this was estimated based on weight and the sizes of fish in a box, if striped bass were already packed for shipping) and any PIT tag numbers detected in the harvest. Information on total harvest (Albemarle Sound commercial fishery), and estimates of harvest

(Roanoke River and Albemarle Sound recreational fisheries) were produced by North Carolina Division of Marine Fisheries (Charlton Godwin, personal communication) and North Carolina Wildlife Resources Commission (McCargo and Dockendorf 2012; 2013; 2014) and were used to estimate the monthly proportion of the harvest from each sector that was scanned for PIT tags. Low reward internal anchor tags were returned to the North Carolina Division of Marine Fisheries by commercial fishers and anglers from any fishery with information on the date, location, and type (i.e., commercial or recreational) of capture and whether the striped bass was harvested or released. When released, sometimes the internal anchor tag was not clipped, although since the tag status was not always correctly recorded, it was assumed that the tag was always clipped. If a fish was caught on multiple occasions (i.e., first as a catch and release with an intact tag), then only the first reported capture was included.

Modeling Methods

Mortality rates were estimated separately for large (900 mm TL or larger) and small striped bass due to drastic differences in observed migration behavior and locations of harvest. The sample size of larger striped bass was small; thus modeling was somewhat simplified (described later) as compared to that for smaller striped bass, but was used to generally compare annual mortality rates between the life stages.

Modeling for striped bass less than 900 mm TL at tagging

Monthly rates of fishing mortality, by sector, and seasonal rates of natural mortality were estimated for striped bass less than 900 mm TL at tagging in the AS-RR system from March 2011 to May 2013. Sonic detections on stationary receivers and returns of high reward internal anchor tags were used to estimate monthly (t) mortality rates using a state-spaced MSCR model, with code modified from Kéry and Schaub (2012). Similar MSCR models combining live and dead recoveries have been used to evaluate movement patterns and the magnitude of different sources of mortality for a variety of species (Kendall et al. 2006; Bischof et al. 2009; Duriez et al. 2009). State-space models have two processes, the state process (i.e., an individual's "true" state) and the observation process (i.e., what was actually observed), modeled by separate categorical distributions in the likelihood. For our model, true states were a function of the individual's survival status (i.e., alive or dead by a specific fishery), as well as status of the individual's high reward internal anchor tag (i.e., intact or cut/lost), with model probabilities denoting transitions between different true states from one month to the next. The observation process links an individual's true to state to what is actually observed; thus allowing

us to account for non-100% detection of live individuals or natural mortality during each month (Kéry and Schaub 2012).

True states for each monthly period (t) were: 1) alive with an internal anchor tag; 2) reported harvest by commercial fishing in the Albemarle Sound ($Fcom_t$); 3) reported harvest by recreational fishing in the Roanoke River (Frr_t); 4) reported harvest by recreational fishing in the Albemarle Sound (Frs_t); 5) reported harvest by combined recreational and commercial fishing in the Pamlico Sound system (estuary and tributary rivers; Fp_t); 6) reported harvest of the internal anchor tag, but release of the individual fish ($Fcrp_t$); 7) natural mortality (M_s); 8) alive without an internal anchor tag (i.e., the tag was cut or lost); and 9) undetermined type of death (i.e., death after removal or loss of the internal anchor tag). Jiang et al. (2007) developed a tag return model for striped bass to incorporate catch and release by evaluating tag return probabilities in terms of tag "death" (i.e., tag removal from the population) as distinguished from actual fish death, which is calculated indirectly. This concept works for our striped bass tag returns, since we have removal of internal anchor tags via both catch and release and tag loss. Transition probabilities between true states in our model are modified from Hightower et al. (2001) and are seen in Figure 2, where total monthly instantaneous mortality of high reward internal anchor tags (ZT_t) is estimated by the following:

$$ZT_t = Fcom_t + Frr_t + Frs_t + Fp_t + Fcrp_t + M_s + TagL$$

and survival for high reward internal anchor tags (ST_t) was estimated as $\exp(-ZT_t)$. $TagL$ was the instantaneous rate of internal anchor tag loss and was estimated using information from recapture of PIT and low reward internal anchor tagged striped bass during spawning ground surveys. Specifically, the number of striped bass recaptured after some number of months at large (with a detected PIT, a readable internal anchor, or both) and the number with a readable internal anchor tag were used to estimate $Ret.IA$ using a binomial likelihood; $TagL$ was the instantaneous rate of tag loss (Jiang et al. 2007). Internal anchor tag loss was considered independent of PIT tag loss and loss of both tags was not addressed, but would be minimal. After an internal anchor tag is lost or cut, a subsequent death cannot be identified to a specific mortality component. Natural mortality (M_s) was estimated seasonally (March-May, June-August, September-November, December-February) since monthly estimates were very imprecise and seasonal estimates appeared to adequately capture variability. Total monthly instantaneous mortality (Z_t) for striped bass (458-900 mm TL) was estimated as:

$$Z_t = Fcom_t + Frr_t + Frs_t + Fp_t + Fcr_t + M_s$$

where Fcr_t is the monthly instantaneous rate of mortality associated with catch and release and was estimated indirectly as $Fcrp_t * p.CR_t$, with $p.CR_t$ equal to the monthly mortality rate

associated with an incidence of catch and release (Kerns et al. 2012). Since we only identified one instance of immediate mortality associated with catch and release in our study and catch and release mortality appears associated with water temperature (Nelson 1998; Bettinger et al. 2005; Millard et al. 2005), we used data on hooking mortality of striped bass in the Roanoke River from Nelson (1998) in a logistic regression to estimate this mortality as a function of water temperature (CRa = intercept for logistic regression model and CRb = slope for impact of temperature). The monthly estimate of the proportion of caught and release striped bass expected to perish ($p.CR_t$) was estimated using average monthly water temperature at the USGS gauging station at Halifax in the Roanoke River. Although potentially important, long-term survival impacts of catch and release as well as impacts of multiple incidents of catch and release were not assessed. Monthly survival (S_t) for striped bass was estimated as $\exp(-Z_t)$. Two annual rates of total fishing (F_a, all fisheries combined) and natural mortality (M_a) were calculated from May 2011 to April 2012 and from May 2012 to April 2013 as the sum of all monthly estimates during those periods. One estimate of annual total instantaneous mortality (Z_a) was calculated based on both years to compare to striped bass greater than 900 mm TL (see below).

For the observation process, we accounted for non-detection of an individual's true state. It was assumed that all intact high reward tags on caught striped bass were returned and information was reported without error; thus, there was no non-detection of harvest or catch and release of an individual with an intact internal anchor tag. All sonic-tag detections of live striped bass (with or without an intact internal anchor tag) on stationary receivers were collapsed into monthly intervals within the MSCR model; thus, an individual detected at any time within a month was considered alive and detected for that month. Monthly detection probabilities (p_t) were estimated since detection was impacted by the number of functional stationary receivers available during that month. Detection was also impacted by individual differences such as tag delay period and location within the system, which would be partially accounted for by monthly estimates. Detections of natural mortality were rare; thus one mean detection probability ($p.M$) was estimated for all months within the MSCR model. Although expulsion of surgically implanted sonic-tags has been observed for other species (Boone et al. 2013), we assumed no sonic-tag loss in our study, since we detected no evidence of such over the study period (i.e., retrieving a high reward-tagged fish at harvest that did not have a sonic-tag or a sonic tag detection pattern that did not match a reported catch timing or location, etc.). Delayed (i.e., after one month) sonic-tag expulsion that resulted in death is theoretically possible and would appear

as natural mortality; however, we have no information to allow for its inclusion and thus it was assumed to be minimal.

Mortality rate estimation from striped bass tagged with a PIT and a low reward internal anchor tag was completed using an instantaneous rates formulation of the Brownie tag return model (Brownie et al. 1985; Hoenig et al. 1998a). Independent multinomial likelihoods were developed for PIT tag detections (by biologists in fish houses and creels) and for low reward tag returns (from anglers and fishers), since detections were independent of returns. Although striped bass were tagged approximately weekly during the spawning run, all individuals tagged during a given month were collapsed into a monthly cohort for analysis.

