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Juvenile and Adult Striped Bass Mortality and Distribution in an Unrecovered Coastal Population

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Abstract

Striped Bass *Morone saxatilis* fisheries have been important in the eastern United States since the 1700s, but many populations have declined from historic levels. Enhancement programs, harvest reduction, water quality improvements, and habitat restoration have led to successful recoveries for specific stocks. However, these efforts have not been successful for the Striped Bass population in the Neuse River of North Carolina. Possible mechanisms inhibiting recovery of this population include overharvest, high discard mortality, poor water quality, and altered flow regimes. These mechanisms and their impacts on the Neuse River population are unclear; therefore, to gain insight, we estimated mortality and distribution of the population. Specifically, we tagged 100 hatchery-reared phase II juveniles (202–227 mm TL) and 111 resident adults (349–923 mm TL) with acoustic transmitters (a subset of 50 adults was also tagged with external high-reward tags). We used telemetry to monitor movement and seasonal distribution from December 2013 until September 2015. Telemetry and tag reporting data informed mortality models, and we estimated that annual discrete total mortality of phase II stocked juveniles was 66.3% (95% credible interval [CI] = 47.4–82.4%). Annual discrete total mortality of adults was 54.0% (95% CI = 41.5–65.4%). Adult discrete natural mortality was 20.1% (95% CI = 8.7–39.1%), and neither juvenile nor adult natural mortality was correlated with seasonal variation in dissolved oxygen, temperature, or salinity. These results show that poststocking mortality is significant and that juvenile mortality should be considered when establishing stocking goals. Additionally, adult natural mortality is within the range predicted by maximum age and by previous studies; however, adult total mortality is higher than targeted rates. These results can help to inform management decisions and develop measures to rebuild depressed Striped Bass populations like that in the Neuse River.

The Striped Bass *Morone saxatilis*, a North Atlantic anadromous species, has contributed to important fisheries in the eastern United States since the 1700s (Merriman 1941; Hawkins 1980). However, as is the case with other North Atlantic diadromous species, many Striped Bass

populations have declined from historic levels (Pearson 1938; Merriman 1941; Koo 1970; Rulifson and Manooch 1990; Limburg and Waldman 2009). In response, research to identify mechanisms contributing to the decline and subsequent recovery efforts have been undertaken to

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rebuild specific stocks along the Atlantic seaboard (Richards and Rago 1999). Through research, the roles of harvest (Hawkins 1980; USDOI and USDOC 1993; NCDMF and NCWRC 2013), water quality (Polgar et al. 1976; Setzler-Hamilton et al. 1981; Buckler et al. 1987; Breitburg et al. 2009), flow regimes (Rulifson and Manooch 1990; Burdick and Hightower 2006), and environmental factors (Rulifson and Manooch 1990; Richards and Rago 1999) have been identified as key components in the conservation of Striped Bass.

In 1984, Congress passed the Atlantic Striped Bass Conservation Act, which required all states to adhere to an interjurisdictional management plan (Atlantic Striped Bass Conservation 1984). In addition to strict federal fishing regulations, statewide policies were implemented. For example, enhancement programs were established in Maryland, Delaware, and Virginia, which led to stocking over 7 million fingerling Striped Bass into the Chesapeake Bay from 1985 to 1993 (Weaver et al. 1986; USDOI and USDOC 1993); and in North Carolina, where over 53,000 fingerling Striped Bass were stocked into the Roanoke River from 1981 to 1996 (NCDMF and NCWRC 2013). In combination, significant harvest restrictions, flow regime management, and substantial stocking efforts brought about remarkable improvements; the Chesapeake Bay and Roanoke River stocks were declared fully recovered in 1995 and 1997 (Richards and Rago 1999; NCDMF and NCWRC 2013).

Unfortunately, not all restoration efforts have led to successful recoveries. Like the Chesapeake Bay and Roanoke River stocks, the Neuse River stock of North Carolina collapsed (NCDMF and NCWRC 2013); by 1984, restoration efforts that included federal fishing restrictions and a stocking program were implemented. The U.S. Fish and Wildlife Service stocked approximately 125,000 phase I (defined by size; 35–50 mm TL) juvenile Striped Bass into the Neuse River annually from 1994 to 2014 (except 2002, 2010, and 2011), and about 100,000 phase II (150–200 mm TL) juveniles were stocked into the river during alternate years from 1992 to 2006 and then every year thereafter (except 2008; NCDMF and NCWRC 2013). Furthermore, the removal of the Quaker Neck Dam at river kilometer (rkm) 225 in 1998 restored access to more than 48% of historical spawning grounds (120 km of potential mainstem spawning habitat and 1,488 km of potential tributary spawning habitat) for Striped Bass and other anadromous fishes in the Neuse River (Hawkins 1980; Beasley and Hightower 2000; Burdick and Hightower 2006). After the dam's removal, Striped Bass once again returned to these historic spawning grounds, as evidenced by the presence of eggs and larvae collected throughout this reach (Burdick and Hightower 2006).

Despite implementation of restrictive harvest regulations, substantial stocking for nearly two decades, and

dam removal, the management goals for the Neuse River Striped Bass population have not been achieved. The fisheries management plan outlined by the North Carolina Wildlife Resources Commission (NCWRC) and the North Carolina Division of Marine Fisheries (NCDMF) aims to (1) rebuild a self-sustaining population that will support sustainable harvest while conserving adequate spawning stock and maintaining a broad age structure; and (2) protect the integrity of habitats to support growth, survival, and reproduction (NCDMF and NCWRC 2013). However, there has been no evidence of a substantive increase in abundance or age structure of Striped Bass in the Neuse River. Although there are no population abundance estimates from formal stock assessments, CPUE has remained low and has not increased since 1992, and virtually no fish over age 10 have been observed in the Neuse River population (Homan et al. 2012; NCDMF and NCWRC 2013). Limited available historical information suggests that the Neuse River population was likely always smaller than the Roanoke River population, but the absence of larger, older fish in the population is troubling. Furthermore, there is no evidence of natural Striped Bass recruitment to the juvenile stage. Barwick et al. (2009) sampled juveniles during summer in 2006 and 2007; based on oxytetracycline marks in otoliths, all individuals were confirmed to be hatchery progeny. Likewise, application of parentage-based tagging (PBT) methods showed that in 2016, all 610-mm and smaller Striped Bass sampled in the Neuse River ($n = 116$) were hatchery reared; only larger fish, likely from year-classes that predated the PBT program, were of unknown origin (Jeremy McCargo, NCWRC, personal communication).

Low population abundance, a truncated age distribution, and a lack of recruitment are complex issues that have most likely been caused by a combination of fishing-related and environmental factors at multiple life stages. Even with harvest limits, populations may be impacted by recreational catch-and-release mortality, commercial discard mortality (i.e., bycatch), or harvesting of the most fecund individuals. High numbers of Striped Bass are caught recreationally (e.g., 10,927 individuals in 2014) in the Neuse River, and the majority (~90%) of those caught are released (due to both angler choice and regulations; NCDMF and NCWRC 2013). Even though the fate of released individuals has been estimated in previous studies (Nelson 1998; Graves et al. 2009), the estimated rates vary considerably. More population-specific information on the fate of individuals after catch and release would improve our understanding of the impact of catch-and-release angling on the overall population. Furthermore, overall fitness of the population may be reduced due to harvest of the largest and most fecund individuals. Olsen and Rulifson (1992) found that in the Roanoke River, age-3 Striped Bass produced about 180,000 eggs, whereas age-10 fish

produced over 2 million eggs. Smaller females not only display lower fecundity but also produce eggs (and subsequent larvae) that are up to 20% smaller than those produced by larger females (Monteleone and Houde 1990); smaller sizes can reduce the survival of embryos and larvae (Secor 1990) and can ultimately reduce juvenile recruitment (Cowan et al. 1993).

Environmental factors, including poor water quality and low streamflow, may also impede stock recovery. Excessive nutrient loading in the Neuse River has contributed to seasonal hypoxia, which can lead to reductions in egg hatching (Turner and Farley 1971), increases in larval mortality (Rogers et al. 1977) and juvenile mortality (Chittenden 1971), and decreases in growth rates of juvenile fish via both direct and indirect mechanisms (Campbell and Rice 2014). Mortality of juvenile Striped Bass can occur at dissolved oxygen (DO) levels at or below 3.0–3.6 mg/L (Chittenden 1971; Coutant 1985), and all ages of Striped Bass avoid DO concentrations below 2–3 mg/L (Coutant and Benson 1990). Streamflow may be another driver; Striped Bass eggs depend on velocities between 0.31 and 5.0 m/s, as flows outside this range can increase egg mortality (Mansueti 1958; Albrecht 1964; Regan et al. 1968; Beasley and Hightower 2000).

To better understand the lack of recovery by Striped Bass in the Neuse River, we estimated mortality rates at different life stages and explored distribution patterns with survival and spawning implications. Specifically, through the use of telemetry, we evaluated natural mortality of stocked juvenile and resident adult Striped Bass and investigated potential correlations between mortality and water quality. Additionally, with a combination of high-reward tags and telemetry, we evaluated the discard mortality (a combination of recreational catch-and-release and commercial discard mortality) and harvest mortality (a combination of recreational and commercial harvest) of adult Striped Bass. Lastly, we evaluated seasonal distribution of Striped Bass, including up-river migration during the spring.

METHODS

Study area.—The Neuse River originates northwest of Raleigh, North Carolina, at the confluence of the Eno and Flat rivers and flows southeast approximately 435 km to the Pamlico Sound. The watershed drains 16,000 km² of productive and rapidly developing urban, industrial, and agricultural areas and contains about 16% of the state's population (NCDENR 2002; Burkholder et al. 2006). The upper third of the river lies within the Piedmont region and has a relatively high gradient (USGS 1995). The river slows and broadens as it crosses the coastal plain, with an average discharge of 82 m³/s near Kinston, North Carolina (USGS 1995). At New Bern, North Carolina, the

Neuse River abruptly widens and changes from a flowing river to a wind-mixed estuary until it empties into the Pamlico Sound (Burkholder et al. 2006). We monitored Striped Bass throughout the entire Neuse River; however, more detailed data were collected in the lower Neuse River from rkm 46 to rkm 66 and in the lower 9 km of the Trent River (hereafter collectively referred to as the “study area”; Figure 1). The stocking location for Striped Bass was situated approximately in the middle of our study area (Figure 1).

