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ARTICLE

Modeling the Effects of Vital Rate Manipulation and Management Scenarios to Predict the Population Impact of Restoration Programs on an Unrecovered Coastal Population of Striped Bass

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Abstract
Striped Bass *Morone saxatilis* have supported important fisheries along the Atlantic coast of North America. However, the species experienced major declines due to overharvest, water quality degradation, and dam construction. Restoration efforts have been successful for specific stocks but unsuccessful for the Striped Bass population in the Neuse River of North Carolina. Ongoing research programs have estimated stage- and source-specific mortality rates to identify mechanisms associated with the lack of recovery of the population. These demographic data are useful; however, they give little insight into the effectiveness of potential restoration programs. To develop effective management strategies, we used estimated mortality rates from the literature to build an age-structured population model. We estimated that if vital rates remained constant, the Neuse River adult Striped Bass population would consist of 18,457 individuals (95% credible interval = 8,176–34,314). We then conducted a life stage simulation analysis to determine the adult population abundance and age structure that would result from a 50% decrease of the following: juvenile and adult natural mortality, recreational discard and harvest, and commercial discard and harvest. Finally, we simulated the potential impacts of six possible management scenarios on population abundance and age structure. We determined that the abundances of adults (age 3+) and older adults (age 6+) were most sensitive to natural mortality of juveniles and adults and next most sensitive to commercial harvest and discard. We further estimated that eliminating all fishing mortality would have the greatest impact on the population and would result in a 26-fold increase in abundance of age-6+ adults. Our results suggest that high mortality rates are preventing the development of a sufficient abundance of adult spawning stock. We recommend that managers use this model to identify the most effective management scenario—given specific goals and constraints—to help increase Striped Bass abundance in the Neuse River.

The Striped Bass *Morone saxatilis* is a diadromous species that is native to the Atlantic coast of North America from the St. John's River, Florida, to the St. Lawrence River, Canada (Pearson 1938). Since the 1700s, Striped Bass have supported important commercial and recreational fisheries along the Atlantic states (Merriman 1941; Hawkins 1980). However, the species experienced major declines from historic levels (Pearson 1938; Koo 1970; Rulifson and Manooch 1990; Richards and Rago 1999; Limburg and Waldman 2009) due to overharvest (Hawkins 1980; USDOI and USDOC 1992), water quality degradation (Rathjen and Miller 1957; Polgar et al. 1976; Setzler-Hamilton et al. 1981; Hall et al. 1984; Buckler et al. 1987; Mehrle et al. 1987), environmental factors (Richards and Rago 1999), and dam construction (Rulifson 1991). Reduced fishing pressure (Ballou 1987), enhancement programs (Weaver et al. 1986; USDOI and USDOC 1992; NCDMF and NCWRC 2013; Callihan

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et al. 2014), improved water quality (Sloan et al. 1983; Albert 1988; Richards and Rago 1999), and increased access to spawning habitat (NCDMF and NCWRC 2013) have led to recoveries of some stocks; examples include those in the Chesapeake Bay and Roanoke River (Richards and Rago 1999; NCDMF and NCWRC 2013). Unfortunately, not all restoration attempts have been successful.

In the late 1800s the Neuse River population supported the second-largest Striped Bass fishery in North Carolina (after the Roanoke River population; Yarrow 1874). This population was described as "exceedingly plenty," and by 1880 nearly 16,000 Striped Bass were harvested annually from the lower Neuse River (Yarrow 1874; McDonald 1884). However, by the 1930s Striped Bass harvest had severely declined (Chestnut and Davis 1975). Recovery efforts were implemented in the Neuse River, and by the 1980s recreational and commercial harvest restrictions (e.g., season, size, and catch limits) were in place to reduce fishing pressure (NCDMF and NCWRC 2013). The North Carolina Wildlife Resources Commission (NCWRC) and North Carolina Division of Marine Fisheries (NCDMF) developed a fisheries management plan that aims to rebuild the Neuse River Striped Bass population to an adequate spawning stock that maintains a broad age structure and supports a sustainable harvest (NCDMF and NCWRC 2013). To achieve this goal, fishing restrictions have been implemented for the commercial fishery, including a 46-cm minimum size limit with a spring harvest season only (January 1–April 30) and a 10-fish daily landing limit (NCDMF and NCWRC 2013). On average, annual harvest of Striped Bass from the Neuse River is 2,700 kg, which comprises 3% of the state's total Striped Bass commercial harvest (NCDMF and NCWRC 2013). Since 2008, recreational harvest in the Neuse River has also been restricted to a 46-cm minimum size, a protective no-harvest slot of 56–69 cm in inland waters, a set season (October–April), and a creel limit of 2 fish/d (NCDMF and NCWRC 2013). In addition to strict harvest limits, the NCWRC, in collaboration with the U.S. Fish and Wildlife Service, established an enhancement program during the mid-1990s; about 125,000 phase I (25–75 mm TL) juvenile Striped Bass were stocked annually from 1994 to 2014 (except 2002, 2010, and 2011) in the lower Neuse River, and about 100,000 phase II (125–200 mm TL) juveniles were stocked in alternate years from 1992 to 2006 and then every year thereafter (except 2008; NCDMF and NCWRC 2013). In addition, the Quaker Neck Dam was removed from river kilometer 225 in 1998 (Burdick and Hightower 2006), providing improved access to spawning habitat. The Quaker Neck Dam had reduced the historical migratory range of Striped Bass by about half, and its removal restored access to more than 120 km of potential main-stem spawning habitat and 1,488 km of potential tributary spawning habitat (Burdick and Hightower 2006).

