EXPLORING CAUSAL FACTORS OF SPAWNING STOCK MORTALITY IN A RIVERINE STRIPED BASS POPULATION

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Abstract.—The recovery of the Atlantic Striped Bass *Morone saxatilis* stock in the 1990s is an important example of effective natural resources management. Implementation of Atlantic States Marine Fisheries Commission (ASMFC) harvest regulations reduced mortality, protected older and more fecund females, and contributed to the formation of dominant year-classes in the 1980s and 1990s. However, Striped Bass stocks south of Albemarle Sound, NC are not subject to ASMFC management plans, and many populations have failed to attain recovery goals. Catch-curve analyses indicate the Neuse River Striped Bass population continues to experience similar spawning stock exploitation rates as those implicated in the decline of the Atlantic Migratory and the Albemarle Sound/Roanoke River stocks in the 1970s. From 1994–2015, Striped Bass instantaneous fishing mortality in the Neuse River ranged 0.12–0.84 and exceeded the overfishing threshold in 12 of 22 years. A global linear model using environmental and exploitation factors accounted for 55% of the variability in spawning stock discrete annual mortality. An information-theoretic approach was used to elucidate the best linear model predicting discrete annual mortality. The best model included previous-year gill net effort and same-year commercial harvest (ω_i = 0.64, R^2 = 0.50). Model-averaged coefficients for gill net effort and commercial harvest suggest total exploitation impacts that are congruent with other studies of Neuse River Striped Bass. Results indicate that reducing exploitation to target levels will require substantial reductions in gill net effort in areas of the Neuse River where Striped Bass occur. Reducing exploitation may increase spawning stock biomass and advance the age structure of spawning females, conferring an increased likelihood of successful recruitment and production of dominant year-classes during periods of favorable environmental conditions.

Striped Bass *Morone saxatilis* populations sustained severe declines in abundance throughout the Atlantic coast in the 1970s following several years of record commercial harvest combined with poor recruitment (Boreman and Austin 1985; Richards and Deuel 1987). In North Carolina, Striped Bass commercial landings declined 80% between 1973 and 1983 (Boreman and Austin 1985). Recovery efforts began with the development of the Atlantic States Marine Fisheries Commission's (ASMFC) Interstate Fisheries Management Plan for Striped Bass (IFMP) in 1981 (Richards and Rago 1999). A centerpiece of the IFMP and its amendments was harvest restrictions to curtail exploitation. The harvest provisions of the IFMP were implemented in North Carolina beginning in 1984, along with an expansion of Striped Bass stocking programs and continued development of optimized streamflow releases from Roanoke Rapids dam to improve spawning conditions in the Roanoke River (NCDENR 2004; NCDENR 2013). Albemarle Sound/Roanoke River Striped Bass were declared recovered in 1997 (NCDENR 2004).

In North Carolina, Striped Bass populations south of Albemarle Sound are not subject to compliance with ASMFC management plans due to their minimal contribution to the Atlantic Migratory Stock (Merriman 1941; Greene et al. 2009). These populations are collectively managed as the Central Southern Management Area (CSMA) stock under a collaborative agreement by the North Carolina Division of Marine Fisheries (NCDMF; coastal waters) and the North Carolina Wildlife Resources Commission (NCWRC; inland waters). Of the populations comprising the CSMA, Neuse River Striped Bass were among the first to receive targeted monitoring and management actions (Hammers et al. 1995).

Although Striped Bass are documented as historically utilizing all major coastal North Carolina rivers (Smith 1907), the Neuse River population was among the most studied by early ichthyologists. In the 19th century, the population was subject to the second largest Striped Bass fishery in North Carolina after the fisheries prosecuted on the Albemarle Sound/Roanoke River stock. Yarrow (1877) described Striped Bass in the Neuse River as "exceedingly plenty" and reported 3,000 were sold to New Bern fish houses from January–April, 1873 (Yarrow 1874). By 1880, almost 16,000 Striped Bass were harvested and shipped from New Bern to northern cities, with an additional unknown quantity consumed locally during the fishing season (McDonald 1884). Despite their former abundance, declines were evident before the end of the 19th century, leading McDonald (1884) to note that ". . . the supply has materially decreased . . . owing to overfishing and the erection of obstructions." By 1939, only 318 kg of Striped Bass were commercially harvested in Craven County, North Carolina (Chestnut and Davis 1975).

Although fishing records during World War II are sparse, acquisition of fishing vessels and labor for the war effort likely reduced Striped Bass harvest and allowed for stock rebuilding. Fishing restrictions and labor shortages were eased towards the end of the war, leading to the harvest of 18,000 kg of Striped Bass in Craven County in 1945 (Anderson and Power 1949). However, construction of Quaker Neck dam in 1952 prohibited access to essentially all spawning habitat (Burdick and Hightower 2006). Few Striped Bass were collected during an investigation initiated to examine angler complaints regarding a decline in the recreational catch of Neuse River Striped Bass in the 1960s (Miller 1975), and commercial landings did not again exceed 4,500 kg until 2010 (NCDMF unpublished data). It is possible that the intensity of post-war fishing in the lower Neuse River combined with an inability to access suitable spawning habitat led to the near extinction of the population.