Juvenile fish tagging.—We surgically implanted individually coded Vemco V7 ultrasonic transmitters (4 × 18 mm, 1.4 g in air; Vemco Ltd., Halifax, Nova Scotia) into 50 hatchery-raised, phase II juvenile Striped Bass (mean = 209 mm TL; range = 202–227 mm) at the Edenton National Fish Hatchery on December 18, 2013. Transmitters were programmed to include a 5-d fast and 25-d slow emission rate over a 30-d cycle. During the fast emission period, transmitters emitted a signal every 15–45 s, and on the remaining days the transmitters emitted a signal every 200–300 s, which resulted in a 212-d battery life. Before surgery, all surgical tools were sterilized in an autoclave. Tools that were reused on surgery day were disinfected in glutaraldehyde for at least 15 min and were rinsed with deionized water (Wagner et al. 2011). Acoustic transmitters were also disinfected in glutaraldehyde overnight and were rinsed with deionized water. All fish were anesthetized to stage-3 sedation (i.e., partial loss of equilibrium; Summerfelt and Smith 1990) in an aerated, 70-L induction tank containing 50 mg/L of tricaine methanesulfonate (MS-222) buffered with sodium bicarbonate. After fish exhibited partial equilibrium loss, they were transferred to a surgery table. During surgery, the fish were kept anesthetized by continuously irrigating the gills with a 30-mg/L solution of buffered MS-222. Wearing a new pair of latex surgical gloves, the surgeon used a sterile scalpel to make a small incision (approximately equal to the width of the transmitter) along the linea alba and posterior to the pelvic girdle (Wagner et al. 2011). The transmitter was inserted into the body cavity through the incision, which was then closed using two or three interrupted sutures (polydioxanone absorbable synthetic monofilament 3-0 FS-1; Ethicon, Cornelia, Georgia; Wagner et al. 2011). After surgery, fish were allowed to recover from anesthesia in an aerated 150-L tank treated with Stress Coat (Aquarium Pharmaceuticals, Franklin, Tennessee). Water temperature in all tanks was monitored, and water was replaced as needed to minimize temperature fluctuations.

On the day after surgery, juvenile fish were transported in a 379-L hauling tank and released near New Bern, North Carolina (Figure 1), along with a subset of the 113,800 phase II juveniles that were stocked in 2013. We wanted to monitor juveniles for at least 365 d poststocking, but because of limited transmitter battery

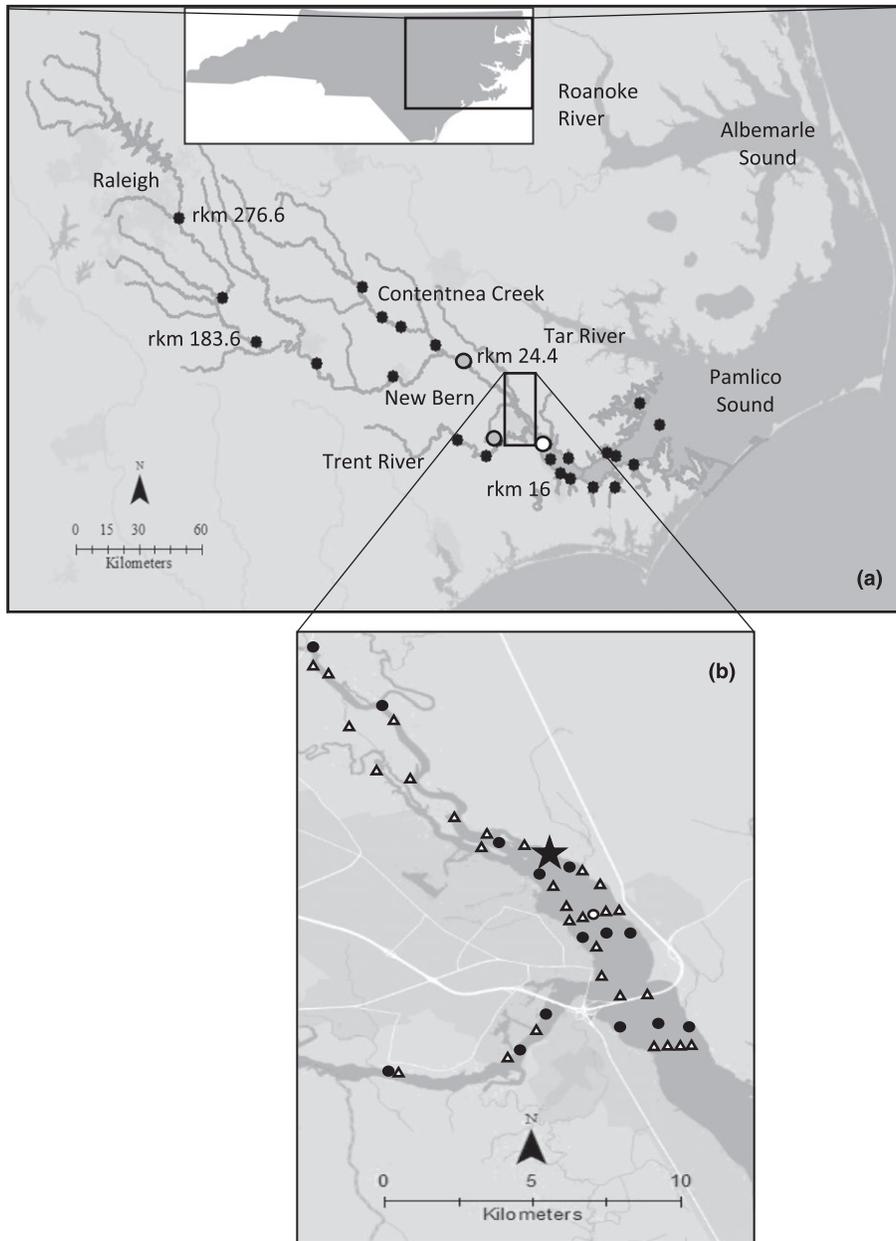


FIGURE 1. (a) Map of the entire Neuse River and its tributaries in North Carolina (black circles = receivers that were located outside of the study area; gray circles = receivers in the Neuse and Trent rivers that marked the beginning boundary for up-river migration; white circle = receiver where 14 juvenile Striped Bass were detected); and (b) map of the study area in the Neuse and Trent rivers (star = stocking location; closed circles = monthly water quality monitoring stations; open circle = location of the water quality data sondes; triangles = receivers at the boundaries and inside the study area).

life we could not do this with one set of transmitters. Therefore, we tagged a second group of 50 juveniles (mean = 215 mm TL; range = 192–245 mm) from the same cohort (assumed based on size). These fish were collected via electrofishing at various locations throughout the study area during May 7–22, 2014. After capture the fish were placed in a 530-L holding tank and were transported (1–10 km) to shore, where a surgery station was

located. As with the first cohort of juveniles, we implanted individually coded Vemco V7 ultrasonic transmitters via the surgical protocol described above. The transmitters were identical to those used in the first group of juveniles except that improved programming technology increased efficiency and thus increased the battery life to 300 d. After recovery from surgery fish were immediately released at the surgery location.

Adult fish tagging.—We tagged 111 subadult and adult Striped Bass (range = 349–923 mm TL; hereafter, “adults”) that made up two cohorts. These included legally harvestable fish as well as some individuals that were below minimum harvest size (457 mm) or within the no-harvest slot limit (559–686 mm; joint and inland waters). The first cohort comprised 50 fish (mean TL = 485 mm; range = 349–720 mm) that were collected by electrofishing throughout the study area from February 21 to March 14, 2014. As with field-collected juveniles, captured adult fish were placed in a 530-L holding tank and were transported (1–10 km) to shore, where a surgery station was located. Individually coded Vemco V13 ultrasonic transmitters (13 × 36 mm; 11 g in air) were implanted into all adults by using the surgical protocol outlined above. Transmitters were programmed identically to those of the juvenile fish but had a 612-d battery life because of the larger battery size. Each fish was also tagged externally with a high-reward (\$100) Floy FM-95W internal anchor tag (5 × 16-mm disk; Floy Tag, Inc., Seattle). A scale was removed about 2 cm posterior to the tip of the left pectoral fin; then a lateral incision of approximately 0.5 cm was made with a scalpel at the location of the removed scale, and the tag’s anchor was inserted through the incision. The second cohort consisted of 61 adults (mean TL = 672 mm; range = 556–923 mm) that were collected by electrofishing throughout the Neuse River from March 2014 to April 2015. These Striped Bass were tagged in accordance with the surgical protocol outlined above except that the fish were immobilized by electronarcosis (anesthesia accompanied by muscle relaxation through electrical inhibition; Hudson et al. 2011).

Transmitter retention study.—To evaluate the possibility of surgery-related mortality and transmitter loss, we conducted a 30-d retention study with 30 phase II juvenile Striped Bass at the Edenton National Fish Hatchery in December 2013. Half of the fish were treated identically to the acoustic-tagged juveniles, except that instead of implanting live transmitters we implanted replica transmitters of identical size and weight. The remaining 15 fish were controls, which were also treated identically (i.e., handled, anesthetized, etc.) except that they did not undergo surgery. The replica-tagged and control fish were randomly selected and interspersed with acoustic-tagged fish during tagging to ensure similar conditions. After undergoing treatment, fish were held in 6,000 L of hatchery water within an 8.9-m³ circular holding tank and were fed fish pellets daily. Water temperature and DO were recorded each day, and fish behavior and survival were monitored. After 30 d, we euthanized all fish in an overdose solution of MS-222 (>200 mg/L) and inspected the internal and external condition of the fish and the incision site.