PIT tags were detected by scanning harvest in three fishery sectors (s): Albemarle Sound commercial, Roanoke River recreational, and Albemarle Sound recreational; thus PIT tag detections contributed directly to estimates of $Fcom_t$, Frr_t, Frs_t. Within the multinomial likelihood there were three cell probabilities per month (t) for each released cohort (i), and each represented the expected number of PIT tag detections from one of the three fishery sectors (s). The expected number of PIT tags detected would be the product of the total number tagged, exploitation in that sector (s) by month (t), and any nuisance parameters. Cohort (i) cell probabilities ($PIT\ Cell p_{its}$) for monthly periods (t) and for each of the three sectors (s) were represented by the following:

$$PIT\ Cell\ p_{its} = p.S_{ts} * p.Ret * TagS * CS_{it} * \frac{F_{ts}}{Z_t} * (1 - \exp(-Z_t))$$

where $p.S_{ts}$ is the proportion of harvest from sector (s) scanned during month (t), $p.Ret$ is the proportion of PIT tags retained, $TagS$ is immediate tagging survival, CS_{it} is cumulative survival for individuals within cohort (i) from tagging until month (t), $\frac{F_{ts}}{Z_t}$ is the proportion of total instantaneous mortality (Z_t) during month (t) attributed to fishery sector (s), and $(1 - \exp(-Z_t))$ is total mortality for month (t). The proportion of harvest, by sector, that was scanned was estimated from a binomial distribution, with information on the total number of striped bass scanned and total harvest (either estimated or known). Unlike low reward tag loss, PIT tag loss did not appear to increase over time and thus it was assumed that an initial tag loss value would be appropriate; it was similarly estimated using a binomial likelihood within the larger integrated model. Initial survival from capture and tagging with an internal anchor and PIT tag was assumed to be 99%. For the first period after release, an additional parameter was included to account for multiple release dates within the month and non-mixing (Hoenig et al. 1998b; Waterhouse and Hoenig 2011). Since striped bass were tagged throughout the spawning period at the spawning grounds at Weldon, newly tagged individuals were not available until

tagged (i.e., not all were tagged at the start of the month) and even once tagged, were not immediately available to fisheries in the Albemarle Sound (newly tagged individuals were assumed to be immediately available to the Roanoke River recreationally fishery, since captures have been reported even from the day of release). Thus, newly released cohorts were set as available to the Roanoke River Recreational fishery (NMRR) at the average time an individual was released during the month, which was almost half way into the month (0.45). Newly tagged individuals were set as available to Albemarle Sound fisheries (NME) based on the number of these tags that were returned from Albemarle Sound fisheries during that month, compared to what would be expected based on total harvest in all fisheries and the number returns from those cohorts in the Roanoke River recreational fishery, which was 0.07.

Returns of standard reward internal anchor tags directly contribute to estimates of all sources of harvest mortality (i.e., $Fcom_t$, Frr_t, Frs_t, Fp_t), as well as patterns in catch and release for legal-sized striped bass ($Fcrp_t$). Within the multinomial likelihood there were five cell probabilities (i.e., five $Low\ Reward\ Cell p_{its}$) per month ($t$) for each released cohort (i), and each represented the expected number of low reward tags returned from each sector including: Albemarle Sound commercial, Roanoke River recreational, Albemarle Sound recreational, Pamlico combined, and combined catch and release. For tag cohorts (i), $Low\ Reward\ Cell p_{its}$ for all monthly periods (t) and for each of the five sectors (s) was represented by the following:

$$Low\ Reward\ Cell\ p_{its} = p.RR_s * TagS * CST_{it} * \frac{T_{ts}}{ZT_t} * (1 - \exp(-ZT_t))$$

where $p.RR_s$ is standard reward reporting rating by sector (s), CST_{it} is cumulative survival for a cohort of low reward tags (i) from tagging until month (t), $\frac{T_{ts}}{ZT_t}$ is the proportion of total instantaneous mortality (i.e., removal) of tags (ZT_t) during month (t) attributed to fishery sector (s), and $(1 - \exp(-ZT_t))$ is total removal for standard reward internal anchor tags for month (t). Three standard reward tag reporting rates were estimated within the model: Albemarle Sound commercial ($p.Com$), Roanoke River recreational ($p.RR$), and Other combined ($p.O$); $p.Com$ was associated with harvest in the Albemarle Sound Commercial fishery, $p.RR$ was associated with harvest in Roanoke River recreational fishery, as well as catch and release during the month of release since striped bass were tagged in the Roanoke River, and $p.O$ was associated with all other harvest and catch and release. Similar to the PIT tag likelihood for fish, a non-mixing parameter (i.e., NMRR for cell probabilities associated with the Roanoke River and NME for all other areas) was included in $Low\ Reward\ Cell p_{its}$ during the month after release to account for the spatial and temporal timing of release.

In addition to the two tagging approaches, catch-at-age data collected by North Carolina Wildlife Resources Commission were used in a catch-curve analysis (i.e., linear regression of the natural log of percentages caught by estimated age) to contribute to annual estimates of total mortality (Z_a). Only catches of striped bass aged as 3-10 years were included in analysis, since those individuals were generally 458-900 mm TL (McCargo and Dockendorf 2012; 2013; 2014) and thus would correspond to the sizes of striped bass included in this analysis.

Modeling for striped bass 900 mm TL or greater at tagging

An integrated model including MSCR and tag return likelihoods were used to estimate mortality rates for striped bass greater than 900 mm TL at tagging. In contrast to smaller striped bass mainly detected and harvested in the AS-RR system with some harvest and detection in the Pamlico system, all large sonic-tagged female striped bass appeared to spend only about one month in the AS-RR system (during the spawning period in late April to early May) and all other detections were from coastal areas of the Atlantic Ocean. In addition, most tag returns from striped bass at least 900 mm TL at tagging were from recreational harvest in the ocean, with one commercial harvest in the AS-RR system during the spawning period. Given that sample sizes were small, we included movement data and tag returns from May 2011 to December 2013 to estimate fishing and natural mortality for the AS-RR system and the Atlantic Ocean. Similar to Rudd et al. 2014, periods were not modeled as months, but as live detections or returns from one of the two locations within the year, such that periods 1, 3, and 5 were live detections or returns from the AS-RR system during the springs in 2011, 2012 and 2013 and periods 2, 4, and 6 were live detections or returns in the Atlantic Ocean during summer through the winter after those spring spawning periods. Since we did not detect any PIT tagged striped bass in the ocean and only one high reward tag was returned from the ocean, we used a stochastic variable (a uniform from 0.2 to 0.4) as an estimate of reporting rate for low reward internal anchor tags in the tag return cell probability. This range for reporting rate would generally be expected given estimated recreational reporting rates for smaller striped bass (see results). We modeled and incorporated internal anchor tag retention assuming that $TagL$ would be the same for larger striped bass, as it was for smaller individuals (i.e., we used the same data). We did not include any non-mixing parameter. Since stationary receiver coverage was very high in the Roanoke River, especially on the spawning grounds and few fish appeared to be missed during the entire period of Atlantic Ocean residence (i.e. 11 months), detection within each period was high, so we estimated one mean detection probability to be assigned to all periods. We did not detect any natural mortality and thus all natural mortality was assessed

indirectly by the cessation of detections on stationary receivers. We had no indication that any large striped bass were caught and released in any location and thus catch and release and any associated mortality was assumed to be negligible. We estimated average monthly rates of fishing and natural mortality for the AS-RR system (FAS and MAS, respectively) and for the Atlantic Ocean (FO and MO, respectively) and calculated average annual rates of fishing (F_a), natural (M_a), and total (Z_a) instantaneous mortality for these large females based on the amount of time spent in each area (i.e., 1 month in the AS-RR system and 11 months in the Atlantic Ocean).