Focused recovery efforts in the Neuse River began with the implementation of an annual stocking regime in 1992 (intermittent stocking began as early as 1931) and annual spawning grounds surveys in 1994. Also in 1994, a 11,340-kg commercial harvest quota was established for the entire CSMA stock (NCDENR 2004). The removal of Quaker Neck Dam in 1998 allowed unobstructed access to approximately 120 km of historical spawning habitat (Burdick and Hightower 2006). Finally, gill net use was prohibited in NCWRC-managed inland waters in 2001 (NCDENR 2013).

Recovery efforts were first formalized in 2004 as part of the North Carolina Estuarine Striped Bass Management Plan (NCDENR 2004) jointly developed by NCDMF and NCWRC. Unweighted linearized catch-curve analyses of age-structures collected on the Neuse River spawning grounds indicated overfishing was occurring (NCDENR 2004), leading to the implementation of gill net restrictions in 2008 (established minimum distance from shore and use of tie-downs during closed harvest season; NCDENR 2013). A stock assessment conducted in 2010 using unweighted linearized catch-curves again documented high mortality, but the assessment was deemed unsuitable for management use due to large confidence intervals around the mortality estimate. However, the need for continued conservation management measures was supported by truncated size and age distributions, low catch per unit effort, and an absence of older fish in spawning grounds samples. Therefore, biological reference points were selected for Neuse River Striped Bass using the Albemarle Sound/Roanoke River stock assessment, leading to the establishment of F_{Target} = 0.33 and $F_{\text{Threshold}}$ = 0.41 (NCDENR 2013; NCDENR 2014a).

Spawning grounds electrofishing assessments indicate size and age distributions have not expanded since the 2010 stock assessment (Rachels and Ricks 2015). Additionally, recent results utilizing parentage-based tagging (PBT) indicate hatchery fish comprise at least two-thirds of the spawning stock (O'Donnell et al. 2016) and may approach 100% stocking contribution (Rachels and Ricks 2015; O'Donnell et al. 2016). The development of recommendations for catch-curve best practices (Smith et al. 2012) render former Neuse River Striped Bass stock assessments obsolete and present an opportunity to re-evaluate spawning grounds age-structure data. Our objectives were two-fold: to improve the precision of catch-curve mortality estimates using current methodology and an expanded time series, and to use linear modeling in an information-theoretic approach (Burnham and Anderson 2002) to elucidate factors responsible for driving the observed mortality rates.

Methods

Study area.—The Neuse River flows approximately 400 km from its origin at the confluence of the Eno and Flat rivers before discharging into Pamlico Sound (Figure 1). The lower 60 km is a wind mixed mesohaline estuary, although salinity can range 0–27‰ depending on precipitation and streamflow (Burkholder et al. 2006). The Neuse River estuary has been classified as Nutrient Sensitive Waters since 1988 and experienced numerous algae blooms and fish kills during the 1990s resulting from nitrogen and phosphorus inputs (Burkholder et al. 1995; Burkholder et al. 2006; Rothenberger et al. 2009).

Mortality estimation.—From 1994–2015, boat-mounted electrofishing (Smith-Root 7.5 GPP; 120Hz; 5000–7000 W) was used to collect Striped Bass from the spawning grounds during annual spawning migrations (March–May). Collections primarily occurred between RKM 230 (river kilometer; from confluence with Pamlico Sound) and RKM 352. Few Striped Bass were collected above Quaker Neck Dam (RKM 230) before its removal in 1998.

Striped Bass were measured for total length (TL; mm), weighed (g), and sex was determined by applying pressure to the abdomen and observing the vent for discharge of milt or eggs. Scales were removed from the left side of each fish between the dorsal fin and lateral line for aging. From 1994–2014, 15 fish of each sex per 25-mm size-class were aged by either directly reading scales (1994–2010) or reading scale impressions on acetate slides (2011–2014). A 20% subsample of each size-class was aged by a second reader. Discrepancies between primary and secondary readers were resolved by jointly reading and reaching consensus (NCWRC and NCDMF 2011). In 2015, a partial pelvic fin clip from each fish was preserved in 95% ethyl alcohol to determine hatchery or wild origin using PBT. Hatchery-origin fish were aged using PBT, while fish of unknown origin were assigned ages with sex specific age-length keys developed using scale-aged fish from 2010–2014.

The Chapman-Robson estimator was used to estimate instantaneous total mortality (Z) for each year in the time series following the recommendations of Smith et al. (2012). Age at full recruitment to the catch-curve was the age of peak catch plus one year (peak plus criterion). An overdispersion parameter $\hat{c}$ (Burnham and Anderson 2002; Smith et al. 2012) was calculated for each year to correct the standard error of the mortality estimate and to assess structural fit of the Chapman-Robson estimator to the age-structure data ($\hat{c} > 4$ indicates poor model fit; Burnham and Anderson 2002). Instantaneous fishing mortality (F) was calculated for each year by subtracting instantaneous natural mortality ($M = 0.246$; Bradley 2016) from Z. Uncertainty in the mortality estimates was characterized by calculating the relative standard error (Z/SE; RSE) and bootstrapping from the distributions of Z and M (Gamma distributed; Bolker 2008) to estimate 90% F confidence intervals.