Telemetry.—We used a combination of passive and active tracking to continuously monitor the distribution

and movement of tagged juvenile and adult Striped Bass within our study area from December 2013 to September 2015. We placed 30 Vemco VR2W 69-kHz passive receivers within and at the boundaries of the study area (Figure 1); the receivers continuously recorded the identity of any transmitters detected. Additionally, 25 receivers were placed over a much larger reach of the Neuse River extending from near Milburnie Dam (rkm 277; Raleigh, North Carolina) to the river mouth (Figure 1); this allowed us to detect possible up-river spawning migration and emigration into the sound or the ocean.

After conducting the range test protocol outlined by Vemco, we determined that tagged juveniles could be detected up to about 200 m from a receiver and that tagged adults could be detected up to about 400 m from a receiver. The receiver arrangement changed throughout the study in response to vandalism and fish distribution; however, the boundaries remained relatively fixed. At the upper bounds of the study area (on both the Neuse and Trent rivers), we established gates consisting of a down-river receiver separated by approximately 1 km from an up-river receiver, which allowed for identification of emigrants and immigrants (Figure 1). At the lower boundary of the study area, we placed a transect of receivers approximately 400 m apart across the river. We were only able to use one transect of receivers at this lower boundary because the river was very wide (1.8 km). Because there was not a true gate on this boundary, we assumed that a fish had emigrated downstream in two situations: (1) if the fish was detected as moving from an up-river receiver to the lower transect or (2) if the fish was detected on the lower transect and subsequently either was detected on a receiver downstream from the study area or was not detected in the study area for at least 1 month. In addition to passive tracking, we manually searched the study area for tagged fish (juveniles and first adult cohort only) every month for 4–5 d (i.e., during the fast emission period) at 600 fixed listening points by using a Vemco VR100 manual receiver and an omnidirectional hydrophone. Many locations that were manually searched had subpar conditions for telemetry (e.g., shallow water and cypress trees); therefore, we conducted a range test in these locations via the Vemco protocol and determined that the manual receiver had a 100-m detection range for juveniles and a 200-m detection range for adults in areas with subpar conditions. Therefore, the listening points were separated by approximately 200 m and covered the entire study area. We listened at all 600 points during the fast emission portion of the cycle within each monthly tracking period unless weather conditions prevented us from tracking all locations. When this occurred, receiver data were inspected to identify locations where fish had not passed, and those areas were skipped. At sites where fish were located, we used a GPS receiver to record the location in Universal

Transverse Mercator coordinates. When we were unsure whether a fish moved between two consecutive months, we also used a unidirectional hydrophone that allowed us to determine fish location more precisely (within ~4 m under calm conditions; Brown et al. 2015).

Water quality monitoring.—Spatial and temporal variation in water quality in the study area was monitored by manual data collection from June 2014 to September 2015. During each manual tracking trip, we collected vertical profiles of water quality throughout the water column at 14 fixed sites that were distributed throughout the study area (Figure 1). We recorded temperature and DO at 1-m intervals from the surface to the bottom by using a manually deployed sonde (YSI 600 XLM; YSI, Inc., Yellow Springs, Ohio). To summarize DO conditions during the study we calculated the proportion of samples on each date (all depths and locations combined) that corresponded to certain DO concentrations (0.0–1.9, 2.0–3.59, 3.6–4.99, and ≥ 5.0 mg/L). Because monthly vertical profiles only provided a snapshot of water conditions, we also deployed two water quality sondes (YSI Model 6600 EDS) that recorded DO and salinity every 15 min from June to September 2014 (sondes also recorded temperature; however, due to the small horizontal fluctuations in temperature, the vertical profiles were sufficient). The sondes were placed in the same location within the middle of the study area (Figure 1) in approximately 3 m of water but at different depths (0.5 and 1.5 m from the bottom). Sondes were downloaded, cleaned, and recalibrated approximately every 2 weeks. Patterns of water quality and monthly mortality rates (described below) were inspected to determine whether there was a correlation between mortality and poor water quality (low DO and high temperature).

Analysis of telemetry data.—We followed the procedures of Hightower and Harris (2017) to build a Bayesian multistate capture–recapture model in OpenBUGS (open-source software; Spiegelhalter et al. 2010), allowing us to estimate the instantaneous rate of total mortality (mortality at a particular moment; additive) and the discrete rate of total mortality (rate of mortality in a given time period; nonadditive) for juvenile and adult Striped Bass as well as component rates (individual types of mortality; e.g., natural mortality) for adults. The models were fitted with a state-space model (Kery and Schaub 2012; Servanty et al. 2014) using \log_e scale prior distributions for instantaneous mortality rates (Ellis et al. 2017).

Juvenile Striped Bass were too small for harvest (also, given the size of terminal tackle used by anglers, catch and discard of juveniles is unlikely). Therefore, we used a multistate model with only two possible states: alive and natural mortality. Live juveniles could remain in the alive state or could transition to natural mortality. Using the telemetry data, we made three types of observations:

detected as dead (state = natural mortality), detected as alive (state = alive), and not detected (state = alive or natural mortality). Based on this information, the multistate model was able to estimate the probability of detection and monthly mortality. These parameters were then used to calculate discrete and instantaneous values for monthly and annual survival and total mortality. We assumed that any transmitter detected in the same location during three or more consecutive sampling trips represented a mortality (Hightower et al. 2001; Kerns et al. 2016), whereas any transmitter that was detected in different locations represented a live juvenile. All undetected fish were assumed to be located in the study area, as we assumed 100% detection of all emigrated fish, and these individuals were censored. The first month after release was considered a “probationary period,” and only fish that remained alive after 30 d poststocking entered the model. The probationary period minimized the effects of any death or behavioral response associated with tagging (Thompson et al. 2007). Other model assumptions included the following: (1) transmitter loss or failure was negligible; (2) every fish had an equal probability of being detected during each tracking period; (3) every fish had an equal chance of surviving from one search period to the next; and (4) all fish acted independently of each other.

For adult fish, we explored component mortality rates including natural, discard (a combination of recreational catch-and-release mortality and commercial discard mortality), and harvest (a combination of recreational and commercial harvest). To estimate these parameters, we used telemetry and high-reward tags (Pollock et al. 2004; Kerns et al. 2016; Hightower and Harris 2017). The adult model had seven possible states for each individual (Figure 2): (1) alive with an external tag, (2) discard survivor, (3) alive with no external tag, (4) natural mortality, (5) nonharvest mortality, (6) discard mortality, and (7) harvest. Fish that were alive could stay alive (alive with an external tag), die of natural causes (natural mortality), be harvested (harvest), be caught and discarded and die within 30 d (discard mortality), or be discarded and remain alive (discard survivor; Figure 2). Fish could only be classified as discard survivors for one period (as this state signified that a catch event occurred during that month), after which the discard survivors could remain alive and transition into the alive state with no external tag; could die due to nonharvest mortality (this term includes all mortality other than harvest mortality, such as natural mortality and undetected discard mortality; it is not simply natural mortality, as the fish did not have an external tag and therefore could have died due to undetected discard mortality); or could be harvested (harvest; Figure 2). Fish that were alive but without an external tag could likewise remain alive (alive with no external tag), could die due to nonharvest mortality, or could be

harvested (Figure 2). A combination of telemetry and tag return data was used to determine the observation state. As described above for juveniles, if an adult's transmitter was detected in the same location during three or more consecutive sampling trips, we assumed that it represented a mortality; however, the source of the mortality depended on previous history. It was assumed to be (1) a natural mortality if the fish had an external tag, (2) a nonharvest death if the external tag had previously been clipped, or (3) a discard mortality if the fish had been reported as caught and released during the previous month. If there was a change in location between periods we assumed that the fish was alive. The model used the estimated true and observational states to estimate the monthly total instantaneous mortality rate (Z), the monthly component instantaneous mortality rates, and the probabilities of detection and death due to being caught and discarded. Discrete mortality rates and annual rates were calculated internally to obtain estimates of precision. In addition to the assumptions of the juvenile model, we assumed that harvest and discard events were detected with a probability of 1.0 for adults that still had external tags based on the expectation of a 100% reporting rate for high-reward tags (Pollock et al. 2001; Hightower and Harris 2017).

One limitation of the multistate model was that survival estimates were only informed by data collected from within the study area. Because adult Striped Bass resided both inside and outside of the study area, we conducted a second analysis using a Cormack–Jolly–Seber (CJS) model in OpenBUGS, which allowed us to estimate survival rates over the entire river. Because this model did not depend on information obtained from active tracking the second cohort of adult Striped Bass could also be included, but any information from active tracking and tag returns was omitted. Juveniles were not included in the CJS model for two reasons. First, we assumed that mortality rates differed between juveniles and adults. Second, juveniles seldom were outside of the study area, and when they were, they did not move enough to generate many detections on the receivers. Like the multistate model, adult fish entered the CJS model at 30 d postsurgery (any fish that died before 30 d never entered the model), and the monthly periods were the same for both models. Because the receiver array had limited coverage, any fish that was detected was assumed to be moving and therefore alive (with the exception of individuals having continuous detections on a single receiver; in such cases, we assumed that mortality occurred within the receiver range). Undetected fish could be alive or dead, but the longer an individual went undetected, the more likely the individual was to be dead. By using detection encounters the CJS model was able to estimate the probability of detection and monthly apparent survival. These parameters were then used to calculate the average and apparent rates of monthly and annual

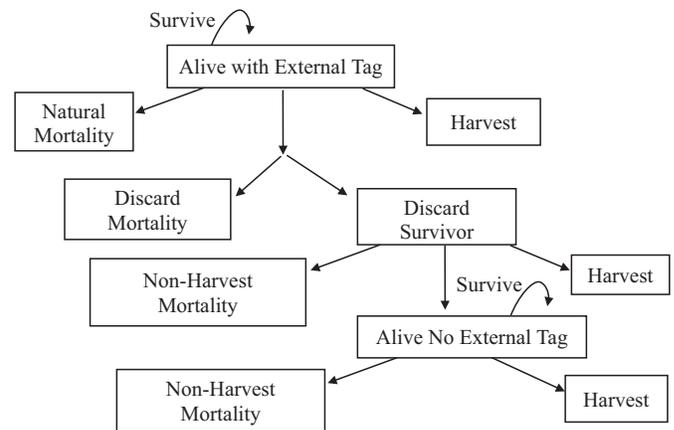


FIGURE 2. Multistate model for adult Striped Bass, indicating all possible states (boxes) and transitions (arrows; after Harris and Hightower 2017). Nonharvest mortality included fish that died from natural causes or undetected discard mortality (i.e., the fish no longer had an external tag, so the discard event could not be identified). Fish that disappeared from the study site undetected were assumed to be harvest events.

survival and total mortality. Unlike the multistate model, which estimated true survival within the study area, the CJS model was restricted in that it estimated the apparent survival rate (ϕ), as there was no efficient receiver gate to detect emigrations at the mouth of the Neuse River. Apparent survival is distinguished from true survival in that apparent survival (hereafter referred to as “survival”) combines the probability of survival and the probability of not permanently emigrating from the river (i.e., $\phi = 1 - \text{mortality} - \text{emigration}$), whereas true survival deals with only mortality. Although it is possible that some adult Striped Bass emigrated permanently, emigration out of the Neuse River is rare (Hawkins 1980; NCDMF and NCWRC 2013; Callihan et al. 2014).