Despite nearly two decades of reduced harvest, enhancement programs, and increased access to historical spawning grounds, however, the Neuse River Striped Bass population has not recovered; relative abundance has remained low and the size distribution has remained truncated. Since 1994, NCWRC biologists have conducted weekly electrofishing surveys each spring to monitor the spawning population. In 2014, annual CPUE was 12 fish/h, 98% of fish were age 7 or younger, and no individual older than age 10 was observed (Rachels and Ricks 2015). By comparison, in the Roanoke River, the annual CPUE was 169.5 fish/h, 98% of fish were age 7 or younger, and the maximum age collected was 14 (Smith et al. 2016). Additionally, and perhaps more troubling, there is no evidence of recruitment by Striped Bass to the juvenile stage. Barwick et al. (2009) sampled extensively for age-0 Striped Bass throughout the Neuse River during summer in 2006 and 2007 and collected only five individuals (three were confirmed as hatchery origin; two were of uncertain origin). Since 2010, the NCWRC has been using parentage-based tagging methods and genetic microsatellite markers to identify Striped Bass of hatchery origin in the Neuse River. In the most recent sample (2016; $n = 113$), all 610-mm and smaller fish were identified as being of hatchery origin. Fish of uncertain origin only became more common at larger sizes, where fish were more likely to be from year-classes predating the parentage-based tagging program (J. W. McCargo, NCWRC, personal communication).

Low population abundance, a truncated age distribution, and a lack of natural recruitment are complex issues that are most likely attributable to a synergy of fishing and environmental causes. Ongoing research programs have estimated stage- and source-specific mortality rates in an effort to identify mechanisms associated with the lack of recovery of the Neuse River Striped Bass population. For example, Bradley et al. (2018) acoustically tracked 100 hatchery-reared phase II juvenile Striped Bass and 111 resident adults in the Neuse River. They concluded that 66% (95% credible interval [CI] = 47–82%) of juveniles died within the first year after stocking and that adult mortality was lower (annual discrete total mortality = 0.54, 95% CI = 0.43–0.66; annual discrete natural mortality = 0.20, 95% CI = 0.09–0.39). During 2004–2009, the NCDMF used recreational creel survey data and commercial independent gill-net survey data to estimate harvest and discard in the Neuse River. The NCDMF estimated that 38% of the fishing-related mortality of Striped Bass in the Neuse River was attributable to commercial harvest, 28% to commercial discard, 22% to recreational harvest, and 12% to recreational catch-and-release mortality (hereafter, "recreational discard mortality"; NCDMF and NCWRC 2013).

These detailed demographic data are useful to estimate, but they give little insight into the effectiveness of potential restoration programs. To develop effective management strategies, vital rates that have the largest effect on population performance must be identified (Morris and Doak 2002; Johnson et al. 2010).

In this study we used mortality estimates for Neuse River juvenile and adult Striped Bass to develop an age-structured population model. We then conducted a life stage simulation analysis to assess the impact of manipulating each vital rate on the abundance of age-3 and older (age-3+) individuals (hereafter, "adults") and a subset of adults consisting of age-6+ individuals (hereafter, "older adults"). Finally, we simulated the potential impacts of six possible management scenarios on adult population abundance and older adult population abundance.

METHODS

Vital rate parameter estimation.— Stage- and source-specific mortality rates were available for the Neuse River Striped Bass population (Table 1; NCDMF and NCWRC 2013; Bradley et al. 2018). Mortality of phase II hatchery-reared juveniles, total mortality of adults, and natural mortality of adults were reported by Bradley et al. (2018). We calculated fishing mortality by assuming that total mortality was a fully additive form of natural and fishing mortality, which occurred continuously throughout the year:

$$\text{Total mortality} = \text{natural mortality} + \text{fishing mortality}.$$

Component rates of fishing mortality were further broken down by using harvest and discard mortality estimates provided by NCDMF and NCWRC (2013). We calculated rates for recreational harvest, commercial harvest, recreational discard mortality, and commercial discard mortality by multiplying the total fishing mortality rate by the specific fishing mortality proportion (Table 1). For example, the rate for recreational harvest was calculated by the following equation:

$$\text{Recreational harvest rate} = \text{total fishing mortality rate} \times \text{recreational harvest proportion}.$$

No mortality rates were available for individuals below harvest size ("subadults"); therefore, we assumed that the mortality of subadults was equal to adult total mortality but with no harvest. Discard mortality was assumed equal between adults and subadults because gill nets with varying size selectivity are allowed in the Neuse River. Specifically, gill nets with mesh sizes as small as 6.35-cm bar mesh are allowed (NCDMF and NCWRC 2013), which efficiently catch subadult-sized Striped Bass (Trent and Hassler 1968).

Population abundance estimates.— We estimated population abundances of adult and older adult Striped Bass by using the following equation:

$$\text{Abundance} = \text{births} + \text{immigration} - \text{deaths} - \text{emigration}.$$

To do this, we developed an age-structured population model in program R (Supplement 1). Because there is no evidence of Striped Bass natural recruitment in the Neuse River (Barwick et al. 2009; NCDMF and NCWRC 2013), no reproductive rates were estimated. Instead, the number of "births" was simply the number of phase II juveniles (age 1) that have been stocked annually from 2009 to 2015 (Table 1). A considerable number of phase I juveniles have historically been stocked (40% of all juveniles stocked in the Neuse River from 2009 to 2014 were phase

TABLE 1. Estimate (median, annual instantaneous rate), variance, and source of each parameter used in the age-structured population model for Neuse River Striped Bass. Variances for subadult total mortality and adult total mortality are not provided, as these values were not used in the model.