Mortality modeling.—Linear models were developed to evaluate environmental and exploitation factors that potentially influence discrete annual mortality ($A = 1 - e^{-Z}$) over the time series 1994–2015. We hypothesized that low dissolved oxygen and warm summer temperatures may lead to increased natural mortality. Hypoxic conditions can be prevalent in the Neuse River estuary during the summer months as a result of nutrient loading and water column stratification (Luettich et al. 2000; NCDENR 2001). These hypoxic conditions have been implicated in many of the 236 fish kills occurring between 1996 and 2015 that primarily affected Atlantic Menhaden *Brevoortia tyrannus* in the Neuse River Basin (NCDENR 2001; NCDEQ 2015a). Hypoxic events and resulting fish kills have also been implied as negatively affecting Striped Bass (NCDENR 2013). Water quality data were obtained from the Neuse River Estuary Modeling and Monitoring Project (ModMon; UNC 2016), which is one of the few programs that has continuously monitored water quality in the lower Neuse River since 1994. The summer (June–August) mean surface dissolved oxygen (mg/L) and summer mean surface water temperature (°C) at ModMon station 30 (RKM 57) were used as environmental factors. Results of an acoustic telemetry study (Bradley 2016) determined the highest densities of adult and juvenile Striped Bass occur in the vicinity of the selected ModMon station.

In addition to the suite of environmental factors, several long-term data sets were available from NCDMF to allow investigation of the effects of exploitation. Beginning in 1994, a mandatory trip ticket program was implemented to monitor commercial landings at the first point of sale. Information collected by this program include harvest (kg) landed by species, gear type, and location (NCDENR 2013). Neuse River Striped Bass commercial harvest was used as a direct exploitation factor (NCDMF unpublished data). However, gill net fisheries continue to pursue other marketable species after the Striped Bass harvest season is closed. Therefore, the annual number of gill net trips in the Neuse River was used as a measure of gill net effort that potentially accounts for harvest, discard, and unreported or miss-reported mortality (NCDMF unpublished data). Unfortunately, measures of recreational fishing effort for Striped Bass were not available for the entire time series. A recreational creel survey has been conducted annually in the lower Neuse River since 2004, yet there is limited information for prior years (for exceptions see Borawa 1983; Rundle et al. 2004). Several NOAA Fisheries recreational fishing surveys were investigated for potential use as a surrogate recreational fishing effort metric, including the Marine Recreational Information Program (MRIP), the Marine Recreational Fisheries Statistics Survey (MRFSS), and the Coastal Household Telephone Survey (CHTS). However, these surveys lacked the data resolution necessary to assess Neuse River recreational fisheries.

Since age-structure collections occurred in the spring, it was likely that factors occurring throughout the previous year (gill net effort) or during the previous summer (dissolved oxygen and surface water temperature) had greater influence on the estimated mortality rate than same-year measures. Therefore, these predictor variables were modeled using a one-year time lag. Commercial harvest was not modeled using a time lag since the commercial Striped Bass harvest season occurs in the early spring before electrofishing collections on the spawning grounds; any effects of commercial harvest should be detected using same-year measures. Striped Bass discrete annual mortality was nonstationary, therefore the global model was of the form

$$A'_t = \beta_0 + \sum(\theta_i X'_{i,t-1}) + \theta_C X'_{C,t} + \varepsilon_t \ ,$$

where A'_t and $X'_{i,t}$ are first-differenced to ensure stationarity and remove serial correlation, as given by

$$A'_t = A_t - A_{t-1} \ ,$$

and

$$X'_{i,t} = X_{i,t} - X_{i,t-1} \ ,$$

where A = discrete annual mortality, β_0 = intercept, X = variable i, θ_i = effect of variable X_i, t = year, C = commercial harvest, and ε = is an independently and identically distributed white noise vector.

Twelve ecologically relevant models incorporating dissolved oxygen, surface water temperature, gill net effort, and commercial harvest were assessed using the information-theoretic framework described in Burnham and Anderson (2002). Due to the small sample size, the second order information criterion (AIC_c) was computed for each model and differenced from the model with the smallest AIC_c (Δ_i) to assess the relative strength of the models. After ensuring that A' and X' differencing removed time trends (β_0 = 0; α = 0.05) the intercept was removed from final models and AIC_c and Δ_i were recalculated. This resulted in very slight improvements in model fit. Akaike weights (ω_i) were calculated to evaluate the relative likelihood of each model (Burnham and Anderson 2002). The relative importance of each predictor variable was assessed by decomposing global model variance using the LMG method (Grömping 2007). Model-averaged estimates of the effect of each predictor variable were calculated by multiplying the coefficients of each factor in the models in which they appeared by the Akaike weight of that model (Burnham and Anderson 2002). The model-averaged effect for gill net effort and commercial harvest was multiplied by the 1994–2015 mean number of gill net trips and mean harvest, respectively, to estimate each factor's long term average effect on discrete annual mortality ($\Delta A \equiv u$; discrete annual fishing mortality). Linear models were fit using ordinary least squares (OLS) regression in package "dynlm" in R 3.2.5.