Characterization of seasonal distribution.—Seasonal distribution maps were created to show the general movement and distribution patterns of adult Striped Bass (both cohorts) throughout the year. Maps were not created for juveniles because there was minimal detection of juveniles outside of the study area. Scaled monthly detections of adult Striped Bass (number of fish detected/number of fish at large when released) were calculated from 4 receivers located within the study area and 27 receivers that were distributed outside of the study area in the Neuse and Trent rivers. The number of adults at large when released (i.e., 111 fish) was used rather than the number of available fish because in every month, there were undetected fish for which fates were unknown; therefore, we did not know the number of individuals that were truly available. Scaled monthly detections were then combined and mapped to create seasonal distribution maps for spring

(April–June), summer (July–September), fall (October–December), and winter (January–March).

We determined the distance of up-river migration in the Neuse and Trent rivers for the first cohort of adult Striped Bass. We excluded the second cohort of adults, as many of those fish were collected up-river and thus could have been a biased sample for use in exploring up-river behavior. Juveniles were also omitted, as they did not migrate up-river. A fish was classified as having migrated if it was detected on the first up-river receiver in the Neuse River (rkm 24.4) or on the first up-river receiver in the Trent River (rkm 16); any fish that did not move at least this distance up-river was considered not to have migrated. Likewise, a fish was designated as having ended its migration when it was detected on the above-mentioned receivers while moving down-river. Distance of migration was defined as the maximum distance an individual fish moved up-river, which was based on up-river receiver detections. We used a generalized linear mixed model to evaluate the effects of fish length (TL at tagging) on whether a fish migrated up-river, with year as a fixed effect and fish as a random effect. All adults from the first cohort that were confirmed to be alive after April 30, 2014, and after April 30, 2015, were included in the first and second years, respectively. To measure the influence of fish length on the distance of up-river migration we used a linear mixed model that included fish TL at tagging as the independent variable and the distance migrated as the explanatory variable, with year and individual fish as fixed and random effects. In this model, we only included fish that migrated up the Neuse River. Fish that did not migrate and fish that migrated up the Trent River were excluded because distances migrated up different rivers were not directly comparable.

RESULTS

Mortality Estimates

Juvenile cohort.— There was no transmitter loss or mortality for replica-tagged or control Striped Bass at the end of the 30-d retention study. Only minor inflammation was observed, and all incisions were healed or healing in every fish but one. The latter individual had lost both of its sutures, the incision site was not healed, and the wound was open and inflamed.

After accounting for the probationary period, we restricted our analyses to include 58 phase II juvenile Striped Bass that were confirmed to be alive at least 30 d after release (a total of 18 fish died within the probationary period; 9 disappeared within the first period and were not detected again; 10 disappeared within 30 d and were later detected as dead, but we were unable to determine the date of mortality; and 5 emigrated from the study area within

30 d and never re-entered). We observed 16 natural mortalities throughout the study period (Table 1). In accordance with this, our multistate model estimated moderately high natural mortality for juvenile Striped Bass, and the annual Z of the first cohort of juveniles was higher than that of the second cohort of juveniles: 1.318 (95% credible interval [CI] = 0.676–2.315) versus 0.939 (95% CI = 0.406–1.87). Annual Z estimated by combining the data from the two cohorts was 1.087 (95% CI = 0.643–1.735), and annual discrete mortality was 66.3% (95% CI = 47.4–82.4%; Table 2). Median monthly instantaneous total mortality values ranged from 0.001 (95% CI = 0.000–0.045) in January 2014 to 0.340 (95% CI = 0.138–0.665) in February 2014 (Figure 3). Mortality estimates were highest in late-winter and summer months (Figure 3), but the uncertainty around estimates was large and seasonal patterns were not obvious. Estimated detection probability was 0.801 (95% CI = 0.754–0.843).

First cohort of adults.— Adult Striped Bass experienced lower mortality rates than juveniles. After we accounted for the probationary period, 46 fish belonging to the first cohort were included in the model (i.e., those confirmed alive at the beginning of the analysis). Of these adults, we confirmed five natural mortalities, four recreational discard survivors, and one recreational harvest from within the study area (Table 1). Outside of the study area we were not able to observe natural mortalities, but we did receive tag reports that confirmed four recreational discard events and one commercial discard event (Table 1). Although these catch events occurred outside of the study

TABLE 1. Observed fate at the end of the study (or at the end of battery life) for juvenile and adult Striped Bass from the first cohort (tagged and released into the Neuse River). Throughout the study there were seven adult recreational discard survivors and one adult commercial discard; the latter occurred at the end of the study, so that fish’s fate after discard was not determined.

Life stage, fate	Number observed
Juvenile, alive	14
Juvenile, natural mortality	16
Juvenile, not detected (in study area)	13
Juvenile, not detected (outside of study area)	15
Juvenile, total	58
Adult, alive	9
Adult, natural mortality	5
Adult, harvest (recreational)	1
Adult, discard mortality (recreational)	1
Adult, not detected (in study area)	1
Adult, not detected (outside of study area)	29
Adult, total	46

area, all four fish from the recreational catches soon immigrated back into study area, and we were able to confirm that three survived and one died (Table 1). The commercial discard did not swim back into the study area and was not detected again on receivers (this event occurred 2 months before the end of the study). There were no confirmed commercial harvests. Our multistate model used information obtained within the study area only (because of model assumptions) and from the first cohort of adults only (model assumptions required all fish to have external high-reward tags); any information obtained outside of the study area or from the second cohort of adults was not used. Because of low sample size the model did not distinguish between commercial and recreational harvests or discards. Annual Z was 0.394 (95% CI = 0.197–0.739), and annual discrete total mortality was 32.6% (95% CI = 17.9–52.3%). Median monthly instantaneous total mortality values ranged from 0.005 (95% CI = 0.000–0.066) in May 2014 to 0.100 (95% CI = 0.006–0.470) in May 2015 (Figure 4). There was no seasonal pattern, and all 95% CIs of monthly mortality overlapped one another (Figure 4). The model estimated the following annual discrete rates for adult Striped Bass: natural mortality was 20.1% (95% CI = 8.7–39.1%), discard mortality was 0.0% (95% CI = 0.0–3.3%), and harvest mortality was 10.8% (95% CI = 3.5–26.1%; Table 2). Estimated monthly detection probability was 0.987 (95% CI = 0.974–0.995).

Both cohorts of adults.—After accounting for the probationary period, we restricted the CJS analysis for the entire Neuse River to 86 adult Striped Bass that were confirmed to be alive at least 30 d after surgery. Annual Z was 0.776 (95% CI = 0.537–1.061), and annual discrete total mortality was 54.0% (95% CI = 41.5–65.4%). Monthly Z -values ranged from 0.001 (95% CI = 0.000–0.038) in October 2014 to 0.175 (95% CI = 0.052–0.352) in August 2014 (Figure 4). As with the multistate model,

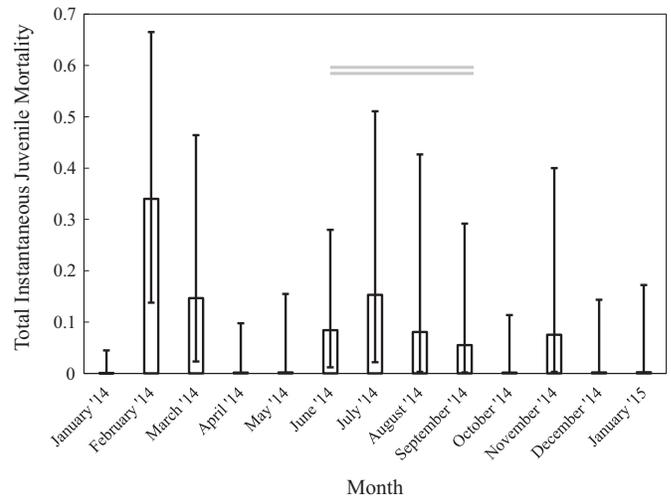


FIGURE 3. Median monthly instantaneous total mortality estimates from the multistate model for phase II juvenile Striped Bass ($n = 58$) in the Neuse River, 2014–2015. Error bars indicate 95% credible intervals. The gray compound bar at the top of the graph denotes months with average water temperatures greater than 25°C and average dissolved oxygen concentrations less than 3.6 mg/L.

there was no obvious seasonal pattern. Detection probability varied, so period-specific estimates were included. Detection probabilities were above 70% for all months other than January 2015 (detection probability = 0.66).

Water Quality

Water temperature varied seasonally; however, spatial variation (location and depth) was less than 2°C for average water temperature at a specific depth. Therefore, water temperatures for all locations and all depths were averaged for each sampling date. Average water temperature varied from 6.2°C in January 2015 to 29.8°C in July 2015 (Figure 5).