Parameter	Estimate	Variance	Source
Number of juveniles stocked	100,754	NA	NCDMF (unpublished data)
Juvenile mortality	1.087	0.078	Bradley et al. (2018)
Subadult total mortality	0.456	NA	Bradley et al. (2018)
Adult total mortality	0.776	NA	Bradley et al. (2018)
Adult natural mortality	0.243	0.013	Bradley et al. (2018)
Total fishing mortality	0.533	0.031	Bradley et al. (2018)
Recreational discard mortality	0.064	0.0004	NCDMF and NCWRC (2013), Bradley et al. (2018)
Commercial discard mortality	0.149	0.002	NCDMF and NCWRC (2013), Bradley et al. (2018)
Recreational harvest	0.117	0.001	NCDMF and NCWRC (2013), Bradley et al. (2018)
Commercial harvest	0.203	0.004	NCDMF and NCWRC (2013), Bradley et al. (2018)

I juveniles), but they contributed only 1% of adult fish that were recaptured and genetically traced to hatchery origin, compared to 99% for phase II fish (K. J. Dockendorf, NCWRC, personal communication). Furthermore, the NCWRC stopped stocking phase I juveniles in 2015; thus, even this minimal contribution will end. Cohort abundance was then estimated by applying annual instantaneous juvenile, subadult, and adult component mortality rates to calculate the number of individuals of each age-class still living at the end of the year. Juveniles (age 1; assumed to begin on January 1 of the year following birth, which was approximately the same date the juveniles were stocked) were assumed to transition to subadults on January 1 of the next year (~1 year after stocking); subadults (age 2) were assumed to transition to adults after 1 year (Rachels and Ricks 2015); and adults (age 3+) remained adults (but were considered to enter the subset of older adults after 3 years, i.e., at age 6). Maximum age was assumed to be 30 years. Emigration and immigration were assumed to be negligible, as studies have shown that the Neuse River Striped Bass population is mainly riverine and nonmigratory (Marshall 1977; Hawkins 1980; NCDMF and NCWRC 2013; Callihan et al. 2014).

Life stage simulation analysis.— To determine life history parameters that had the greatest impact on the Neuse River Striped Bass population, we followed Johnson et al. (2010) as a guide and conducted life stage simulation analyses. Specifically, we generated 1,000 matrices of component mortality rates; in each simulation, the population vector for each year was multiplied by a randomly drawn matrix (rates were assumed constant within each matrix), where mortality rate values were generated from gamma probability distributions (Bolker 2008) given the medians and variances (Table 1). Each matrix was projected 20 years—the time period to achieve a stable stage distribution in the population. The resulting population abundances of adults and older adults were then calculated and compared to the estimated baseline abundances (estimated baseline using nonmanipulated vital rate values) to assess the impact of each scenario. Population abundance was used instead of population growth because there is no natural recruitment. Consequently, abundance in the system is additive rather than multiplicative, and as long as vital rates are held constant the growth rate will always be 1.0. The initial baseline abundance and age distribution were compared with observed relative abundance and age distribution data collected by NCWRC during 2015 spring sampling.

The first life stage simulation analysis we performed was a sensitivity analysis to identify age- and cause-specific mortality rate "importance" in terms of the potential effects on population abundances. We simulated a 50% proportional decrease of the following mortality rates individually: juvenile mortality, natural mortality of adults and subadults (hereafter, "adult natural mortality"), recreational discard mortality, recreational harvest mortality, commercial discard mortality, and commercial harvest mortality. Next, we simulated the potential impacts of six plausible management actions: (1) doubling the number of fish stocked, (2) eliminating all harvest (recreational and commercial), (3) eliminating all recreational fishing mortality (harvest and discard), (4) eliminating all commercial fishing mortality (harvest and discard), (5) eliminating all fishing and discard mortality, and (6) doubling the number of fish stocked while also eliminating all harvest.

RESULTS

The baseline model predicted few individuals over age 9, which is consistent with field observations (Table 2). Baseline adult population abundance was estimated to be 18,457 individuals (95% CI = 8,176–34,314), with 1,809 older adults (95% CI = 720–4,107; Table 3).

Results from the sensitivity analysis showed that adult and older adult abundances were most sensitive to juvenile and adult natural mortalities; interestingly, however, juvenile mortality affected adult abundance the most, while adult natural mortality affected older adult abundance the most (Table 3; Figure 1). Both adult and older adult abundances were moderately sensitive to commercial harvest and discard mortality and were least affected by recreational harvest and discard mortality (Table 3; Figure 1).

All modeled management scenarios would increase abundances above baseline, and some scenarios were

TABLE 2. Abundance and percentage of adult Striped Bass age-classes as predicted by the baseline population model and as observed by Rachels and Ricks (2015) during field sampling in the Neuse River in spring 2015. Age 3 had lower gear susceptibility, so the observed abundance and percentage of age 3 are not included.

	Baseline prediction		Observed catch	
Age	Abundance	Percent	Abundance	Percent
3	9,985	NA	NA	NA
4	4,526	54	106	45
5	2,137	25	74	31
6	983	12	27	11
7	443	5	22	9
8	211	2	3	1
9	94	1	2	<1
10	42	<1	1	<1
11	19	<1	0	NA
12	9	<1	0	NA
13	4	<1	0	NA
14	2	<1	0	NA
15	1	<1	0	NA

TABLE 3. Predicted population abundance, 95% credible interval (CI), maximum age with 10 or more individuals, and the resulting proportional change (prop. change) in abundance of Striped Bass adults (age 3+) and older adults (age 6+) in the Neuse River 20 years after simulated manipulation of each vital rate.