Hybrid Striped Bass.—The trip ticket program does not differentiate between Striped Bass and hybrid Striped Bass *M. chrysops x M. saxatilis*, although fish house sampling has monitored for the occurrence of hybrid Striped Bass in commercial harvest since 2000 (NCDMF, unpublished data). Hybrid Striped Bass constituted a considerable proportion of the Neuse River commercial harvest in 2014 and 2015 (48% and 22%, respectively), however they did not exceed 5% of the commercial harvest in any other year. Additional model runs were conducted after adjusting commercial harvest data from 2000–2015 with the proportion of hybrid Striped Bass occurring in fish house samples.

Runaround gill net modeling.—Runaround gill nets are commonly used to target Striped Mullet *Mugil cephalus* and Spotted Seatrout *Cynoscion nebulosus* (NCDENR 2014b; NCDEQ 2015b) and have seen an increase in use relative to other gill netting methods in the Neuse River (accounted for 4% of gill net trips in 1994, increase to 39% by 2015). Striped Mullet and Spotted Seatrout occur sympatrically with Striped Bass. The lack of quantitative data regarding Striped Bass catch in runaround gill nets warrants runaround gill net effort inclusion in the gill net effort predictor variable. However, common practices in the runaround gill net fishery have been assumed to minimally affect Striped Bass (C. Godwin, NCDMF, personal communication). Therefore, the modeling procedures in the preceding section were repeated with runaround gill net trips removed from the gill net effort predictor variable.

Model assumptions.—Assumptions for OLS time series regression depart from those considered in classical linear modeling. Assumptions of time series regression include mean of zero, constant variance, and constant covariance structure through time (stationarity; Hyndman and Athanasopoulos 2014). The Augmented Dickey-Fuller test (ADF; $\alpha = 0.05$; Hyndman and Athanasopoulos 2014) assumes H_0 = nonstationary, and was employed in R package "stats" to assess stationarity in the mortality time series. The partial autocorrelation function (PACF; Derryberry 2014) was utilized in R package "stats" to examine the potential for autocorrelation in the spawning stock discrete annual mortality time series. Multicollinearity among the predictor variables was assessed by calculating variance inflation factors (VIFs; Fox and Weisburg 2006) using R package "car". Variance inflation factors are generally considered to indicate the presence of multicollinearity if any VIF exceeds 10 (see O'Brien 2007).

Results

Mortality Estimation

The number of Striped Bass collected on the spawning grounds varied throughout the time series, ranging from 58 fish in 2006 to 403 fish in 2003 (Table A.1). Recruitment to the catch-curve typically occurred at age 4 or age 5 (Table A.2). Although the oldest Striped Bass encountered on the spawning grounds was an age-13 female collected in 2005, only 73 of the 4,549 (1.6%) fish collected during the time series were age 9 or older.

The Chapman-Robson mortality estimator generally performed well, as $\hat{c} > 4$ in only 3 of 22 years (Table A.2). Mortality estimates were reasonably precise (RSE < 30%) and only exhibited a high degree of uncertainty in 2008. Instantaneous total mortality varied considerably throughout the time series, ranging from 0.36 to 1.08. Mortality was generally lowest during the period 1997–2007 and highest during the period 2008–2011. Instantaneous fishing mortality ranged 0.12–0.84 (Table A.2; Figure 2) assuming the instantaneous natural mortality rate given by Bradley (2016) remained constant throughout the time series. Fishing mortality was greater than $F_{\text{Threshold}}$ in 12 of the 22 years.

Mortality Modeling

Model assumptions.— The ADF test indicated spawning stock discrete annual mortality was nonstationary (p = 0.181). Therefore, all modeled variables were first-differenced (Hyndman and Athanasopoulos 2014). The PACF indicated a correlation between A_t and A_{t-1} of 0.34, indicating weak autocorrelation. We did not consider this level of autocorrelation sufficient to warrant modeling as an AR(1) process given the small sample size and potential for model overspecification. Variance inflation factors ranged 1.1–2.5, indicating a low likelihood of multicollinearity among predictor variables.

Model results.—The best linear model supported by the data contained gill net effort and commercial harvest as predictors of discrete annual mortality (Table 1). The global model containing all predictor variables accounted for 55% of the variability in spawning stock mortality, while the best model accounted for 50%. Every model receiving at least modest support as the best model ($\Delta_i < 7$) incorporated gill net effort as a predictor variable.

Gill net effort was the most important predictor of spawning stock mortality relative to the four predictor variables examined (Table 2; Figure 3). Commercial harvest was the second most important predictor of spawning stock mortality, while summer dissolved oxygen and surface water temperature did not substantially influence spawning stock mortality (Tables 1 & 2). Multiplying the model-averaged gill net coefficient by the mean number of gill net trips for 1994–2015 (2,421 trips) suggests the average effect of gill net effort on discrete annual mortality is 0.29 (u = 0.29). Using the same procedure for commercial harvest (3,199 kg) suggests an average effect of 0.08 (u = 0.08).

Hybrid Striped Bass.—Adjusting commercial harvest did not appreciably change model results. The model-averaged commercial harvest coefficient was 2.27×10^{-5} after adjusting for the proportion of hybrid Striped bass observed in fish house sampling, compared to 2.37×10^{-5} without the adjustment. Multiplying the model-averaged coefficient from the adjusted data with the adjusted mean annual commercial harvest (3,062 kg) results in an average effect on discrete annual mortality of 0.07. Given the minimal change in model results and an inability to adjust commercial harvest before 2000, models adjusting for hybrid Striped Bass were not considered further.