TABLE 2. Annual instantaneous and discrete mortality rate estimates and 95% credible intervals (CIs) for Striped Bass juveniles (predicted by the multistate model only) and adults (predicted by the multistate and Cormack–Jolly–Seber [CJS] models) in the Neuse River.

Life stage, type of mortality	Annual instantaneous mortality rate		Annual discrete mortality rate	
	Estimate	95% CI	Estimate	95% CI
Juvenile, natural (both cohorts)	1.087	0.643–1.735	0.663	0.474–0.824
Juvenile, natural (cohort 1)	1.318	0.676–2.315	0.732	0.491–0.901
Juvenile, natural (cohort 2)	0.939	0.406–1.87	0.609	0.336–0.846
Adult, natural (multistate)	0.243	0.089–0.527	0.201	0.087–0.391
Adult, harvest (multistate)	0.131	0.041–0.346	0.108	0.035–0.261
Adult, discard (multistate)	0.000	0.000–0.041	0.000	0.000–0.033
Adult, total (multistate)	0.394	0.197–0.739	0.326	0.179–0.523
Adult, total (CJS)	0.776	0.537–1.061	0.540	0.415–0.654

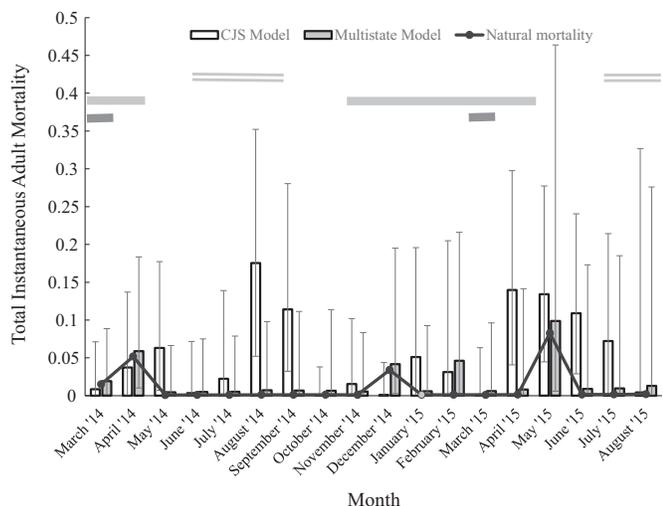


FIGURE 4. Median monthly instantaneous total mortality and natural mortality estimates from the multistate model ($n = 46$) and median monthly instantaneous total mortality estimates from the Cormack–Jolly–Seber (CJS) model ($n = 86$) for adult Striped Bass in the Neuse River, 2014–2015. Error bars represent 95% credible intervals. The light-gray compound bar at the top of the graph denotes months with average water temperatures greater than 25°C and average dissolved oxygen concentrations less than 3.6 mg/L. The light-gray bar indicates the recreational harvest season and the dark-gray bar indicates the commercial harvest season.

The DO concentrations also varied temporally, but unlike temperature, DO varied spatially (location and depth). Monthly samples taken throughout the study area showed that in June–October of both years (with the exception of July 2014), there were samples with DO less than 3.6 mg/L; August–October 2014 and June–September 2015 samples had DO concentrations below 2.0 mg/L (Figure 5). Additionally, during these months average water temperature was above 25°C, with little temporal or spatial variation (Figure 5). However, oxygenated water was available; for every month during the study, over 50% of all samples had DO concentrations of 3.6 mg/L or greater, and June 2015 was the only monthly sample in which no locations had DO concentrations above 5.0 mg/L (Figure 5). Likewise, continuous samples from the sondes showed that DO concentrations varied throughout the summer (Figure 6). Although DO concentrations below 2 mg/L were observed at both depths, sonde data showed that oxygen stratification did occur, and the deep sonde (0.5 m from the bottom) recorded more frequent and prolonged periods of DO below 2.0 mg/L than did the shallow sonde (1.5 m from the bottom; Figure 6). Sonde data indicated that salinity varied from 0.0‰ to 7.9‰ (shallow sonde) and from 0.0‰ to 9.3‰ (deep sonde).

The multistate model predicted peaks in juvenile mortality during June–September 2014, when water

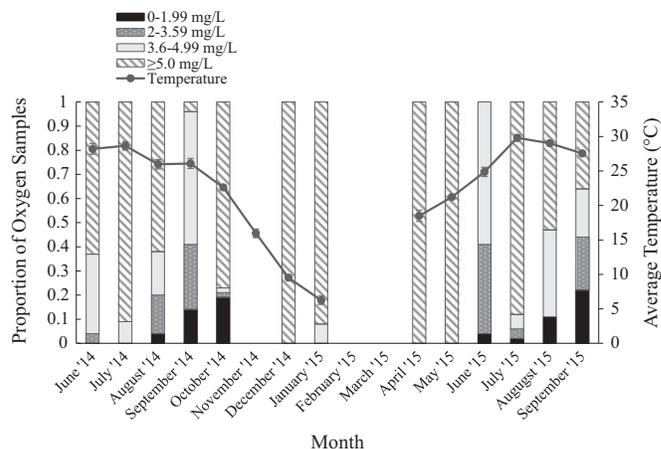


FIGURE 5. Dissolved oxygen (DO) concentrations and water temperatures throughout the Neuse River study site, 2014–2015. Oxygen concentration is expressed as the proportion of locations (Figure 1) and depths during each monthly sampling trip with a DO level of 0.0–1.99, 2.0–3.59, 3.6–4.99, or ≥ 5.0 mg/L. Water temperature is reported as the average (\pm SD; all locations and all depths) from each monthly sampling trip. Due to equipment failure, DO was not recorded in November 2014, and neither DO nor temperature was recorded in February and March 2015.

temperature was above 25°C and hypoxic water was present (Figure 3). However, median juvenile mortality was highest in February 2014 (water quality data not available), a month when water temperature has historically been the coldest and when oxygenated water is always available. Natural mortality predicted by the multistate model was highest in April, December, and May 2014; however, none of those months had poor water quality (temperature > 25°C and DO < 3.6 mg/L).

Seasonal Distribution

Juvenile Striped Bass resided year-round in the study area, and only one receiver outside of the study area had significant detections of juveniles: 14 juveniles were detected on the first receiver downstream from the study area during summer 2014 (Figure 1). Only four juveniles were detected on other receivers outside of the study area. These detections were infrequent and showed no migration patterns. Adult Striped Bass also resided year-round in the study area and downriver of it (Figure 7). Distribution between years was similar; however, detection probability was lower in winter 2015 than in all other seasons. There was no obvious temporal migration into the sound or the ocean, although two individuals (621 and 670 mm TL) were detected in the Tar River. During the spring, adults migrated up-river, and nearly all up-river detections ceased by summer months (Figure 7). Other than the spring up-river migration, year-round distribution of adult Striped Bass remained relatively constant.

Up-river migration of adults during the spring was affected by fish size, with larger fish being more likely to

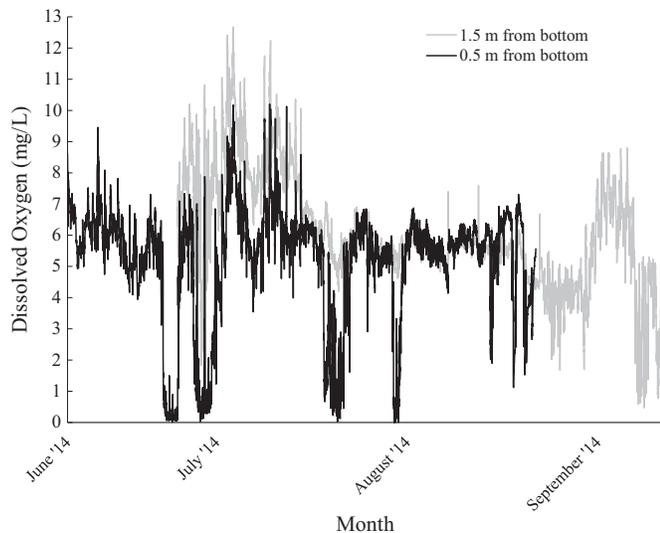


FIGURE 6. Dissolved oxygen concentrations recorded by data sondes in the Neuse River during summer 2014. The black line represents data from the sonde placed 0.5 m from the bottom, and the gray line represents data from the sonde placed 1.5 m from the bottom. Water depth was approximately 3 m at the sonde location. Due to equipment failure, some periods have no values.

migrate. Twenty-five (60%) of 42 available adults made up-river migrations (21 in the Neuse River; 4 in the Trent River) during spring 2014, and 9 (47%) of 19 available fish made up-river migrations (6 in the Neuse River; 3 in the Trent River) during spring 2015. The farthest detected migration for any fish was a movement to rkm 276.6. Results from the generalized linear mixed model showed a positive effect of fish length on migration probability (coefficient for length [mean \pm SE] = 0.31 ± 0.11 ; $T = 2.83$, $df = 17$, $P < 0.02$; log odds ratio increased by 0.31). Year did not affect whether a fish migrated (coefficient for year = 0.23 ± 0.66 ; $T = 0.35$, $df = 17$, $P < 0.80$). However, for the fish that migrated, neither fish size nor year affected the up-river migration distance (coefficient for length = 0.054 ± 0.16 , $F = 0.29$, $df = 3$, $P > 0.80$; coefficient for year = 15.24 ± 33.01 , $T = 0.46$, $df = 3$, $P < 0.70$).

DISCUSSION

Our results indicated that 66% of juvenile Striped Bass died within the first year after stocking in the Neuse River. Adult Striped Bass experienced moderate mortality rates within the study area; however, mortality rates throughout the entire Neuse River were much higher. This variation could be attributable to higher levels of fishing mortality occurring outside of the study area. There were some peaks in juvenile mortality during months in which water quality appeared to be poor, but the patterns were inconsistent, and there was no correlation between adult natural mortality and poor water quality. Given the

estimated adult natural mortality rate, adult target mortality for Striped Bass throughout the Neuse River would be 38.9% (Rachels and Ricks 2015)—much lower than the estimated total mortality. These results indicate that decreasing the fishing mortality of Striped Bass in the Neuse River may help to achieve a mortality level closer to the target rate. If larger fish are disproportionately targeted, the negative effects of high exploitation rates on spawning success may be compounded, as up-river migration was positively affected by fish size. Based on our results, we recommend that managers explore different stocking methods for possibly decreasing the poststocking mortality of juveniles, implement stricter exploitation guidelines (i.e., stricter harvest quotas for recreational and commercial anglers and/or stricter gill-net regulations to reduce commercial bycatch), and use these results to guide future research initiatives.