Vital rate	Adult abundance	95% CI	Prop. change	Maximum age	Older adult abundance	95% CI	Prop. change
Baseline	18,457	8,176–34,314	N/A	11	1,809	720–4,107	N/A
50% reduction in:							
Juvenile mortality	32,714	13,767–58,915	1.77	12	3,135	1,217–6,901	1.73
Adult natural mortality	26,866	11,543–50,864	1.46	14	3,794	1,472–8,373	2.10
Commercial discard mortality	23,623	10,779–44,856	1.28	13	2,827	1,144–6,411	1.56
Commercial harvest	22,873	10,742–44,197	1.24	13	3,024	1,168–6,716	1.67
Recreational harvest	20,898	9,385–41,094	1.13	12	2,403	882–5,554	1.33
Recreational discard mortality	20,411	9,261–38,844	1.11	12	2,200	833–4,913	1.22

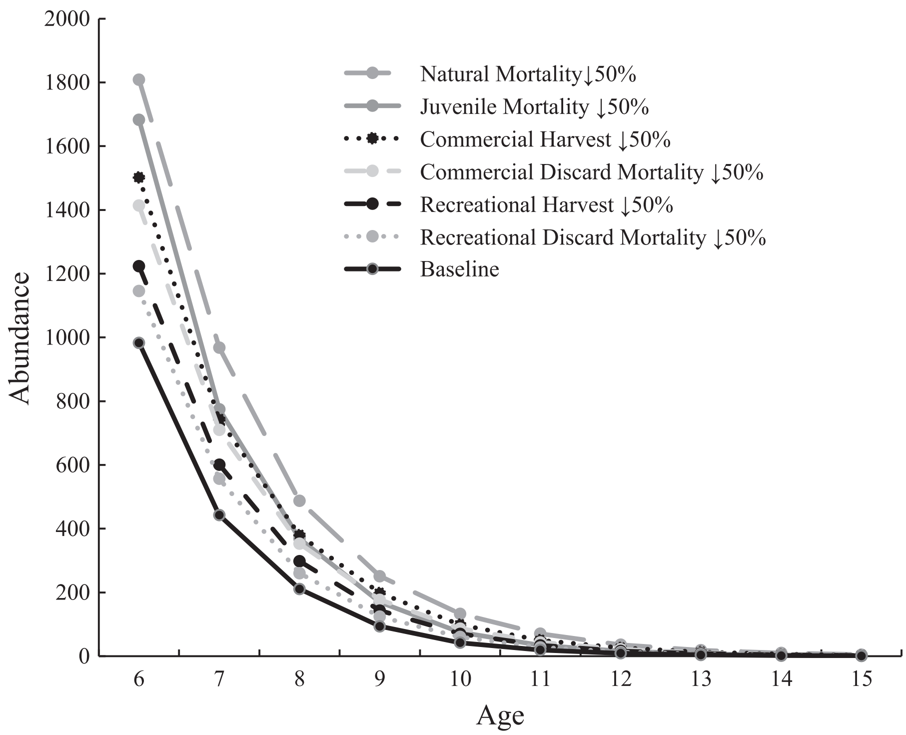

FIGURE 1. Predicted abundance of older adult Striped Bass (ages 6–15) in the baseline simulation and after a simulated 50% decrease in each component mortality rate.

predicted to generate substantial increases. In particular, the population abundances of adults and older adults were predicted to increase 5.36- and 26.38-fold, respectively, if all harvest mortality and discard mortality were eliminated (Table 4; Figure 2). Doubling the number stocked while eliminating all harvest was not as effective, but it still resulted in 4.06- and 10.54-fold increases in adult and older adult abundances (Table 4; Figure 2). The elimination of all commercial mortality was the third most effective management strategy to increase adult and older adult abundances (2.56- and 7.31-fold increases). Eliminating all recreational mortality was the least effective management scenario (1.54- and 2.66-fold increases; Table 4; Figure 2). Interestingly, some management scenarios affected adult and older adult abundances differently. The management scenario that affected adult abundance the least was eliminating all recreational mortality (1.54-fold increase), while doubling the number stocked had the least effect on older adult abundance (2.00-fold increase; Table 4; Figure 2). In all but one management scenario

TABLE 4. Predicted population abundance, 95% credible interval (CI), maximum age with at least 10 individuals, and the resulting proportional change in abundance of Striped Bass adults (age 3+) and older adults (age 6+) in the Neuse River after a 20-year simulation of each management scenario.

Management scenario	Adult abundance	95% CI	Prop. change	Maximum age	Older adult abundance	95% CI	Prop. change
Baseline	18,457	8,176–34,314	N/A	11	1,809	720–4,107	N/A
Eliminate harvest and discard mortality	98,996	44,135–193,500	5.36	>30	47,725	19,243–102,829	26.38
Double the number stocked and eliminate harvest	74,877	33,579–141,133	4.06	20	19,059	7,769–41,386	10.54
Eliminate all commercial mortality	47,289	21,570–88,722	2.56	20	13,232	5,533–28,930	7.31
Double the number stocked	36,915	16,353–68,628	2.00	12	3,618	1,439–8,214	2.00
Eliminate all harvest	37,439	16,790–70,567	2.03	18	9,530	3,884–20,693	5.27
Eliminate all recreational mortality	28,440	12,514–53,020	1.54	14	4,814	1,909–10,610	2.66