Runaround gill net models.—With runaround gill nets removed, the best linear model remained the model with gill net effort and commercial harvest predictor variables (Table A.3). The model-averaged gill net effort coefficient with runaround gill nets removed was 1.53×10^{-4} (SE = 3.4×10^{-5}). Multiplying this model-averaged gill net coefficient by the 1994–2015 mean number of gill net trips (without runaround gill nets; 1951 trips) results in an average effect of 0.30 (u = 0.30). The overall effect of gill net effort on mortality did not change, as reductions in gill net trips due to the exclusion of runaround gill nets were offset by an increase in the estimated gill net coefficient. Due to the similarity in results, models without runaround gill net effort were not considered further.

Discussion

Catch-curve analysis indicates the Neuse River Striped Bass spawning stock has been subjected to overfishing throughout much of the last two decades. The 22-year mean fishing mortality rate in this study ($F = 0.46$) is similar to the 18-year mean rate ($F = 0.47$) that preceded the depletion of Albemarle Sound/Roanoke River Striped Bass in the 1970s (Hassler et al. 1981; NCDENR 2013). These high fishing mortality rates also approach the level of exploitation that was determined to be a major factor in the Atlantic Striped Bass stock collapse (ASMFC 1989; Richards and Rago 1999). Mortality has not trended towards F_{Target}, despite the development of two comprehensive management plans and increasingly restrictive recreational and commercial harvest regulations (see Appendix 14.5 in NCDENR 2013).

Linear modeling indicates gill net effort is the most important factor influencing spawning stock mortality among the exploitation and environmental factors examined. Gill net effort accounted for substantially greater variability in spawning stock mortality than commercial harvest, and the model-averaged coefficient identifies gill net effort discrete annual fishing mortality $u = 0.29$. This suggests that the commercial multispecies gill net fishery imparts substantial mortality even when the Striped Bass harvest season is closed. The reason for this mortality is obscure, but may be attributable to dead discard mortality; over-quota and high-grading mortality; avoidance, predation, and drop-out mortality; or unreported, miss-reported and illegal harvest (ICES 1995; Gilman et al. 2013; Uhlmann and Broadhurst 2015; Batsleer et al. 2015). In particular, discard mortality should be carefully considered as Clark and Kahn (2009) found that Striped Bass are acutely susceptible to discard mortality in multispecies gill net fisheries. Furthermore, Striped Bass discards in the large mesh gill net fishery were identified as the primary source of mortality within the CSMA (NCDENR 2013). The effect of gill net effort on discrete annual mortality as estimated by linear modeling is within 3% of the estimated effect of cryptic mortality in a cohort-based model ($u = 0.26$; Table B.3 in Rachels and Ricks 2015), while the effect of commercial harvest was identical to the estimated commercial harvest discrete annual fishing mortality rate in that study.

Contrary to exploitation factors, the environmental factors examined did not account for much variability in spawning stock mortality. Although numerous Atlantic Menhaden fish kills have occurred due to hypoxic conditions throughout the time period encompassing this research, it appears these events have relatively little impact on Striped Bass spawning stock mortality. Campbell and Rice (2014) observed that estuarine fish can rapidly detect and avoid hypoxic areas in the Neuse River. They also found that habitat compression due to hypoxic conditions likely reduced growth rates in juvenile Spot *Leiostomus xanthurus* and Atlantic Croaker *Micropogonias undulatus*. Movement out of hypoxic areas could increase predation mortality due to habitat compression and prey aggregation (Campbell and Rice 2014), although it should be noted that Striped Bass are an apex predator in the lower Neuse River and rarely experience predation at older ages. Neuse River Striped Bass also exhibit the fastest growth rates among coastal NC Striped Bass populations (Rachels and Ricks 2015). It is likely that negative impacts of hypoxic conditions or water temperatures exceeding Striped Bass thermal optima would manifest through reduced growth rates before mortality effects are observed. Nonetheless, the parameter coefficients for summer mean dissolved oxygen and summer mean surface water temperature indicate the potential for increased spawning stock mortality as dissolved oxygen decreases and water temperature increases. However, these effects were minimal—approximately 2% change in discrete annual mortality per unit change in temperature or dissolved oxygen—compared to the effects of gill net effort and commercial harvest.

The inability to include recreational angling as an exploitation factor reduces the amount of variability in spawning stock mortality that can be accounted for in this study. The median annual recreational harvest during 2004–2015 was 2,337 kg and is similar to the median commercial harvest of 3,355 kg for the same time period (NCDMF unpublished data). Thus, the actual commercial harvest and recreational harvest exploitation rates are similar, an observation supported by simulation studies (Rachels and Ricks 2015; Bradley 2016). It is likely that inclusion of factors that represent recreational harvest and discard would perform comparably to the results of the commercial harvest factor used in linear modeling. However, time dynamic trends in the level of recreational fishing effort or harvest could influence its importance relative to commercial harvest in a regression analysis. In fact, recreational effort declined dramatically 2005–2010, concurrent with increases in discrete annual mortality (Figure A.1). The continued collection of recreational creel survey data is warranted to elucidate long-term effects of angling on Neuse River Striped Bass mortality.