Mortality of the first juvenile cohort was higher than that of the second juvenile cohort. The difference in mortality was not entirely unexpected, as the second cohort of juveniles was collected from among individuals that had successfully survived more than 5 months poststocking and were presumably more competent and better acclimated to their surroundings. We suggest that poststocking survival could be increased by allowing juveniles to become more acclimated before they are stocked. For example, Baltzegar (2010) found that survival of juvenile Striped Bass increased if individuals were acclimated to the salinity level.

Previous studies estimating the mortality of phase I juvenile Striped Bass have produced equivocal results: estimates of phase I monthly discrete survival have ranged from 9–41% in the Sacramento–San Joaquin Estuary, California (Turner and Chadwick 1972) to 88–89% in Smith Mountain Lake, Virginia (Moore et al. 1991; Sutton 1997). These results indicate strong site-dependent mortality rates and suggest a limited ability to generalize patterns from one system to another. We are aware of no previous investigations that have estimated the mortality of phase II juvenile Striped Bass. This additional information will be useful in the long-term assessment of stocking programs (e.g., determining the number and size or age of individuals to stock; Wallin and Van Den Avyle 1995) and in the development of fisheries management strategies.

It should also be noted that our estimate of annual juvenile mortality may be negatively biased. We censored mortalities that occurred within the first 30 d because of the potential link to surgical complications. However, any immediate poststocking mortality during that period caused by stocking, handling, transportation, or some combination of these factors would have also been excluded. Ideally, we would have been able to determine whether the mortality of the censored individuals was caused by stocking effects or surgery effects, as stocking-

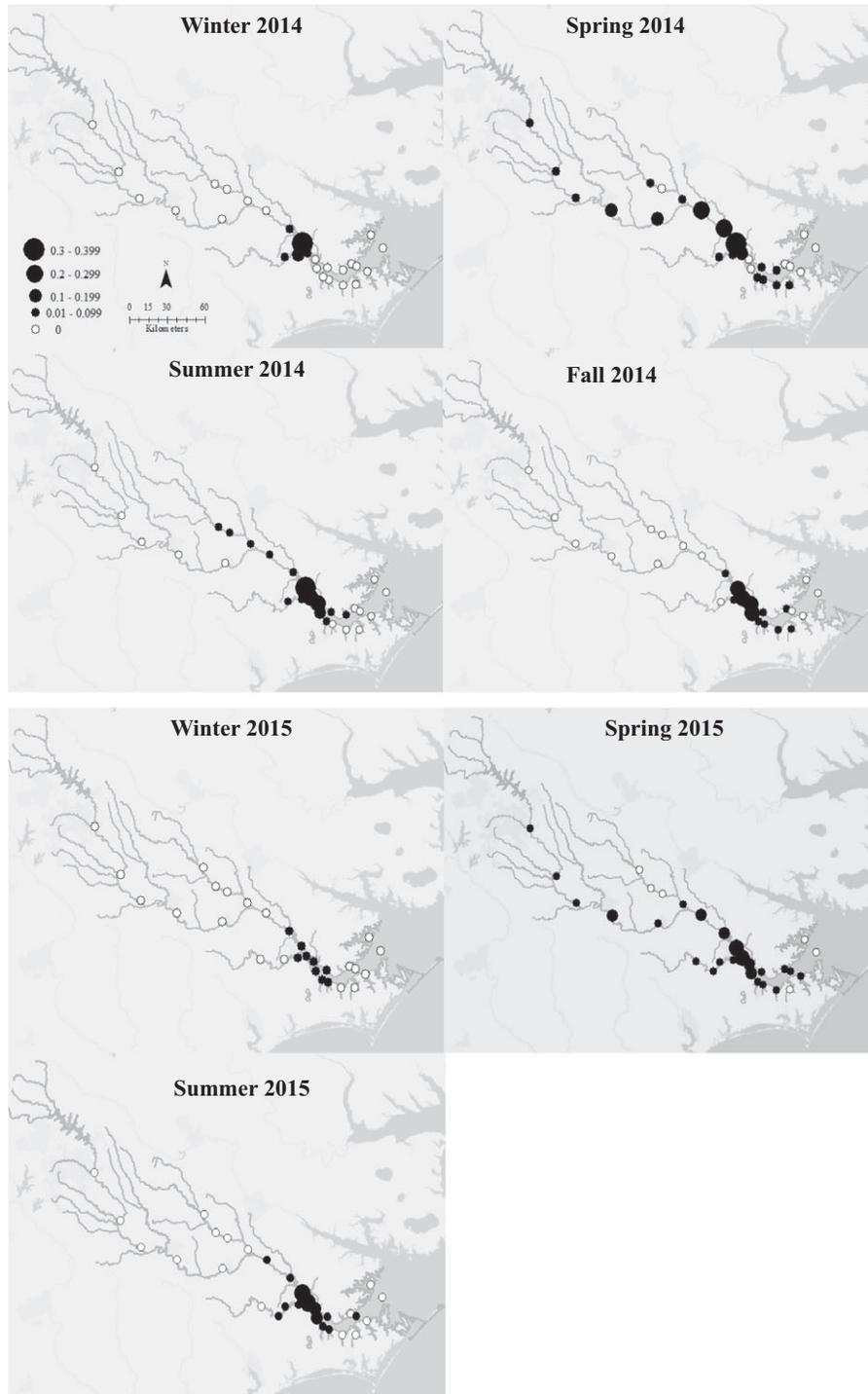


FIGURE 7. Seasonal distribution of adult Striped Bass throughout the entire Neuse River. Black circles represent receivers where Striped Bass were detected; circle size is scaled in proportion to the number detected. Small white circles represent receivers where no Striped Bass were detected. There were 54 tagged fish in winter 2014, 70 in spring 2014, 70 in summer 2014, 70 in fall 2014, 70 in winter 2015, and 111 in spring 2015.

related mortality should be considered in an overall assessment of juvenile survival. Even though we observed no mortalities in our transmitter retention study (which assessed surgery effects only), we believe that the majority

of the censored individuals died due to surgery effects, as the numbers of censored individuals were similar between the two cohorts. Among the first cohort, which was subjected to stocking, transportation (>2 h), and surgery, 21

individuals were censored, 10 of which were censored because of confirmed mortality within the first month. Likewise, we censored 21 individuals from the second cohort (subjected to surgery effects only), 8 of which were censored due to confirmed mortality within the first month.

Of the two modeling approaches used to estimate total mortality of adult Striped Bass, the CJS model produced what we believe to be a more robust and reliable estimate of total mortality, with even narrower CIs, because it used data from throughout the entire Neuse River rather than from only within the study area. Use of data from throughout the entire river was important because the results showed that tagged individuals resided year-round in locations outside of the study area. Furthermore, evidence suggested that Striped Bass within our study area experienced lower levels of mortality than those outside of the study area, likely because fishing pressure—particularly from the commercial sector—is lower within the study area. Even though commercial fishing is permitted within the study area, there were neither reported harvests (corroborated by the lack of missing fish) nor commercial discards (only one reported commercial discard occurred outside of the study area). However, commercial harvest mortality does affect the overall population, with 1,288 Striped Bass commercially harvested in the Neuse River during 2014 (the most recent estimates available; NCDMF, unpublished data). Any mortality due to commercial fishing was not represented in the total mortality estimate from within the study area; therefore, we believe that total mortality of adults throughout the Neuse River was better estimated by the CJS model. Our assertion is further supported by a previous study: Rachels and Ricks (2015) conducted a Chapman–Robson catch curve analysis and estimated that the annual instantaneous mortality of adult Striped Bass in the Neuse River was 0.86 (SE = 0.1), which corresponds to an annual discrete total mortality rate of 58%, similar to the 54% annual discrete total mortality we estimated with the CJS model. In contrast, Callihan et al. (2014) used a time-at-liberty approach to estimate discrete total mortality of Neuse River Striped Bass from the time of stocking to the time of capture (mean = 2.1 years), resulting in a lower estimate of 48%.

It should also be noted that the CJS estimate represents apparent survival rather than true survival; that is, the mortality estimate included true mortalities along with any permanent emigration events, as our study did not have a gate or transect of receivers at the opening of the Neuse River, and permanent emigrations could go undetected if individuals were not picked up by NCDMF receivers in surrounding rivers. In fact, 2 of the 111 adults (621 and 670 mm TL) tagged in this study were subsequently detected in the Tar River, and they were not detected as

immigrating back into the Neuse River during the study. These detections demonstrate at least temporary emigration from the Neuse River, but evidence suggests that there is little permanent emigration. Tagging studies conducted by Hawkins (1980), NCDMF and NCWRC (2013), and Callihan et al. (2014) indicated that Neuse River Striped Bass are riverine, and therefore any differences between true survival and apparent survival should be negligible. Another limitation of both models is that adults were assumed to experience equal mortality across all sizes; however, harvest mortality would not be equal. Among the 111 tagged adults, 22 fish were below the minimum harvest size at the time of tagging; some of these individuals would have remained below the minimum size throughout the study period, whereas others would have grown into the harvestable length range. Likewise, some individuals were within the no-harvest slot limit at the time of tagging or may have entered (or exited) the slot limit during the study period.