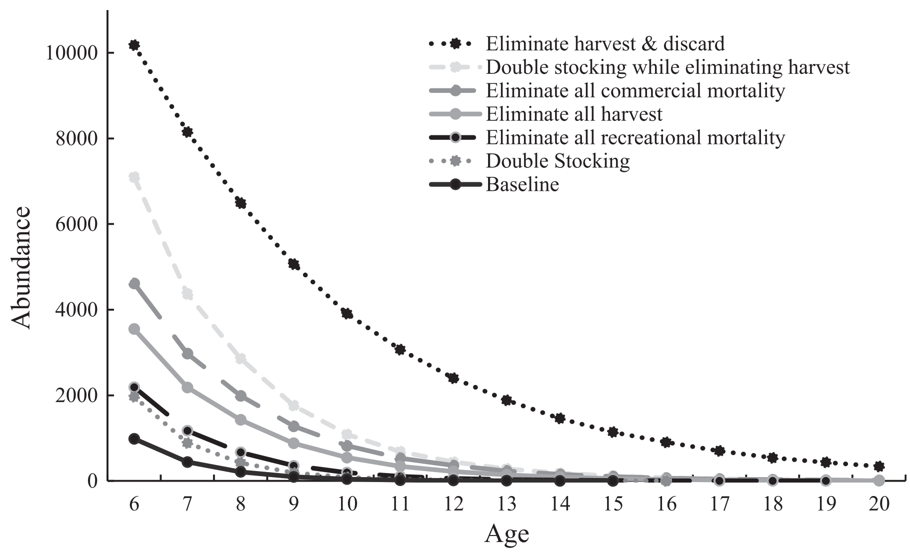

FIGURE 2. Predicted abundance of older adult Striped Bass (ages 6–20) in the baseline simulation and after the simulated implementation of each management scenario.

(doubling the stocking number), older adult abundance responded more strongly than adult abundance.

DISCUSSION

We developed an age-based population model and conducted life stage simulation analyses to better understand the failure of Neuse River Striped Bass population recovery efforts. As expected, our age-based population model estimated a low abundance and truncated age distribution of Striped Bass in the Neuse River. Adult and older adult population abundances were most sensitive to natural mortality of juveniles and adults as well as to commercial harvest and discard mortality. Results showed that eliminating all fishing mortality would have the greatest impact on increasing abundances of adult and older adult Striped Bass in the Neuse River, whereas eliminating all recreational mortality would have the least impact on adult abundance and doubling the number stocked would have the least impact on older adult abundance. Interestingly, the effectiveness of decreasing mortality rates was age specific and not necessarily correlated with the magnitude of the rate. These unintuitive results elucidated the importance of clearly defined management goals (i.e., increasing adult abundance versus increasing the abundance of older ages) and the importance of life stage simulation analyses in identifying the most effective management strategies when trying to rebuild a population and when managing a put-and-take fishery.

Our baseline modeling results predicted a truncated age distribution for Striped Bass in the Neuse River given current vital rates, which is similar to empirical data from monitoring programs (Table 2; Rachels and Ricks 2015). Our baseline model also predicted a low population abundance, although empirical evidence suggests that actual abundance may be even lower than predicted by the model. Given the estimated baseline population abundance, commercial harvest rate, and recreational harvest rate, the model predicted a commercial harvest of 3,391 individuals and a recreational harvest of 2,038 individuals. However, average recreational harvest estimated from NCWRC creel surveys was 1,718 individuals (SD = 740), and average commercial harvest estimated from NCDMF trip tickets in 2013–2014 was 1,284 individuals (SD = 228; C. H. Godwin, NCDMF, personal communication). The discrepancy between predicted and observed harvests is likely due to an overestimation of population abundance as an artifact of underestimating juvenile mortality. Bradley et al. (2018) censored all mortality that occurred within the first month after stocking. Although this assumption eliminated surgery-related mortality, it likely eliminated natural mortality that occurred during the first month poststocking—the period when stocked juveniles are youngest and most naïve.

Low abundance and a truncated age distribution may be contributing to the lack of recovery of the Striped Bass population in the Neuse River by limiting the number and fecundity of individuals that spawn. Bradley et al. (2018) found that fish size affected whether adult fish migrated upriver during the spring, presumably to spawn. Not only are larger fish more likely to make spawning migrations, they also have higher fecundity and can produce offspring with higher survival than smaller and younger 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. In addition to being more numerous, the eggs and subsequent larvae produced by older and larger females were as much as 20% larger than those produced by smaller females (Monteleone and Houde 1990). Ultimately, truncated adult size can reduce juvenile recruitment (Cowan et al. 1993) because the survival of embryos and larvae is positively correlated with their size (Secor 1990).

Results from our life stage simulation analyses were age specific, and the contribution of vital rates to abundance depended on the age of the fish. For example, doubling the number stocked doubled the abundance of adult fish, but this management strategy was the least effective at increasing the abundance of older adults. Generally, manipulation of vital rates had a much greater impact on increasing the abundance of older adults than on increasing the abundance of all adults because of the low number of older adults present in the system. Therefore, relatively small changes in vital rates had major effects on the abundance of older adults. For example, although the management scenario of eliminating all fishing-related mortality resulted in the greatest increases in both adult and older adult abundances, it produced only a 5-fold increase in the abundance of adult fish while achieving a 26-fold increase in the abundance of older adults. These results underscore the importance of developing explicit policy goals, and managers may take different actions depending on whether they want to increase adult abundance or expand the age distribution of Striped Bass.