Periodic strategists such as Striped Bass are resilient to periods of extended recruitment failure through the storage effect (Warner and Chesson 1985; Winemiller and Rose 1992). Recovery is contingent upon building spawning stock biomass by advancing the female age structure to older and more fecund fish (Secor 2000). Although regulating fishing mortality is one of the principal tools available to fisheries managers, “historical precedence is often invoked as a reason to continue unwise fishery management practices” (Richards and Rago 1999). Yet, the effectiveness of coordinated multi-jurisdictional management efforts in significantly reducing exploitation has been demonstrated by the restoration of the Atlantic Striped Bass stock (Field 1997; Richards and Rago 1999).

Current high exploitation rates combined with low stock abundance and a high contribution of hatchery fish to the spawning stock (Rachels and Ricks 2015; Bradley 2016) suggest the expected recovery time of Neuse River Striped Bass continues to be “both uncertain and long” (Hilborn et al. 2014). Our research suggests fisheries managers should reduce exploitation by focusing on reductions in gill net effort in areas of the Neuse River utilized by Striped Bass. Reducing spawning stock exploitation may confer an increased likelihood of recruitment during periods of favorable environmental conditions, thereby leading to improvements in population abundance and increased numbers of wild fish in the spawning stock.

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TABLE 1. Linear models exploring the effect of environmental and exploitation factors on Striped Bass spawning stock discrete annual mortality, 1994–2015. The number of estimated model parameters (*K*) includes the predicting factors and an error term; final model runs did not include an intercept parameter.

Model [a]	*K*	AIC_c	Δ_i	ω_i	R^2
EFFORT, HARV	3	-39.95	0.00	0.64	0.50
EFFORT	2	-36.98	2.97	0.15	0.34
EFFORT, HARV, DO, TEMP	5	-34.88	5.07	0.05	0.55
EFFORT, DO	3	-34.81	5.14	0.05	0.36
EFFORT, TEMP	3	-34.60	5.36	0.04	0.35
EFFORT, DO, TEMP	4	-34.40	5.56	0.04	0.44
HARV	2	-31.68	8.27	0.01	0.14
DO	2	-30.67	9.29	0.01	0.09
HARV, DO	3	-30.38	9.57	0.01	0.20
HARV, TEMP	3	-29.83	10.12	0.00	0.10
DO, TEMP	3	-27.98	11.97	0.00	0.10
HARV, DO, TEMP	4	-27.23	12.72	0.00	0.20

[a] EFFORT = gill net effort, DO = dissolved oxygen, HARV = commercial harvest, TEMP = surface water temperature

TABLE 2. Relative importance of predictor variables affecting spawning stock mortality.

Predictor Variable	Model Averaged Coefficient		Relative Importance (LMG)
	θ	SE	
Gill net effort	1.21×10^{-4}	3.54×10^{-5}	0.62
Commercial harvest	2.37×10^{-5}	1.00×10^{-5}	0.23
Dissolved oxygen	-1.73×10^{-2}	1.63×10^{-2}	0.10
Surface water temperature	2.50×10^{-2}	2.71×10^{-2}	0.05

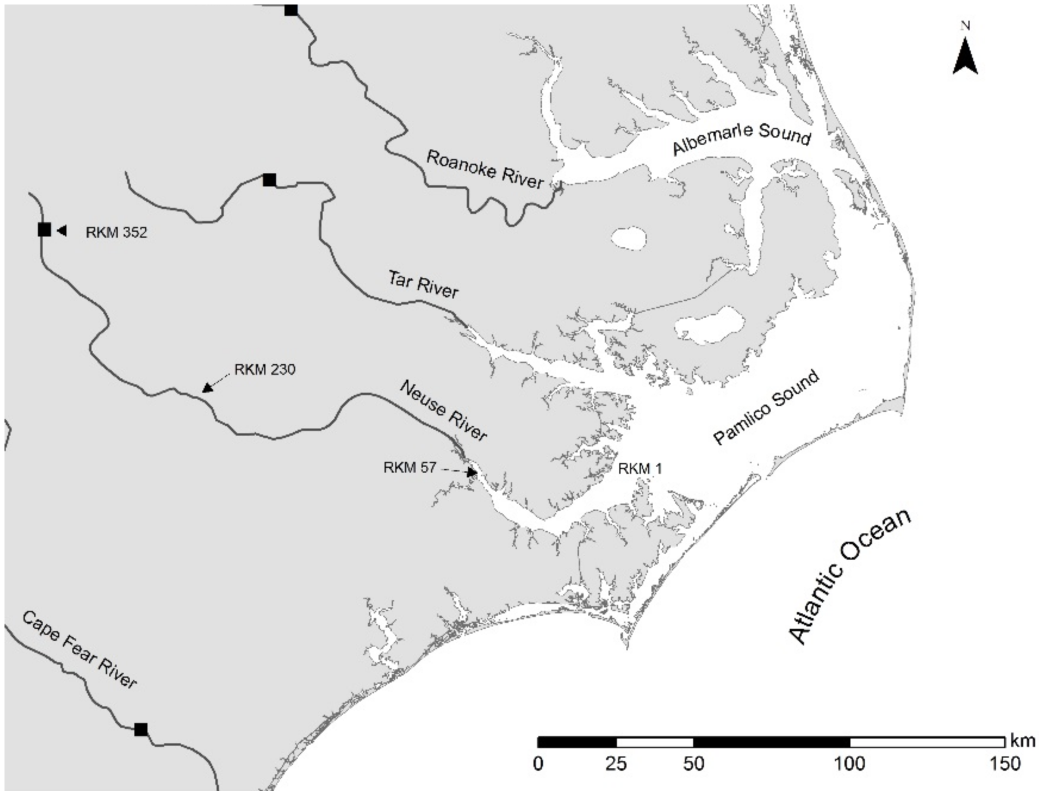

FIGURE 1. Major coastal rivers in North Carolina. Black squares denote the first major impediment to migration for anadromous fish. Important river kilometers in the Neuse River are referenced.