Results

To estimate mortality rates for striped bass 458-900 mm TL, 103 sonic and high reward tagged individuals, 3,617 PIT tagged individuals, and 3,789 internal anchor tagged individuals were included in analysis. Of the 103 sonic and high reward tagged individuals, 7 (6.8%) were reported as harvested through the commercial fishery in Albemarle Sound, 2 (1.9%) were reported as recreationally harvested in the Albemarle Sound, 2 (1.9%) were reported as recreationally harvested in the Pamlico Sound, five (4.9%) were reported as recreationally harvested in the Roanoke River, and 12 (11.7%) were reported as caught and released by one of those fisheries. No striped bass 458-900 mm TL were reported as caught in any other area. All striped bass reported were harvested during legal periods and detection patterns on stationary receivers corroborated angler and fisher reports. All fish reported as catch and release, were caught by recreational anglers in April, May, and June. Five of the 12 were caught in April, during the legal season to harvest, but two of those were released because they were inside the protective slot in the Roanoke River. One individual was caught and released in Albemarle Sound, one was caught and released at the mouth of the Roanoke River, and the remaining 10 individuals were caught and released in the Roanoke River between Williamston and Roanoke Rapids. We detected one mortality associated with catch-and-release; it occurred in mid-June at the mouth of the Roanoke River. Although there was variability in timing and migration behavior into and out of the Roanoke River during the spring spawning period, it did appear that there may have been a behavioral effect of catch and release for striped bass caught below the spawning grounds at Weldon (Figure 3). One of the two fish caught below the spawning grounds fell back just after catch and release, but then continued to Weldon. The other striped bass fell back and did not return to make a spawning migration until the following spring. A similar fall back was seen for a striped bass not reported to be caught and released (Figure 3), but this was not common; thus it is unclear if this individual was a non-reported catch

and release, a lost internal anchor tag followed by catch and release, or if this behavior is part of normal variability. Striped bass caught and released at Weldon showed no fallback behavior.

We scanned 24.5% of the commercial harvest in Albemarle Sound fish houses and detected 41 PIT tags. Much lower percentages of the recreational harvest were estimated to be scanned (8.2% in the Roanoke River and 5.3% in the Albemarle Sound) due to the dispersed nature of those fisheries in both time and space. We detected 10 PIT tags in the Roanoke River recreational fishery and only one in the Albemarle Sound recreational fishery. Standard reward tags could be returned from any fishery at any time and were returned from the commercial (n=37) and recreational (n=45) fisheries in the Albemarle Sound, the recreational fishery in the Roanoke River (n=65), a combined recreational and commercial fishery in the Pamlico Sound (n=4), and as a result of catch and release from any of the above areas (n=138). Standard reward tags from striped bass 458-900 mm TL were not returned from any other locations.

The natural log of the estimated percentage of striped bass in each included age class (i.e., age 3-10) caught in the Roanoke River during the spring spawning survey generally showed a linear pattern of decline with age. The linear pattern of decline is not illustrated for striped bass below age-3 or above age-10. Less than 5% of the spawning population was composed of individuals over the age of seven (Figure 4).

Monthly patterns in fishing mortality rates for striped bass 458-900 mm TL were consistent with monthly periods of legal harvest (Figure 5). Monthly rates of fishing mortality were highest in March and April, when striped bass were conducting the spawning migration and all fisheries were open for harvest. Fishing mortality rates were generally smaller, but not non-existent, during all months when harvest was legal in Albemarle Sound. In contrast, natural mortality was generally highest during the summer and almost non-existent during the rest of the year. Catch and release rates were also highest during the spring spawning migration period, although catch and release was reported during almost all months. Catch and release mortality was very low, since the months of highest catch and release (often April and May) were periods with cool water temperature. Total annual instantaneous fishing mortality was similar between the two years and was lower than total annual natural mortality in both years (Table 2). Overall, the average annual total instantaneous mortality rate for fish 458-900 mm TL was 1.32 (95%: 1.07-1.63), resulting in an annual survival estimate of 27%. The model estimated that total annual mortality rate was at least 1.00 with a probability of 1. Natural mortality in the summer, when most striped bass were in the Albemarle Sound was the largest single monthly component of mortality for striped bass 458-900 mm TL (Figure 5).

Estimated rates for all nuisance parameters can be found in Table 2. PIT tags were retained in 71 of the 74 striped bass included in the PIT tag loss estimation and internal anchor tags were lost or became unreadable over time, with 52 of 61 retained and readable over the 25 months examined. Reporting rates were estimated to be similar for the two recreational fisheries (~1/3) and were generally higher than that for the Albemarle Sound commercial fishery, although 95% credible intervals overlapped for all fisheries. Detection probability was highest during spring, when most sonic-tagged striped bass were concentrated in the Roanoke River, since it did not appear that any striped bass that conducted a spawning run into the Roanoke River was undetected by all stationary receivers there (Figure 6). Detection probability was lowest during the fall, when striped bass were most dispersed throughout the Albemarle Sound, and possibly when striped bass were moving around the least. In general, detection probability declined overtime, as stationary receivers were lost in the Albemarle Sound and the representative individuals had sonic tags with a longer delay (i.e., average delay for fish tagged in 2011 was 60 seconds, as compared to 90 seconds in 2012).

The integrated multi-state model for large striped bass (i.e., those greater than 900 mm TL at tagging) was composed of 14 sonic and high reward tagged females and 122 individuals (females and males) tagged with a PIT and a low reward internal anchor tag. All large females were sonic-tagged at Weldon, the spawning grounds in the Roanoke River, and all were later detected by stationary receivers in the Atlantic Ocean. In addition, all large females that were later detected, were found to return to Weldon to spawn during each spring. Two sonic-tagged individuals were known to be harvested, one recreationally in the Atlantic Ocean off of Massachusetts and the other in the Albemarle Sound commercial fishery during the spring spawning migration. Of the 122 low reward tagged individuals, 9 were reported as recreationally harvested in the Atlantic Ocean off the coasts of Massachusetts, New York, and New Jersey and none were reported from any other areas. Annual estimates of both fishing and natural mortality were lower for larger female striped bass, as compared to individuals between 458 and 900 mm TL, although 95% credible intervals overlapped for annual estimates of fishing mortality (Table 2). In contrast to smaller individuals, annual fishing mortality rates for larger, anadromous females were estimated to be higher than annual instantaneous natural mortality rates. In general, recreational fishing mortality in the Atlantic Ocean appeared to be the largest contributor to total annual mortality for large anadromous striped bass in the AS-RR system, whereas for smaller individuals high natural mortality in Albemarle Sound in the summer, appeared to be the largest contributor to annual mortality, although fishing mortality was also substantial, especially during the spring when harvest occurred for all fisheries.

Discussion

Accurate and precise estimates of mortality rates are essential for appropriate assessment and management of harvested species. The use of an integrated model to assess striped bass mortality rates in the AS-RR allowed us to take advantage of the strengths of multiple data sources to produce estimates that would otherwise be less accurate and precise (Pollock et al. 2004; Kendall et al. 2006 Abadi et al. 2010; Maunder and Punt 2013). The combination of live detection of sonic-tagged individuals on stationary receivers with reported harvest of their high reward tags provided extensive, high quality data on mortality from all sources and was especially valuable for estimating seasonal patterns in natural mortality, since manually searching the entire AS-RR area was logistically impossible. However, low sample sizes would have made estimating seasonal patterns in fishing mortality difficult and imprecise at best, since few individuals with high reward tags were harvested by any fishery at any time during the study. Each tagged fish (as well as maintaining the multiple stationary receivers) was very expensive and congregations of tagged fish, especially during the spring spawning migration, caused clashing on stationary receivers, limiting the total number of individuals tagged using this method. The addition of tag return data improved estimates of seasonal patterns in fishing mortality, since a higher proportion of the population could be tagged with an external tag and thus individuals were returned from all fisheries throughout the season. Tag return models alone can produce valid estimates of fishing mortality rates, as long as reporting rate can be effectively estimated (see Pollock et al. 1991; 2001; 2002), but natural mortality is estimated only indirectly and seasonal patterns could not be assessed during periods without harvest (i.e., April-October in this study). Detections of PIT tags also contributed to identification of fine scale temporal patterns in some fishing mortality rates, but were most beneficial for estimating reporting rates of low reward tags. Detections of PIT tags were very useful in the Albemarle Sound commercial fishery since catch must be reported, making harvest a known (not estimated) value and thus the proportion scanned was known. In addition, scanning a larger proportion of the harvested population in the commercial fishery was possible, as compared to the dispersed (both spatially and temporally) recreational fisheries, since commercially harvested striped bass were concentrated in the limited number of fish houses, which could were often contacted to maximize the proportion scanned for PIT tags. Although time consuming, scanning of harvest by biologists has considerable value, since it alleviates the need to assume that any tags (even those with high rewards) are all reported (Pollock et al. 2001). Inclusion of data on catch-at-age in a catch curve was also useful for establishing overall