Despite the age-specific nature of our modeling results, some general patterns emerged. Reducing juvenile and adult natural mortality, increasing the number stocked while eliminating harvest, and reducing fishing mortality (particularly commercial discard mortality) all had a proportionately large impact on adult and older adult abundances; however, these strategies are not equally feasible. Increasing the number stocked may be one of the easiest "vital rates" for managers to manipulate, as production cost is the main obstacle. Cost per unit of phase II juvenile Striped Bass has been estimated to vary between US$0.94 and $1.94 per fish (Rulifson and Laney 1999; Southerwick and Loftus 2002; Patrick et al. 2006). Managers could evaluate the increased costs versus the predicted increase in Striped Bass abundance to determine whether this strategy is economically feasible and worthwhile.

Decreasing the mortality of stocked juveniles may be possible by improving stocking methods. For example, Baltzegar (2010) determined that the survival of phase II juvenile Striped Bass after stocking was dependent on salinity. She found that individuals raised in hatchery ponds with salinities similar to those at stocking locations experienced higher survival and made a larger contribution to the fishery. Wallin and Van Den Avyle (1995) concluded that stocking of juvenile Striped Bass in brackish water ameliorated stress and could reduce mortality. The average salinity level at the time and location of stocking on the Neuse River varied from 0.03‰ to 15.88‰ (mean = 6.2‰; USGS 2016) during the period 1996–2009; however, the Striped Bass are reared in ponds that vary from 0‰ to 6‰ (S. C. Jackson, Edenton National Fish Hatchery, personal communication). In 2013, juveniles were stocked in the Neuse River at a salinity level of 0.1‰, and fish were likewise held in water with salinity of 0.1‰ at the hatchery. However, the effects of handling may offset the effects of salinity. Wallin and Van Den Avyle (1995) noted that handling had the greatest impact on juvenile survival, and there was no difference in mortality between individuals stocked in brackish water versus freshwater when handling was minimal (Wallin and Van Den Avyle 1995). Likewise, Raquel (1989) determined that handling and trucking of Striped Bass before stocking increased mortality but also noted that increased salinity and oxygen in holding tanks before stocking could decrease mortality.

Natural mortality of adult Striped Bass can be caused by a number of factors, including limited food availability, competitors (Setzler et al. 1980), pollutants (Rathjen and Miller 1957; Polgar et al. 1976; Setzler-Hamilton et al. 1981; Hall et al. 1984; Buckler et al. 1987; Mehrle et al. 1987), thermal stress (Setzler-Hamilton et al. 1981), and poor water quality (Chittenden 1971). It is possible that certain management scenarios could reduce adult natural mortality by reducing pollutants and improving water quality throughout the entire Neuse River watershed; the methods and feasibility to achieve this, if possible, are beyond the scope of this paper and beyond the control of fisheries management agencies in North Carolina. In contrast, reducing fishing mortality would be possible, and our results indicated that eliminating all fishing mortality (harvest and discard) would increase the abundance of adults and older adults more than any other management scenario. Eliminating all Striped Bass harvest would be possible by closing the fishery on the Neuse River; however, the elimination of all discard mortality would be much more difficult. Currently, the majority of recreationally caught Striped Bass are discarded (e.g., 90% of such individuals were released in the Neuse River during 2014). Even if no harvest is allowed, it is unlikely that all anglers would stop fishing for Striped Bass. Additionally, Striped Bass are caught as bycatch in other recreational fisheries (e.g., Largemouth Bass *Micropterus salmoides*, Red Drum *Sciaenops ocellatus*, and Spotted Seatrout *Cynoscion nebulosus*; NCDMF and NCWRC 2013), and these fisheries would continue even if the Striped Bass fishery was closed. However, recreational discard mortality could be reduced by changing fishing practices. Research has shown that recreational discard mortality of Striped Bass is positively correlated with high water temperature, use of live bait, and handling time (Harrell 1988; Diodati 1991; Hysmith et al. 1994; Nelson 1998).

Because commercial bycatch mortality has a greater impact on the Neuse River population than all other sources of fishing mortality, reductions in commercial bycatch mortality would result in a larger response in abundance than similar reductions in any other source of mortality. Striped Bass are caught as commercial bycatch in gill-net fisheries for the American Shad *Alosa sapidissima*, Atlantic Croaker *Micropogonias undulatus*, Red Drum, Southern Flounder *Paralichthys lethostigma*, Spot *Leiostomus xanthurus*, Spotted Seatrout, Striped Mullet *Mugil cephalus*, and Weakfish *Cynoscion regalis* (NCDMF and NCWRC 2013). Although closing all commercial fisheries in the Neuse River is neither plausible nor recommended, there are ways to reduce commercial bycatch. For example, NCDMF and NCWRC (2013) concluded that attendance of gill nets by fishers lowers bycatch mortality because it reduces the time the fish spend in the net and the number of gill nets that are set. Wilson (1999) concluded that restriction of gill nets during months of warm weather reduces Striped Bass mortality. Likewise, Price and Rulifson (2004) concluded that commercial fishers' traditional ecological knowledge can aid in gill-net placement to reduce bycatch of Striped Bass. Establishing more specific regulations on gill nets may allow continued use throughout the Neuse River while reducing Striped Bass bycatch.