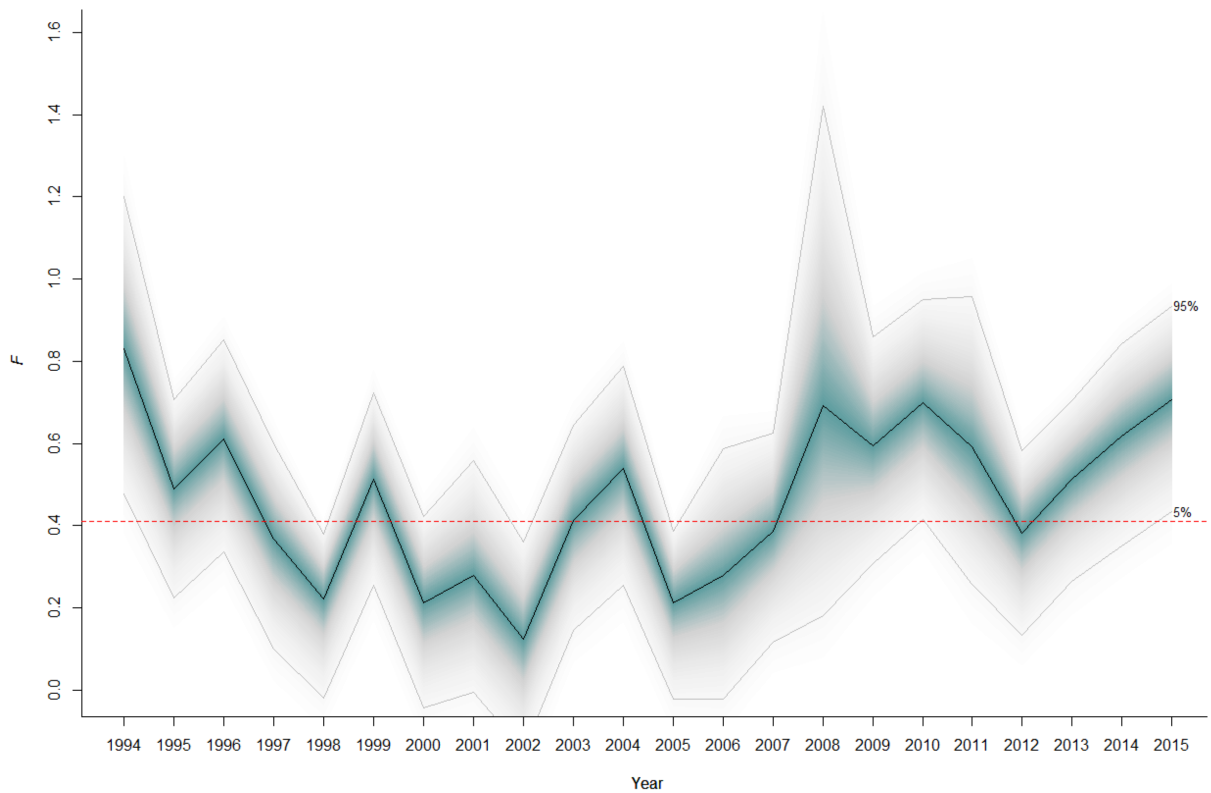

FIGURE 2. Striped Bass spawning stock fishing mortality (*F*) in the Neuse River, 1994–2015. The 90% confidence interval is denoted by grey lines, while the interquartile range is within a green color gradient. The dashed red line represents the overfishing threshold ($F_{Threshold}$ = 0.41).