rates of mortality. Evaluating mortality rates from catch-at-age data involves entirely different assumptions than those for tagging studies; evaluating multiple independent data sources with different assumptions and thus potential biases, likely results in a more accurate evaluation of mortality rates. Bayesian techniques (i.e., Markov-chain Monte Carlo simulation) allowed us to estimate distributions for each included parameter using information from all of these available data sources, analyzed by their component likelihoods (Rhodes et al. 2011; Kéry and Schaub 2012); thus, we could directly produce median estimates with appropriate variability. This makes Bayesian approaches ideal for the evaluation of integrated models such as this.

Although the use of multiple data sources in an integrated model likely reduces potential bias and increases precision, it is important to critically assess both assumptions and estimates. Our results suggested that annual instantaneous mortality is considerably higher than reported in the current striped bass stock assessment for the AS-RR population (Takade-Heumacher 2010). In the current stock assessment, estimates of mortality rates from 1982-2008 are made using a forward projecting catch-at-age model, including catch data from multiple fishery independent surveys and fishery dependent catch data, as well as an assumed natural mortality rate of 0.15 for all ages. Model estimates for fishing mortality ranged from about 0.1 to 1.0, but have declined recently to 0.1-0.4, resulting in an estimate of Z_a that would be considerably less than 1 in most examined years (which had a probability of zero in our model). There are three main potential causes of bias in our estimates that could lead to inflated estimates of M_a: 1) sonic-tag expulsion, 2) delayed tagging mortality (any tag type), and 3) emigration to areas not covered by stationary receivers. Sonic-tag expulsion has been seen for other fish species (Moore et al. 1990; Daniel et al. 2009; Boone et al. 2013) and would result in apparent disappearance of the individual from the population. We did not detect any evidence of sonic tag expulsion (i.e., all striped bass reported as harvested appear to show a pattern of sonic detections as would be expected and often we were able to retrieve the sonic tag from the angler or fisher) and we accounted for expulsion of internal anchor and PIT tags by direct estimation. Delayed tagging mortality is difficult to assess, but likely occurs for sonic-tagged individuals and should not be ignored. Any delayed mortality associated with the tag or tagging process would appear as natural mortality, although we might expect that delayed tagging mortality would result in a less dramatic seasonal mortality pattern. Emigration to areas without coverage by stationary receivers would also appear as natural mortalities, since individuals would cease to be detected on receivers. Although we did not detect evidence of permanent emigration, it is possible that a limited number of individuals migrated undetected north to Chesapeake Bay. Random temporary emigration for short periods of time should be accounted

for by estimating detection probability. In addition, it has been observed that collapsing live detections into bins (i.e., months) can cause bias in survival estimation, although the 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). How this bias influences estimates in an integrated model including live recaptures, dead recaptures, and catch-at-age, is unknown, but considering we generally observed high estimates of survival over estimation periods, we consider the bias to be minimal. In contrast, for many fish species, larger individuals are more responsive to electrofishing stimuli (Saunders et al. 2011; Price and Peterson 2010; Benejam et al. 2012), which could bias our catch curve estimates of total mortality low. A combined approach would result in an estimate that was intermediate (based on sample sizes) and would have high imprecision if there was significant disagreement. Improved methods to assess bias in estimates and goodness of fit for these types of integrated models would be beneficial (Lebreton et al. 1999), but combing different data sources likely improves the accuracy of the overall assessment, especially if final values also appear relatively precise, as seen in our study.

Results from our model suggest that striped bass 458-900 mm in TL in the AS-RR system experience moderate, and fairly similar, rates of fishing mortality from the Albemarle Sound recreational fishery, the Albemarle Sound commercial fishery, and the Roanoke River recreational fishery, as well as low rates of mortality from harvest in the Pamlico Sound and associated with catch and release fishing. As expected, Roanoke River recreational fishing mortality was very concentrated to the early part of the spring spawning run, whereas, Albemarle Sound fisheries were more temporally dispersed, but often peaked during or just before the spawning run, when detections suggested that many striped bass were moving around a lot and often concentrated near the mouth of the Roanoke River. Although natural mortality was very low during most of the year, it was fairly substantial during summer months, when water temperatures peaked in Albemarle Sound. During the summer, striped bass in Albemarle Sound were sometimes observed to be in poor physical condition (i.e., low relative weight and high occurrence of lesions), potentially as a result of thermal stress, which seemed especially prevalent for individuals larger than 325 mm TL (Haeseker et al. 1996). Overall the total instantaneous mortality rate for striped bass in the AS-RR system resulted in an annual survival rate of 27%, potentially resulting in the relatively small proportions of fish over 7 years of age collected during spawning surveys.

In contrast to striped bass less than 900 mm TL, larger anadromous females had a much lower annual instantaneous mortality rate corresponding to an annual survival rate of

61%. Sonic-tagged females over 900 mm TL at tagging spent considerably little time in the Albemarle Sound, appearing to use it only as a corridor to reach spawning grounds in the Roanoke River from the Atlantic Ocean in the spring; however, they experienced the highest natural mortality rates during this short period in the AS-RR system, after conducting the spawning migration (i.e., between leaving the Roanoke River and being detected by stationary receivers in the Atlantic Ocean). Higher natural mortality rates for large anadromous females in the AS-RR system, compared to the Atlantic Ocean, may be a function of spawning stress, warmer water temperatures, reduced feeding, or a combination. It has been suggested that larger individuals can 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 (Dorazio et al. 1994; Secor and Piccoli 2007; Mather et al. 2009; Callihan et al. 2014). After migration, larger anadromous striped bass are then vulnerable to recreational fisheries in northern areas of the Atlantic Coast. Although it appears that basically all individuals over 900 mm TL in the AS-RR system are anadromous, it is unclear what proportion of the Atlantic coast stock is composed of individuals from the AS-RR system (Gauthier et al. 2013; Kneebone et al. 2014) and it likely changes over time. Stock proportions may be affected by the average size at emigration, which may differ between populations (Dorazio et al. 1994; Mather et al. 2009; Callihan et al. 2014). Detections sent from biologists working in various rivers and coastal areas along the Atlantic Coast were incredibly valuable for assessing both mortality rates and movement patterns of large striped bass. Sonic and high reward tagging a larger number of these large anadromous individuals, potentially with larger tags with longer battery life would continue to provide useful information on their mortality rates, movement patterns, and contribution to Atlantic Coast catch.