Although we believe our results have important implications for Striped Bass in the Neuse River and for other put-and-take fisheries, some limitations of our data set should be recognized. This is a simplified model and does not take into account temporal variation, which could have population-level impacts. Shelton and Mangel (2011) used data from a global sample of fish species and concluded that environmental variation greatly alters the consequences of exploitation for the temporal variability of fish populations. Evidence suggests that there is temporal variation (potentially environmental and exploitative) in adult mortality of Neuse River Striped Bass. Rachels and Ricks (2015) used historic catch-at-age data and estimated that total mortality varied from 0.45 to 1.08 during 1994–2014. Other uncertainties may also affect model outputs. For example, subadults may grow to legally harvestable size during the year, and adults may grow into or out of the protected slot limit. In addition, age-2 and older individuals were assumed to all be equally vulnerable to commercial discard mortality, even though commercial discard mortality can be attributed to gill-net bycatch, which has varying size selectivity. Although gill nets with different mesh sizes are deployed in the Neuse River (NCDMF and NCWRC 2013), individuals of different sizes may have unequal vulnerability to harvest. Unfortunately, detailed information on the range and proportional use of different mesh sizes is not available; consequently, we could not factor gill-net selectivity into the analysis. It should also be noted that commercial discard mortality was estimated using data from 2004 to 2009, and since then policies have been implemented in the Neuse River to reduce Striped Bass bycatch (NCDMF and NCWRC 2013). If significant reductions have since occurred, our estimation of the importance of commercial discard could be exaggerated. Conversely, commercial discard mortality was estimated by counting the number of Striped Bass that were dead when discarded. Delayed discard mortality, however, may be common and can occur over an extended period (Davis 2002). For example, delayed mortality has been observed up to 6 d after discard in Atlantic Mackerel *Scomber* *scombrus* (Lockwood et al. 1983), 2 d after discard in Atlantic Halibut *Hippoglossus hippoglossus* (Neilson et al. 1989), 3.5 d after discard in Sole *Solea solea* (Van Beek et al. 1990), and 14 d after discard in Atlantic Herring *Clupea harengus* (Suuronen et al. 1996). Although differences in time of delayed mortality depended on species and environmental factors, counting only initial mortality likely underestimated the commercial discard mortality in our study. There is uncertainty in all estimates of component rates used in this analysis. If improved estimates of discard mortality or other component rates are obtained in the future, they can be incorporated into the model presented here to generate improved predictions of population responses to various management actions. Correlations and density dependence in vital rates could alter the effects of management scenarios in unpredictable ways, which was demonstrated in a Walleye *Sander vitreus* population in Lake Mendota, Wisconsin. Managers increased the number stocked but they did not see the predicted increase in abundance, as angling pressure disproportionately increased (Kitchell 1992). These effects could be explored with the model as additional data become available.

Our results showed that even though the Neuse River Striped Bass population has a low population abundance and truncated age distribution, several management scenarios could greatly increase the abundance and expand the age distribution. Increasing the number of older and more fecund individuals in the Neuse River population may be a necessary prerequisite for successful natural recruitment. However, that alone may not be sufficient because constraints at other life stages (i.e., eggs and larvae) could still inhibit natural recruitment. We recommend that managers use the age-based model we built to identify the most effective management scenario—given their specific goals and restraints—to help increase Striped Bass abundance in the Neuse River while also conducting research at other life stages to determine whether natural recruitment is possible if the spawning stock is high.

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REFERENCES

Albert, R. C. 1988. The historical context of water quality management for the Delaware estuary. Estuaries 11:99–107.

Ballou, R. 1987. The Atlantic Striped Bass Conservation Act: reauthorized and put to the test. Territorial Sea: Legal Defense in the Management of Interjurisdictional Resources 7(3–4):1–12.

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 Southeastern Association of Fish and Wildlife Agencies 63:161–165.

Bolker, R. M. 2008. Ecological models and data in R. Princeton University Press, London.

Bradley, C. E., J. A. Rice, D. D. Aday, J. E. Hightower, J. Rock, and K. L. Lincoln. 2018. Juvenile and adult Striped Bass mortality and distribution in an unrecovered coastal population. North American Journal of Fisheries Management 38:104–119.

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.

Callihan, J. L., C. H. Godwin, and J. A. Buckel. 2014. Effect of demography on spatial distribution: movement patterns of the Albemarle Sound–Roanoke River stock of Striped Bass (*Morone saxatilis*) in relation to their recovery. U.S. National Marine Fisheries Service Fishery Bulletin 112:131–143.

Chestnut, A. F., and H. S. Davis. 1975. Synopsis of marine fisheries of North Carolina. University of North Carolina, Sea Grant Program, Publication UNC-SG-75-12, Raleigh.

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.

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.

Davis, M. W. 2002. Key principles for understanding fish bycatch discard mortality. Canadian Journal of Fisheries and Aquatic Sciences 59:1834–1843.

Diodati, P. J. 1991. Estimating mortality of hook and released Striped Bass. Massachusetts Division of Marine Fisheries, Project AFC-22, Final Report, Salem.

Hall, L. W., L. O. Horseman, and S. Zeger. 1984. Effects of organic and inorganic chemical contaminants on fertilization, hatching success, and prolarval survival of Striped Bass. Archives of Environmental Contamination and Toxicology 13:723–729.

Harrell, R. M. 1988. Catch and release mortality of Striped Bass caught with artificial lures and baits. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 41(1987):70–75.

Hawkins, J. H. 1980. Investigations of anadromous fishes of the Neuse River, North Carolina. North Carolina Division of Marine Fisheries, Special Scientific Report 34, Morehead City.

Hysmith, B. T., J. H. Moczygemba, and G. R. Wilde. 1994. Hooking mortality of Striped Bass in Lake Texoma, Texas-Oklahoma. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 46:413–420.