Natural mortality of Striped Bass can be caused by a number of factors, including predation (mainly on juveniles; NCDMF and NCWRC 2013), competitors and limited food availability (Setzler et al. 1980), pollutants (Polgar et al. 1976; Setzler-Hamilton et al. 1981; Buckler et al. 1987), and poor water quality (Chittenden 1971; Coutant 1985). We explored the correlation between common indicators of water quality (water temperature and DO) and juvenile and adult natural mortality. We observed months with unsuitable temperatures and occasional unsuitable DO concentrations for Striped Bass in the summer; however, there were no consistent peaks in mortality of juveniles or adults during those months. The lack of correlation between natural mortality levels and poor DO could be attributable to the ability of Striped Bass to avoid hypoxic areas, as has been observed in a freshwater reservoir (Cheek et al. 1985) and in saltwater bays (Chittenden 1971; Coutant and Benson 1990). Avoidance of hypoxic areas would have been possible because in all of our monthly observations, at least half of the areas sampled had DO concentrations at or above 3.6 mg/L. Although oxygenated areas were always available, thermal refuge was not available during the summer months as all areas sampled were above the preferred thermal range (18–22°C) and above the upper limit of suitable temperature (25°C) for Striped Bass (Coutant and Benson 1990). However, the consequences of warm water for Striped Bass mortality are unclear. For example, some studies have indicated that Striped Bass experience cessation of feeding (Zale et al. 1990) and poor condition (Coutant 1985) in warm water, whereas other studies have not observed negative impacts under similar conditions (Farquhar and Gutreuter 1989; Thompson et al. 2010; Thompson and Rice 2013). Striped Bass avoidance of poorly oxygenated water and tolerance of warmer water may

have led to our failure to detect a correlation between poor water quality events and the mortality of juvenile and adult Striped Bass in the Neuse River.

Instantaneous annual natural mortality of adults was estimated at 0.243. Although no previous studies have estimated the natural mortality of adult Striped Bass in the Neuse River, this estimate is similar to those generated based on traditional methods. For example, Hoenig's (1983) regression equation (based on maximum age) predicted natural mortality of Atlantic Striped Bass to be 0.15, and the Lorenzen (1996) method (based on fish size) predicted natural mortality (given the average size of adults in this study) to be 0.38. Our estimate of natural mortality is centered between these two estimates. Empirical evidence suggests that natural mortality in Atlantic Striped Bass populations is age specific. Jiang et al. (2007) used 1991–1998 tag return data from tagged Striped Bass in the Chesapeake Bay to estimate natural mortality (along with harvest and catch-and-release mortality). Those authors concluded that natural mortality of Striped Bass ranged from 0.378 to 0.399 (SE = 0.021) for ages 3–5 and ranged from 0.145 to 0.150 (SE = 0.009) for ages 5 and older. Our natural mortality estimate also fell between these two estimates (fish from our study were predicted to be ages 3–9 based on size; NCDMF and NCWRC 2013).

Our natural mortality estimate could be positively biased because any discard mortality events that went unreported were classified as natural mortalities. We have evidence that the reporting rate of high-reward tags was not 100%, even though Pollock et al. (2001) considered the 100% reporting rate to be a valid assumption. During our study there were three instances in which anglers reported recreational discard events but did not clip the tag or record the tag number; in two cases, the angler was aware of the tag value but chose to release it because he thought that the tag would yield more information if the fish was left at large. If any of these fish died our estimate of natural mortality would be positively biased.

The majority of adult Striped Bass made up-river migrations in the spring, presumably to spawn, and there is historical evidence of successful spawning in the Neuse River. Burdick and Hightower (2006) collected Striped Bass eggs and larvae in the Neuse River during 2004. More recently, the NCWRC found evidence of limited spawning: 119 Striped Bass eggs were collected in 2016, of which 64% were viable, and the daily survival rate was 48% (NCWRC, unpublished data). Even with evidence of successful spawning, there has been no evidence of recruitment to the juvenile stage. We believe that the high mortality of adults has led to age truncation in the population and that the bottleneck of older and larger females is a key component in preventing successful recruitment. Older females may produce an order-of-magnitude more eggs than younger females

(Olsen and Rulifson 1992), and older females' eggs have been demonstrated to exhibit increased survival and juvenile recruitment rates (Monteleone and Houde 1990; Secor 1990; Cowan et al. 1993). We believe that expanding the age distribution may be a necessary prerequisite for natural recruitment; however, this alone may not be sufficient because constraints at other life stages (e.g., low survival of eggs and larvae) could still be inhibitory. We await additional research that builds upon our findings to better elucidate the ways in which egg and larval survival can influence natural recruitment.

In summary, our results indicate that high natural mortality of juveniles and high exploitation mortality of adults may be contributing to the lack of recovery of Striped Bass in the Neuse River. This is the first study to (1) estimate the poststocking mortality of phase II juvenile Striped Bass and (2) estimate natural mortality of Striped Bass adults in the Neuse River. We conclude that mortality rates are not correlated to DO and temperature conditions. We found that adult natural mortality is within the expected range based on size, maximum age, and the results of previous studies, and natural mortality of adults is unlikely to be contributing to the low population abundance. Therefore, reductions in fishing mortality may constitute an effective strategy to reach target mortality. Reducing harvest may be particularly important if larger individuals are disproportionately removed, as larger individuals are more likely to spawn (assumed based on upstream migration) and have higher fecundity. Our results suggest that reducing juvenile poststocking mortality and reducing fishing mortality may help to increase the abundance of Striped Bass in the Neuse River.

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REFERENCES

- Albrecht, A. B. 1964. Some observations on factors associated with survival of Striped Bass eggs and larvae. *California Fish and Game* 50:100–113.
- Atlantic Striped Bass Conservation 1984. U.S. Code, title 16, chapter 71A, sections 5151–5158.
- Baltzegar, J. F. 2010. Assessment of multiple stocking strategies of Striped Bass in the Ashley River, South Carolina using multiplexed

- microsatellite panels. Master's thesis. College of Charleston, Charleston, South Carolina.
- Barwick, R. D., J. M. Homan, and C. D. Thomas. 2009. Investigation of Striped Bass recruitment in the Neuse River, North Carolina. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies 63:161–165.
- Beasley, C. A., and J. E. Hightower. 2000. Effects of a low-head dam on the distribution and characteristics of spawning habitat used by Striped Bass and American Shad. Transactions of the American Fisheries Society 129:1316–1330.
- Breitbart, D. L., J. K. Craig, R. S. Fulford, K. W. Rose, W. R. Boynton, D. C. Brady, B. J. Ciotti, R. J. Diaz, K. D. Friedland, J. D. Haggy III, D. R. Hart, A. H. Hines, E. D. Houde, S. E. Kolesar, S. W. Nixon, J. A. Rice, D. H. Secor, and T. E. Targett. 2009. Nutrient enrichment and fisheries exploitation: interactive effects on estuarine living resources and their management. Hydrobiologia 629:31–47.
- Brown, D. T., J. A. Rice, C. D. Suski, and D. D. Aday. 2015. Dispersal patterns of coastal Largemouth Bass in response to tournament displacement. North American Journal of Fisheries Management 35:431–439.
- Buckler, D. R., P. M. Mehrle, L. Cleveland, and F. J. Dwyer. 1987. Influence of pH on the toxicity of aluminum and other inorganic contaminants to East Coast Striped Bass. Water, Air, and Soil Pollution 35:97–106.
- Burdick, S. M., and J. E. Hightower. 2006. Distribution of spawning activity by anadromous fishes in an Atlantic slope drainage after removal of a low-head dam. Transactions of the American Fisheries Society 135:1290–1300.
- Burkholder, J. M., D. A. Dickey, C. A. Kinder, R. E. Reed, M. A. Mallin, M. R. McIver, L. B. Cahoon, G. Melia, C. Brownie, J. Smith, N. Deamer, J. Springer, H. Glasgow Jr., and D. Toms. 2006. Comprehensive trend analysis of nutrients and related variables in a large eutrophic estuary: a decadal study of anthropogenic and climatic influences. Limnology and Oceanography 51:463–487.
- Callihan, J. L., C. H. Godwin, K. J. Dockendorf, and J. A. Buckel. 2014. Growth and mortality of hatchery-reared Striped Bass stocked into nonnatal systems. North American Journal of Fisheries Management 34:1131–1139.
- Campbell, L. A., and J. A. Rice. 2014. Effects of hypoxia-induced habitat compression on growth of juvenile fish in the Neuse River estuary, North Carolina, USA. Marine Ecology Progress Series 497:199–213.
- Cheek, T. E., M. J. Van Den Avyle, and C. C. Coutant. 1985. Influences of water quality on distribution of Striped Bass in a Tennessee River impoundment. Transactions of the American Fisheries Society 114:67–76.
- Chittenden, M. E. 1971. Effects of handling and salinity on oxygen requirements of Striped Bass, *Morone saxatilis*. Journal of the Fisheries Research Board of Canada 28:1823–1830.
- Coutant, C. C. 1985. Striped Bass temperature and dissolved oxygen: a speculative hypothesis for environmental risk. Transactions of the American Fisheries Society 114:31–61.
- Coutant, C. C., and D. D. Benson. 1990. Summer habitat for Striped Bass in Chesapeake Bay: reflections on a population decline. Transactions of the American Fisheries Society 119:757–778.
- Cowan, J. H., K. A. Rose, E. S. Rutherford, and E. D. Houde. 1993. Individual-based model of young-of-year Striped Bass population dynamics II: factors affecting recruitment in the Potomac River, Maryland. Transactions of the American Fisheries Society 22:439–458.
- Ellis, T. A., J. A. Buckel, and J. E. Hightower. 2017. Winter severity influences Spotted Seatrout mortality in a southeast U.S. estuarine system. Marine Ecology Progress Series 564:145–161.
- Farquhar, B. W., and S. Gutreuter. 1989. Distribution and migration of adult Striped Bass in Lake Whitney, Texas. Transactions of the American Fisheries Society 118:523–532.
- Graves, J. E., A. Z. Horodysky, and R. J. Latour. 2009. Use of pop-up satellite archival tag technology to study postrelease survival of and habitat use by estuarine and coastal fishes: an application to Striped Bass (*Morone saxatilis*). U.S. National Marine Fisheries Service Fishery Bulletin 107:373–383.
- Harris, J. E., and J. E. Hightower. 2017. An integrated tagging model to estimate mortality rates of Albemarle Sound-Roanoke River Striped Bass. Canadian Journal of Fisheries and Aquatic Sciences 74:1061–1076.
- Hawkins, J. H. 1980. Investigations of anadromous fishes of the Neuse River, North Carolina. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Special Scientific Report 34, Morehead City.
- Hightower, J. E., and J. E. Harris. 2017. Estimating fish mortality rates using telemetry and multistate models. Fisheries 42:210–219.
- Hightower, J. E., J. R. Jackson, and K. H. Pollock. 2001. Use of telemetry methods to estimate natural and fishing mortality of Striped Bass in Lake Gaston, North Carolina. Transactions of the American Fisheries Society 130:557–567.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. U.S. National Marine Fisheries Service Fishery Bulletin 81: 898–903.
- Homan, J. M., K. R. Rundle, K. W. Ashley, and K. J. Dockendorf. 2012. Review of Striped Bass monitoring programs in the Central Southern Management Area, North Carolina—2011. North Carolina Wildlife Resources Commission, Federal Aid in Sportfish Restoration, Project F-22, Raleigh.
- Hudson, J. M., J. R. Johnson, and B. Kynard. 2011. A portable electronarcosis system for anesthetizing salmonids and other fish. North American Journal of Fisheries Management 31:335–339.
- Jiang, H., K. H. Pollock, C. Brownie, J. M. Hoenig, and R. J. Latour. 2007. Tag return models allowing for harvest and catch and release: evidence of environmental and management impacts on Striped Bass fishing and natural mortality rates. North American Journal of Fisheries Management 27:387–396.
- Kerns, J. A., M. S. Allen, and J. E. Hightower. 2016. Components of mortality within a black bass high-release recreational fishery. Transactions of the American Fisheries Society 145:578–588.
- Kery, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, Massachusetts.
- Koo, T. S. 1970. The Striped Bass fishery in the Atlantic States. Coastal and Estuarine Research Federation 11:73–93.
- Limburg, K. E., and J. R. Waldman. 2009. Dramatic declines in North Atlantic diadromous fishes. BioScience 59:955–965.
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. Journal of Fish Biology 49:627–647.
- Mansueti, R. J. 1958. Eggs, larvae, and young of the Striped Bass. University of Maryland Chesapeake Laboratory Biological Contribution 112.
- Merriman, D. 1941. Studies on the Striped Bass (*Roccus saxatilis*) of the Atlantic coast. U.S. Fish and Wildlife Service Fishery Bulletin 50:1–77.
- Monteleone, D. M., and E. D. Houde. 1990. Influence of maternal size on survival and growth of Striped Bass, *Morone saxatilis*, eggs and larvae. Journal of Experimental Marine Biology and Ecology 140:1–11.
- Moore, M. C., R. J. Neves, and J. J. Ney. 1991. Survival and abundance of stocked Striped Bass in Smith Mountain Lake, Virginia. North American Journal of Fisheries Management 11:393–399.
- NCDENR (North Carolina Department of Environmental and Natural Resources). 2002. Neuse River basin-wide water quality plan. NCDENR, Raleigh.