Although we have separated fish into two distinct size classes (i.e., larger anadromous individuals and smaller resident individuals), size likely impacts mortality on a finer scale for striped bass. For juvenile fish, survival often increases with size, as they become less available to predators (Lorenzen 1996; Sogard 1997). However, natural mortality for larger, but not yet anadromous, striped bass may be more impacted by summer thermal stress in the Albemarle Sound, than for smaller resident individuals (Haeseker et al. 1996). Fishing mortality rates are 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 of striped bass may be more available and targeted by fisheries in Albemarle Sound, especially commercial fisheries. The natural log of catch-at-age data generally appeared to show a fairly linear decline over the ages 3-10, which would suggest that striped bass in this range had similar total mortality, even if specific patterns varied. Striped

bass below age-3 were less represented in the catch likely because they had not fully recruited to the spawning population (i.e., a large proportion did not conduct a spawning migration and remained during the spawning period in Albemarle Sound). Those above age-10 showed a lower mortality rate; however, data from these age classes should be evaluated with great caution, since larger individuals were sometimes targeted in the spring spawning survey and there were very small numbers in each older age class in most years. Callihan et al. (2014) found that migration of AS-RR striped bass to coastal waters generally initiated around 600 mm TL and the proportion to emigrate increased with size. In general, striped bass 700-800 mm TL had the highest probability of being reported as caught in coastal areas adjacent to North Carolina, whereas striped bass were more frequently caught in northern coastal waters starting at 800-900 mm TL. We tagged only a few (n=48, 2 with sonic tags) striped bass 700-900 mm TL, so our mortality results may not apply to the size category that emigrates from the AS-RR system (usually ages 8-10), but does not migrate north. Overall, size likely impacts vulnerability to specific types of mortality; however, our two classifications appear to capture large changes in mortality resulting from the change to an anadromous life history, with the possible exception of striped bass 700-900 mm TL.

Catch and release did not appear to contribute substantially to total mortality, likely because water temperatures during periods of high catch and release rates were adequately low (Nelson 1998; Bettinger et al. 2005; Millard et al. 2005); however, the catch and release fishery may also impact population growth by altering spawning behavior. Although there was considerable variability in spawning migration behavior, we observed that both of the striped bass reported as caught and released below the spawning grounds initiated a fall back behavior after release, with one fish later heading to the spawning grounds and the other abandoning the spawning run for that year. How much this pattern is a function of small sample sizes and natural variability, as compared to the impacts of catch and release, is unknown. This behavior was not observed for striped bass caught-and-released at Weldon. It may be that striped bass caught and released on the spawning grounds do not illustrate a fallback behavior because they are among conspecifics, as compared to during the run, when they might only encounter others in passing. It is also possible that repeated incidence of catch-and-release have a greater impact that identified by our study. Fish size impacts rates of catch-and-release, since undersized striped bass are often reported as released and no individuals over 900 mm TL were reported as caught-and-released. Impacts of catch-and-release mortality on small individuals and how this source of mortality affects population growth warrant further study. Very few large individuals appear to be caught at all in the AS-RR system. Despite their low numbers, the

combination of lower mortality and higher fecundity of large females (Boyd 2011) likely results in their increased importance to population growth and persistence.

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Table 1: Prior distributions for all estimated parameters in the integrated multi-state model for striped bass 458-900 mm TL at tagging (upper table) and over 900 mm TL at tagging (lower table) in the Albemarle Sound-Roanoke River system. Parameters with subscript "t" have independent estimates for each month. Natural mortality was estimated seasonally and has a subscript "s". For all other parameters, only one estimate was produced that was applied to all monthly periods in the model. The two parameters for uniform prior distributions indicate range, whereas they represent mean and precision=1/variance for a normal distribution.

Parameter	Description	Prior Distribution
$Ln(Fcom_t)$	Natural log of monthly fishing mortality for the Albemarle Sound commercial fishery	Uniform (-10,1)
$Ln(Frr_t)$	Natural log of monthly fishing mortality for the Roanoke River recreational fishery	Uniform (-10,1)
$Ln(Frs_t)$	Natural log of monthly fishing mortality for the Albemarle Sound recreational fishery	Uniform (-10,1)
$Ln(Fp_t)$	Natural log of monthly fishing mortality for the Pamlico Sound fishery	Uniform (-10,1)
$Ln(Fcrp_t)$	Natural log of monthly tag mortality associated with the catch and release fishery	Uniform (-10,1)
$Ln(M_s)$	Natural log of seasonal natural mortality	Uniform (-10,1)
$Ret.p$	Retention rate for PIT tags	Uniform (0,1)
$Ret.IA$	Monthly retention rate for internal anchor tags	Uniform (0,1)
CRa	Intercept for logistic regression of catch and release survival as a function of temperature	Normal (0,0.01)
CRb	Slope for logistic regression of catch and release survival as a function of temperature	Normal (0,0.01)
p_t	Monthly detection probability for live detections on stationary receivers	Uniform (0,1)
$p.M$	Detection probability for natural mortality	Uniform (0,1)
$p.Com$	Reporting rate for the Albemarle Sound commercial fishery	Uniform (0,1)
$p.RR$	Reporting rate for the Roanoke River recreational fishery	Uniform (0,1)
$p.O$	Reporting rate for other fisheries combined	Uniform (0,1)
$Ln(N0)$	Intercept for catch curve	Uniform (0,20)
CC_sd	Standard deviation for catch curve	Uniform (0,10)

Parameter	Description	Prior Distribution
$Ln(FAS)$	Natural log of monthly fishing mortality in the Roanoke River-Albemarle Sound	Uniform (-10,1)
$Ln(FO)$	Natural log of monthly fishing mortality in the Atlantic Ocean	Uniform (-10,1)
$Ln(MAS)$	Natural log of monthly natural mortality in the Roanoke River-Albemarle Sound	Uniform (-10,1)
$Ln(MO)$	Natural log of monthly natural mortality in the Atlantic Ocean	Uniform (-10,1)
$Ret.IA$	Monthly retention rate for internal anchor tags	Uniform (0,1)
p	Monthly detection probability for live detections on stationary receivers	Uniform (0,1)
$p.R$	Reporting rate	Uniform (0.2,0.4)

Table 2: Median estimates (with 95% credible intervals) from posterior distributions for mortality rates and all nuisance parameters estimated from the integrated multistate model for the Albemarle Sound-Roanoke River population of striped bass 458-900 mm TL (upper table) and larger than 900 mm TL (lower table).

Parameter	Description	Median (95% interval)
F_{a1}	Annual total instantaneous fishing mortality for year 1 (May 2011-April 2012)	0.53 (0.40 - 0.70)
F_{a2}	Annual total instantaneous fishing mortality for year 2 (May 2012-April 2013)	0.34 (0.23 - 0.52)
M_{a1}	Annual total instantaneous natural mortality for year 1 (May 2011-April 2012)	0.83 (0.63 - 1.05)
M_{a2}	Annual total instantaneous natural mortality for year 2 (May 2012-April 2013)	0.94 (0.63 - 1.29)
Z_a	Average annual total instantaneous mortality (years combined)	1.32 (1.07 - 1.63)
P(Z_a)>1	Probability that annual total instantaneous mortality is greater than 1	1.00 (1.00 - 1.00)
$Ret.p$	Retention rate for PIT tags	0.94 (0.86 - 0.98)
$Ret.IA$	Monthly retention rate for internal anchor tags	0.94 (0.92 - 0.96)
$TagL$	Monthly estimate of internal anchor tag loss	0.06 (0.04 - 0.09)
CRa	Intercept for logistic regression of catch and release survival as a function of temperature	-8.67 (-13.18 - -4.77)
CRb	Slope for logistic regression of catch and release survival as a function of temperature	0.31(0.13 - 0.52)
$p.M$	Detection probability for natural mortality	0.10 (0.08 - 0.13)
$p.Com$	Reporting rate for the Albemarle Sound commercial fishery	0.17 (0.10 - 0.27)
$p.RR$	Reporting rate for the Roanoke River recreational fishery	0.30 (0.21 - 0.43)
$p.O$	Reporting rate for other fisheries combined	0.33 (0.23 - 0.47)
$Ln(N0)$	Intercept for catch curve	12.86 (11.14 -15.03)
CC_sd	Standard deviation for catch curve	1.5 (0.93 - 2.49)