Johnson, H. E., J. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

Kitchell, J. F. 1992. Food web management: a case study of Lake Mendota. Springer-Verlag, New York.

Koo, T. S. 1970. The Striped Bass fishery in the Atlantic States. Chesapeake Science 11:73–93.

Limburg, K. E., and J. R. Waldman. 2009. Dramatic declines in North Atlantic diadromous fishes. BioScience 59:955–965.

Lockwood, S. J., M. G. Pawson, and D. R. Eaton. 1983. The effects of crowding on Mackerel (*Scomber scombrus* L.), physical condition and mortality. Fisheries Research 2:129–147.

Marshall, M. D. 1977. Anadromous fisheries research program—Tar River, Pamlico River, and northern Pamlico Sound. North Carolina Division of Marine Fisheries, Completion Report Project AFCS-10, Morehead City.

McDonald, M. 1884. The rivers and sounds of North Carolina. Pages 625–637 *in* G. B. Goode, editor. The fisheries and fishery industries of the United States, section V. U.S. Commission of Fish and Fisheries, Washington, D.C.

Mehrle, P. M., L. Cleveland, and D. R. Buckler. 1987. Chronic toxicity of an environmental contaminant mixture to young (or larval) Striped Bass. Water, Air, and Soil Pollution 35:107–118.

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.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology; theory and practice of population viability. Sinauer Associates, Sunderland, Massachusetts.

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. NCDMF and NCWRC, Morehead City.

Neilson, J. D., K. G. Waiwood, and S. J. Smith. 1989. Survival of Atlantic Halibut caught by longline and otter trawl gear. Canadian Journal of Fisheries and Aquatic Sciences 46:887–897.

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.

Patrick, W. S., O. Bin, K. A. Schwabe, and P. W. Schumann. 2006. Hatchery programs, stock enhancement and cost effectiveness: a case study of the Albemarle Sound/Roanoke River stocking program 1981–1996. Marine Policy 30:299–307.

Pearson, J. C. 1938. The life history of the Striped Bass, or rockfish, *Roccus saxatilis* (Walbaum). Fishery 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.

Price, A. B., and R. A. Rulifson. 2004. Use of traditional ecological knowledge to reduce Striped Bass bycatch in the Currituck Sound White Perch gill-net fishery. North American Journal of Fisheries Management 24:785–792.

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.

Raquel, R. P. 1989. Effects of handling and trucking on Chinook Salmon, Striped Bass, American Shad, steelhead trout, Threadfin Shad, and White Catfish salvaged at the John E. Skinner Delta fish protective facility. California Department of Fish and Game, Technical Report 19, Sacramento.

Rathjen, W. F., and L. C. Miller. 1957. Aspects of the early life history of the Striped Bass (*Roccus saxatilis*) in the Hudson River. New York Fish and Game Journal 4:43–60.

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.

Rulifson, R. A. 1991. Striped Bass spawning activity and reservoir discharge. NOAA Technical Memorandum NMFS-SEFC-291.

Rulifson, R. A., and R. W. Laney. 1999. Striped Bass stocking programs in the United States: ecological and resource management issues. Canadian Stock Assessment Secretariat Research Document 99/07.

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.

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. NOAA Technical Report NMFS Circular 443.

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.

Shelton, A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. Proceedings of the National Academy of Sciences of the USA 108:7075–7080.

Sloan, R. J., K. W. Simpson, R. A. Schroeder, and C. R. Barnes. 1983. Temporal trends toward stability of Hudson River PCB contamination. Bulletin of Environmental Contamination and Toxicology 31:377–385.

Smith, C. A., J. W. McCargo, and K. M. Patoka. 2016. Characteristics of the 2015 Roanoke River Striped Bass spawning population. North Carolina Wildlife Resources Commission, Inland Fisheries Division, Raleigh.

Southerwick, R. L., and A. J. Loftus. 2002. Investigation and monetary value of fish and freshwater mussel kills. American Fisheries Society, Special Publication 30, Bethesda, Maryland.

Suuronen, P., E. Lehtonen, V. Tschernij, and P. Larsson. 1996. Skin injury and mortality of Baltic Cod escaping from trawl codends equipped with exit windows. Archive of Fishery and Marine Research 44:165–178.

Trent, L., and W. H. Hassler. 1968. Gill net selection, migration, size and age composition, sex ratio, harvest efficiency, and management of Striped Bass in the Roanoke River, North Carolina. Chesapeake Science 9:217–232.

USDOI (U.S. Department of the Interior) and USDOC (U.S. Department of Commerce). 1992. Striped Bass research study: report for 1992. National Marine Fisheries Service, Silver Spring, Maryland.

USGS (U.S. Geological Survey). 2016. National Water Information System: Neuse River at New Bern. Available: http://waterdata.usgs.gov/nwis/inventory/?site_no=02092162. (April 2018).

Van Beek, F. A., P. I. Van Leeuwen, and A. D. Rijnsdorp. 1990. On the survival of Plaice and Sole discards in the otter-trawl and beam-trawl fisheries in the North Sea. Netherlands Journal of Sea Research 26:151–160.

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 124:736–745.

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.

Wilson, C. J. 1999. Mesh size selectivity of gill nets in western Pamlico Sound, North Carolina. Master's thesis. East Carolina University, Greenville, North Carolina.

Yarrow, H. C. 1874. Report of a reconnaissance of the shad-rivers south of the Potomac. Pages 396–402 *in* S. F. Baird, editor. Report of the Commissioner for 1872 and 1873. U.S. Commission of Fish and Fisheries, Washington, D.C.