- NCDMF (North Carolina Division of Marine Fisheries) and NCWRC (North Carolina Wildlife Resources Commission). 2013. Amendment I to the North Carolina Estuarine Striped Bass Fishery Management Plan. North Carolina Department of Environment and Natural Resources, NCDMF, Morehead City.
- Nelson, K. L. 1998. Catch-and-release mortality of Striped Bass in the Roanoke River, North Carolina. *North American Journal of Fisheries Management* 18:25–30.
- Olsen, E. J., and R. A. Rulifson. 1992. Maturation and fecundity of Roanoke River–Albemarle Sound Striped Bass. *Transactions of the American Fisheries Society* 121:524–537.
- Pearson, J. C. 1938. The life history of the Striped Bass, or Rockfish, *Roccus saxatilis* (Walbaum). U.S. Bureau of Fisheries Bulletin 49:825–860.
- Polgar, T. T., J. A. Mihursky, R. E. Ulanowicz, R. P. Morgan II, and J. S. Wilson. 1976. An analysis of 1974 Striped Bass spawning success in the Potomac estuary. Pages 151–165 in M. L. Wiley, editor. *Estuarine processes, volume 1: uses, stresses and adaptation to the estuary*. Academic Press, New York.
- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimate I: an evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* 21:521–532.
- Pollock, K. H., J. Jiang, and J. E. Hightower. 2004. Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Transactions of the American Fisheries Society* 133:639–648.
- Rachels, K. T., and B. R. Ricks. 2015. Neuse River Striped Bass monitoring programs, population dynamics, and recovery strategies. North Carolina Wildlife Resources Commission, Inland Fisheries Division, Raleigh.
- Regan, D. M., T. L. Wellborn, and R. G. Bowker. 1968. Striped Bass development of essential requirements for production. U.S. Fish and Wildlife Service, Bureau of Sport Fisheries, Atlanta.
- Richards, R. A., and R. J. Rago. 1999. A case history of effective fishery management: Chesapeake Bay Striped Bass. *North American Journal of Fisheries Management* 19:356–375.
- Rogers, B. A., D. T. Westin, and S. B. Saila. 1977. Life stage duration studies on Hudson River Striped Bass. University of Rhode Island, Applied Marine Resources Group, National Oceanic and Atmospheric Administration Sea Grant, Marine Technical Report 31, Kingston.
- Rulifson, R. A., and C. S. Manooch III. 1990. Recruitment of juvenile Striped Bass in the Roanoke River, North Carolina, as related to reservoir discharge. *North American Journal of Fisheries Management* 10:397–407.
- Secor, D. H. 1990. The early life history of natural and hatchery-produced Striped Bass. Doctoral dissertation. University of South Carolina, Columbia.
- Servanty, S., S. J. Converse, and L. L. Bailey. 2014. Demography of a reintroduced population: moving toward management models for an endangered species, the whooping crane. *Ecological Applications* 24:927–937.
- Setzler, E. M., W. R. Boynton, K. V. Wood, H. H. Zion, L. Lubbers, N. K. Mountford, P. Frere, L. Tucker, and J. A. Mihursky. 1980. Synopsis of biological data on Striped Bass, *Morone saxatilis* (Walbaum). NOAA Technical Report NMFS Circular 443 and Food and Agriculture Organization Synopsis 121.
- Setzler-Hamilton, E. M., W. R. Boynton, J. A. Mihursky, T. T. Polgar, and K. V. Wood. 1981. Spatial and temporal distribution of Striped Bass eggs, larvae, and juveniles in the Potomac estuary. *Transactions of the American Fisheries Society* 110:121–136.
- Spiegelhalter, D. A., N. B. Thomas, and D. Lunn. 2010. OpenBUGS user manual, version 3.1.2. MRC Biostatistics Unit, Cambridge, UK.
- Summerfelt, R. C., and L. S. Smith. 1990. Anesthesia, surgery, and related techniques. Pages 213–272 in C. B. Schreck and P. B. Moyle, editors. *Methods for fish biology*. American Fisheries Society, Bethesda, Maryland.
- Sutton, T. M. 1997. Early life history dynamics of a stocked Striped Bass (*Morone saxatilis*) population and assessment of strategies for improving stocking success in Smith Mountain Lake, Virginia. Doctoral dissertation. Virginia Polytechnic Institute and State University, Blacksburg.
- Thompson, J. S., and J. A. Rice. 2013. The relative influence of thermal experience and forage availability on growth of age 1–5 Striped Bass in two southeastern reservoirs. Pages 93–120 in J. S. Bulak, C. C. Coutant, and J. A. Rice, editors. *Biology and management of inland Striped Bass and hybrid Striped Bass*. American Fisheries Society, Symposium 80, Bethesda, Maryland.
- Thompson, J. S., J. A. Rice, and D. S. Waters. 2010. Striped Bass habitat selection rules in reservoirs without suitable summer habitat offer insight into consequences for growth. *Transactions of the American Fisheries Society* 139:1450–1464.
- Thompson, J. S., D. S. Waters, J. A. Rice, and J. E. Hightower. 2007. Seasonal natural and fishing mortality of Striped Bass in a southeastern reservoir. *North American Journal of Fisheries Management* 27:681–694.
- Turner, J. L., and H. K. Chadwick. 1972. Distribution of abundance of young-of-the-year Striped Bass, *Morone saxatilis*, in relation to river flow in the Sacramento–San Joaquin Estuary. *Transactions of the American Fisheries Society* 101:442–452.
- Turner, J. L., and T. C. Farley. 1971. Effects of temperature, salinity, and dissolved oxygen on the survival of Striped Bass eggs and larvae. *California Fish and Game* 57:268–273.
- USDOI (U.S. Department of the Interior) and USDOC (U.S. Department of Commerce). 1993. Striped Bass research study, report for 1992. USDOC, National Marine Fisheries Service, Silver Spring, Maryland.
- USGS (U.S. Geological Survey). 1995. Water quality assessment of the Albemarle–Pamlico drainage basin, North Carolina and Virginia—environmental setting and water-quality issues. USGS, Open-File Report 95-136, Raleigh, North Carolina.
- Wagner, G. N., S. J. Cooke, R. S. Brown, and K. A. Deters. 2011. Surgical implantation techniques for electronic tags in fish. *Reviews in Fish Biology and Fisheries* 21:71–81.
- Wallin, J. E., and M. J. Van Den Avyle. 1995. Interactive effects of stocking site salinity and handling stress on survival of Striped Bass fingerlings. *Transactions of the American Fisheries Society* 124:746–745.
- Weaver, J. E., R. B. Fairbanks, and C. M. Wooley. 1986. Interstate management of Atlantic coastal migratory Striped Bass. *Marine Recreational Fisheries* 11:71–85.
- Zale, A. V., J. D. Weichman, R. L. Lochmiller, and J. Burroughs. 1990. Limnological conditions associated with summer mortality of Striped Bass in Keystone Reservoir, Oklahoma. *Transactions of the American Fisheries Society* 119:72–76.