Parameter	Description	Median (95% interval)
FAS	Monthly fishing mortality in the Roanoke River-Albemarle Sound	0.014 (0.001-0.083)
FO	Monthly fishing mortality in the Atlantic Ocean	0.025 (0.011-0.055)
MAS	Monthly natural mortality in the Roanoke River-Albemarle Sound	0.130 (0.000-0.371)
MO	Monthly natural mortality in the Atlantic Ocean	0.001 (0.000-0.027)
F_a	Annual total instantaneous fishing mortality (areas combined)	0.29 (0.13-0.64)
M_a	Annual total instantaneous natural mortality (areas combined)	0.18 (0.01-0.48)
Z_a	Average annual total instantaneous mortality (areas combined)	0.49 (0.23-0.93)
$Ret.IA$	Monthly retention rate for internal anchor tags	0.96 (0.93-0.98)
p	Monthly detection probability for live detections on stationary receivers	0.95 (0.83-0.99)
$p.R$	Reporting rate	0.30 (0.21-0.40)

Figures

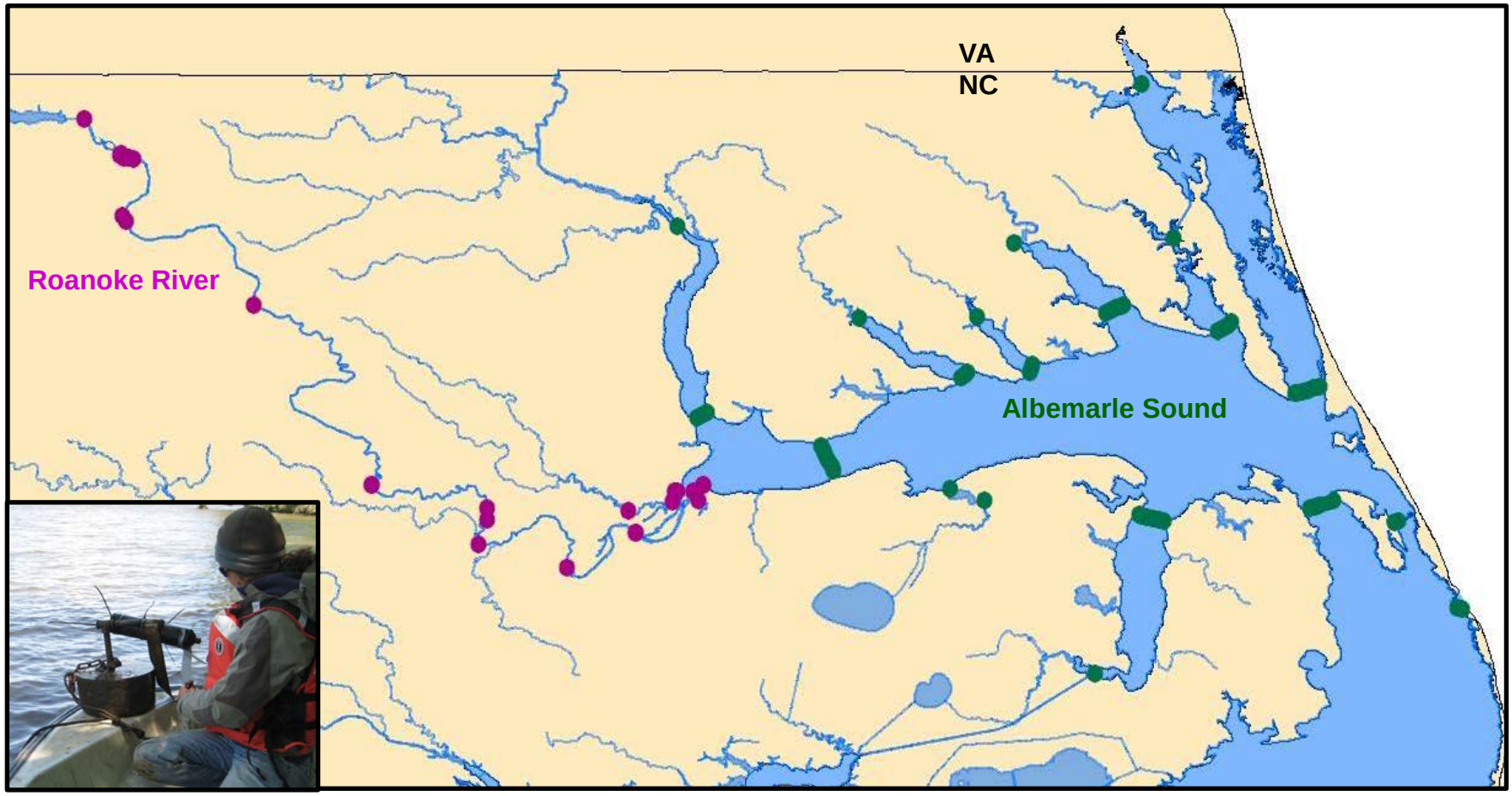

Figure 1: Locations of stationary receivers in the Roanoke River (Pink) and Albemarle Sound (Green), North Carolina.

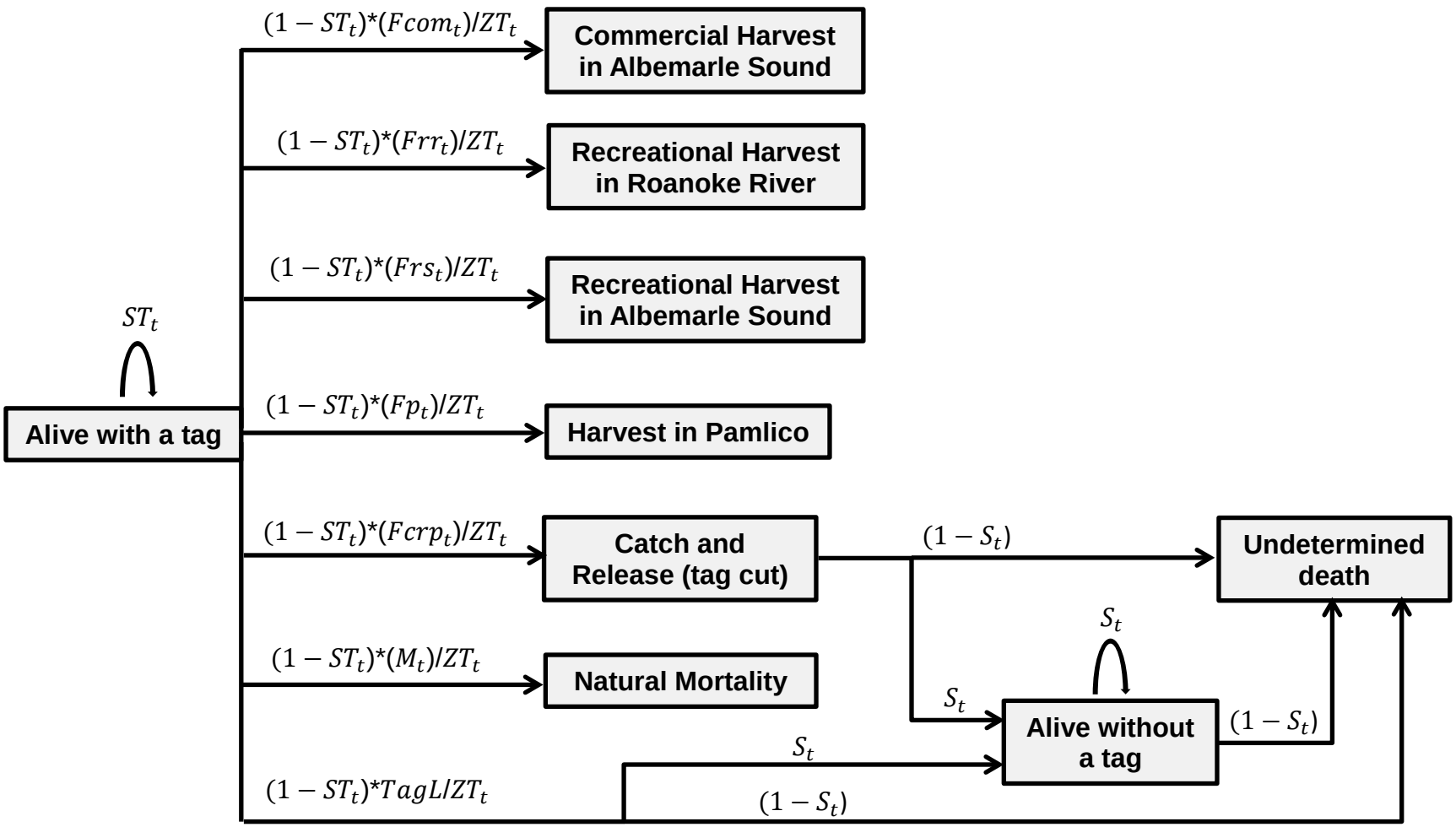

Figure 2: Diagram illustrating all possible true states (grey boxes) and transition probabilities (arrows with equations above) for the multi-state capture recapture model for striped bass 458 to 900 mm TL at tagging in the Albemarle Sound-Roanoke River system, NC. Definitions for parameters in equations can be found in the text.

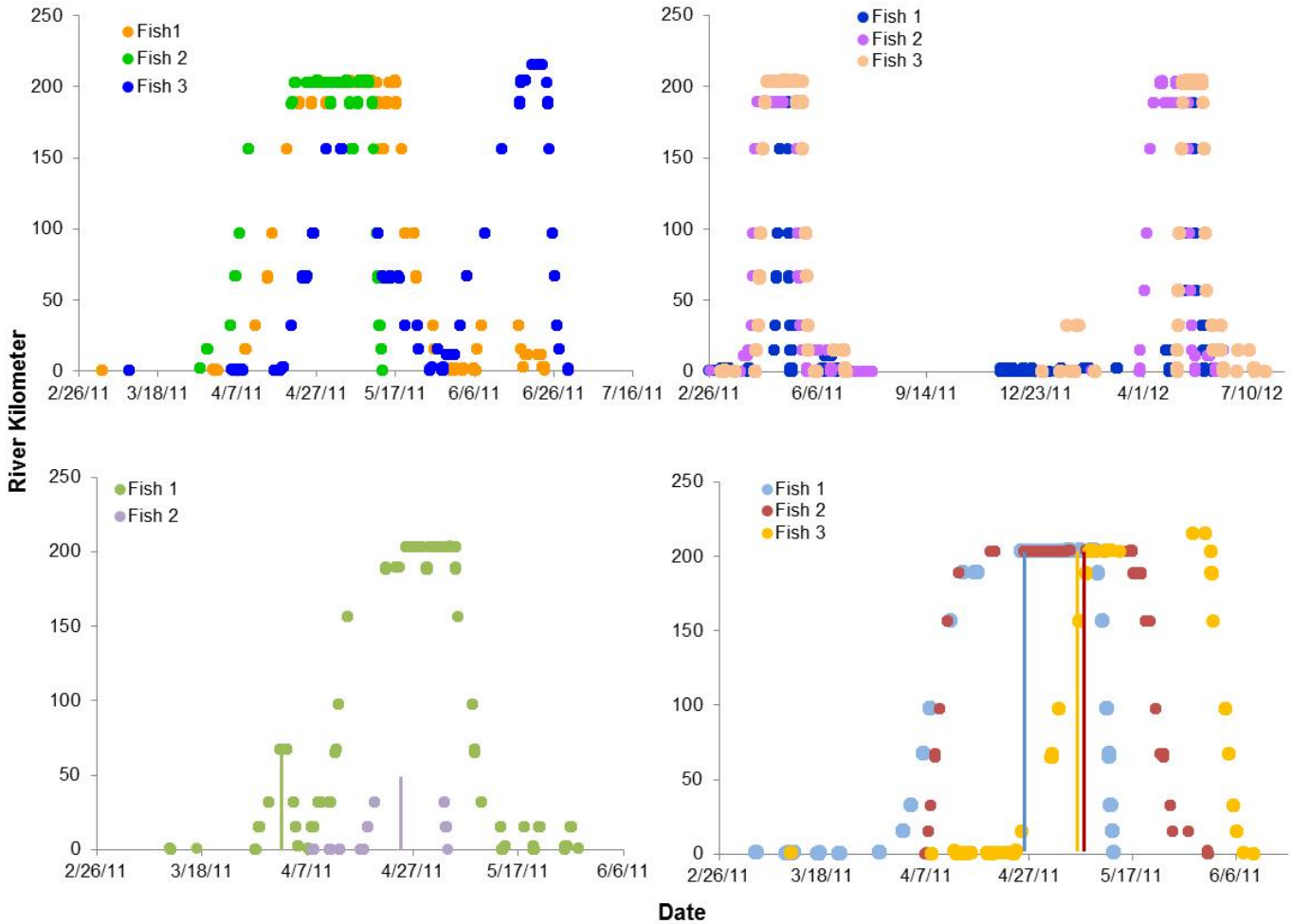

Figure 3: Movement patterns of striped bass 458-900 mm TL in the Roanoke River, NC. Circles indicate detections on stationary receivers, by river kilometer. The upper panel shows examples of movement patterns for striped bass not reported as caught and released in 2011 (left panel) and in 2011 and 2012 (right panel). The lower panel shows all striped bass reported as caught and released below Weldon in the Roanoke River in 2011 (left panel) and three fish reported as caught and released at Weldon (right panel). The line depicts the location and date of reported catch and release for the individual with circles of the same color.

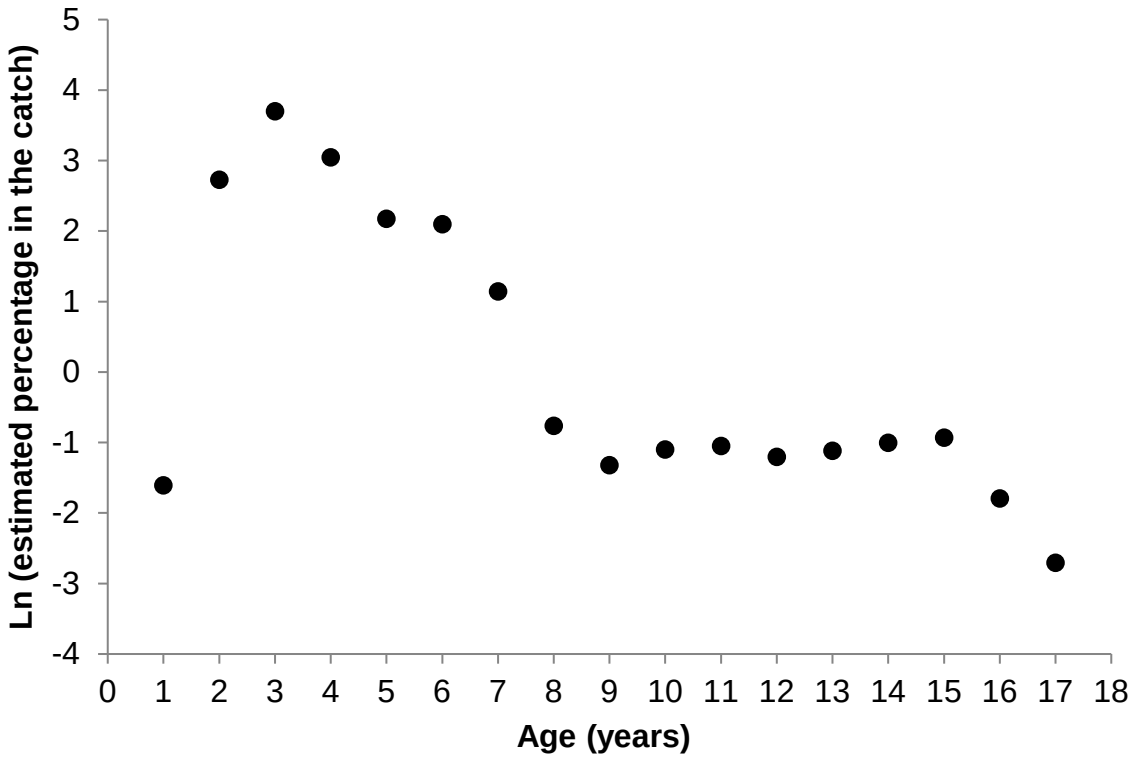

Figure 4: Natural log of the estimated percentage of different age classes of striped bass caught during the spring spawning survey by North Carolina Wildlife Resources Commission and North Carolina Division of Marine Fisheries in the Roanoke River, NC. Percentages were estimated by developing an age-length key, by evaluating scales for age assignment and recording length at collection.

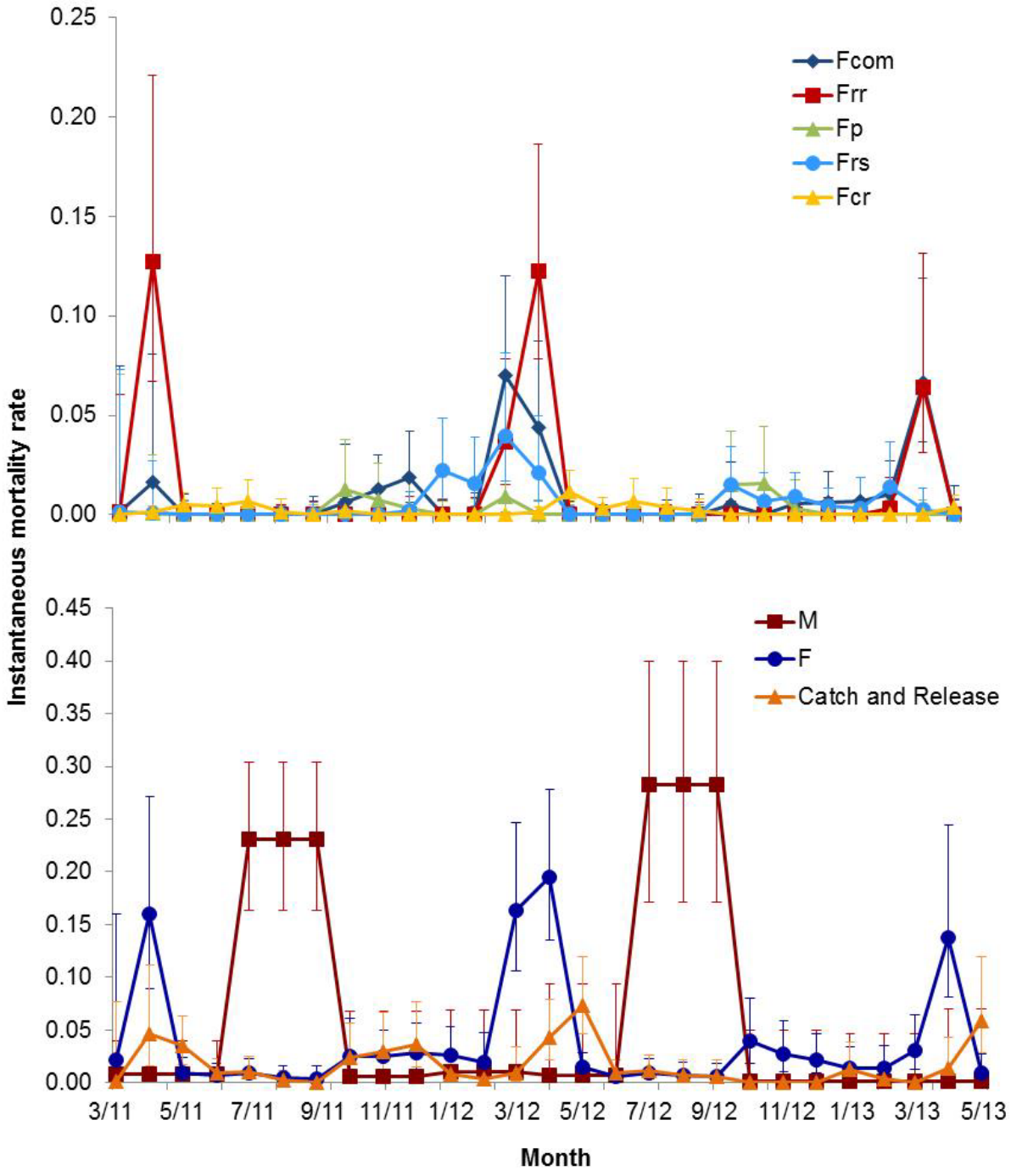

Figure 5: Monthly fishing mortality rates, by sector (upper panel), as well as monthly rates of total fishing mortality (i.e., sum of all fisheries; F), seasonal rates of natural mortality (M) and monthly rates of catch and release (lower panel) for striped bass 458-900 mm TL in the Albemarle Sound-Roanoke River system. "Fcom" = fishing mortality from the commercial fishery in the Albemarle Sound, "Frr" = fishing mortality from the recreational fishery in the Roanoke River, "Fp" = fishing mortality from the recreational and commercial fisheries in the Pamlico system, "Frs" = fishing mortality from the recreational fishery in Albemarle Sound, and "Fcr" = mortality associated with catch and release.

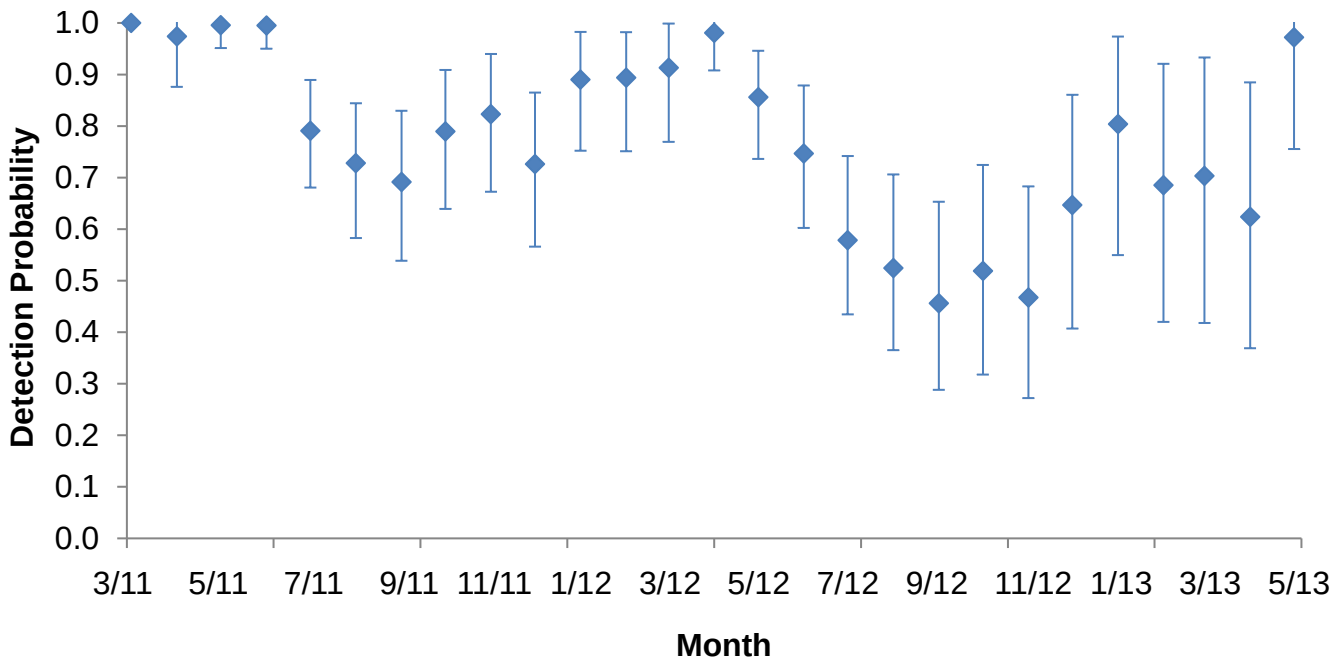

Figure 6: Estimated monthly detection probability for sonic-tagged striped bass 458-900 mm TL in the Albemarle Sound-Roanoke River system.