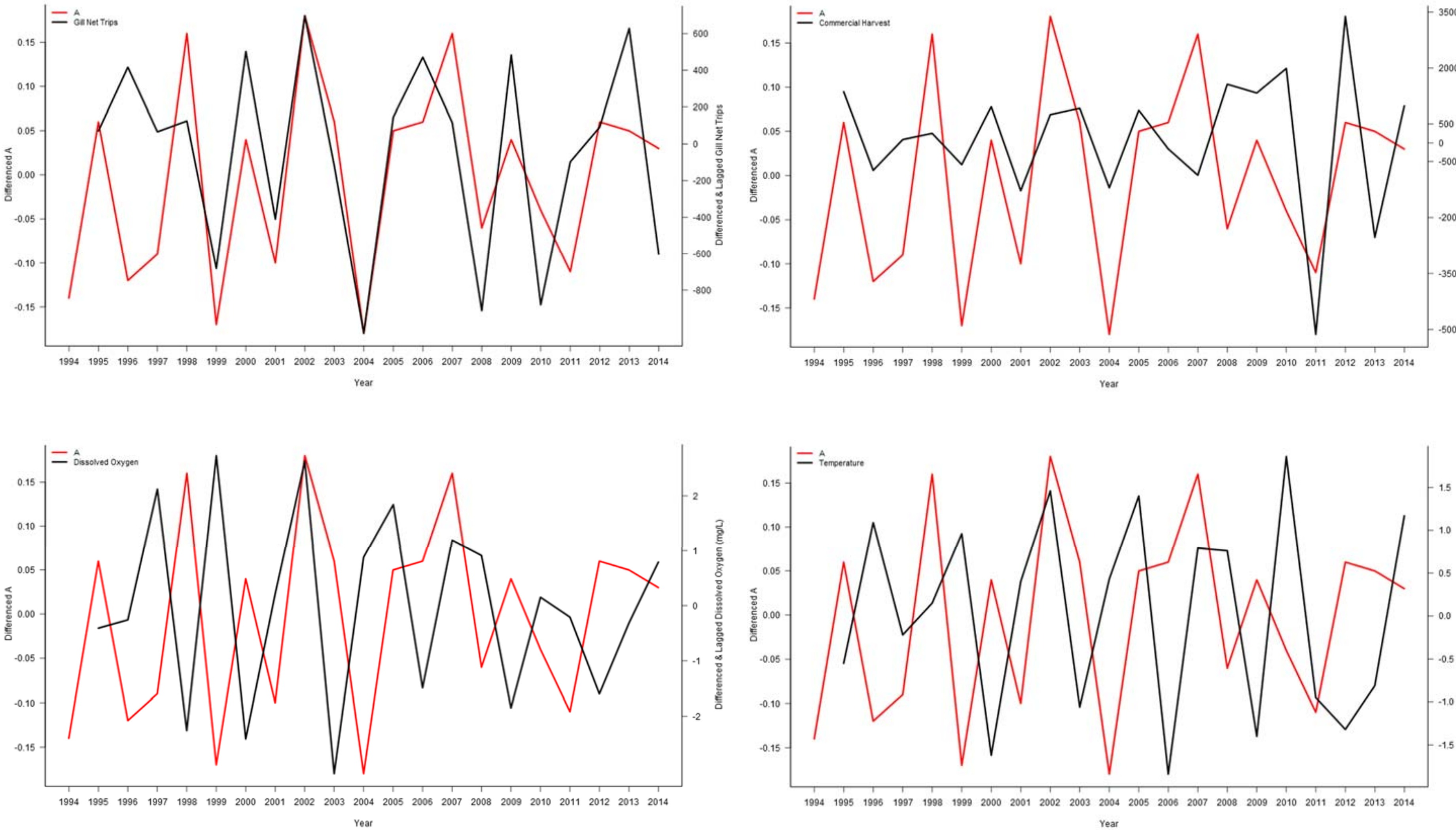

FIGURE 3. Differenced Striped Bass spawning stock discrete annual mortality (*A*) and differenced exploitation and environmental predictor variables. Gill net effort, summer mean surface dissolved oxygen, and summer mean surface water temperature were modeled with one-year time lags.

APPENDIX A

TABLE A.1. Neuse River Striped Bass catch-at-age from spawning grounds electrofishing surveys, 1994–2015.

Age	Year of sample																					
	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
2	1	0	0	3	2	0	1	0	3	0	0	2	4	4	4	6	0	40	5	10	0	26
3	16	36	48	27	69	52	75	10	32	46	8	26	33	72	28	133	70	33	72	105	76	42
4	8	78	40	32	39	89	69	25	9	127	7	25	9	45	38	106	42	48	25	120	106	76
5	22	51	67	27	40	77	101	51	15	132	27	26	5	30	47	88	18	34	22	51	74	60
6	37	27	41	26	27	36	63	44	11	43	26	19	4	7	18	28	8	8	12	29	27	17
7	22	17	14	18	20	20	25	21	17	21	12	10	1	3	3	8	2	7	4	16	22	13
8	11	11	11	8	13	16	16	4	12	23	6	12	0	4	1	0	1	6	2	7	3	4
9	3	1	5	1	5	1	5	0	3	7	2	4	0	3	0	0	0	0	2	3	2	1
10	0	0	0	1	3	1	1	0	0	4	1	0	2	4	2	1	0	0	0	0	1	0
11	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

TABLE A.2. Chapman-Robson mortality estimator metrics and mortality rates for Neuse River Striped Bass, 1994–2015.

Metric [a]	Year of sample																					
	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
N	120	221	226	143	219	292	357	155	102	403	90	125	58	172	141	373	141	176	144	341	311	239
N_c	36	107	71	81	148	151	111	69	67	98	48	97	21	96	24	231	71	55	67	106	129	95
T_c	7	5	6	5	4	5	5	5	4	6	6	4	4	4	6	4	4	5	4	5	5	5
$\hat{c}$	0.57	1.60	1.10	2.23	1.64	1.97	4.17	3.90	5.53	2.20	0.12	1.81	1.57	2.52	3.19	4.96	0.13	2.41	0.85	0.42	1.51	0.90
Z	1.08	0.73	0.85	0.61	0.45	0.75	0.45	0.52	0.36	0.65	0.78	0.44	0.53	0.63	0.98	0.84	0.94	0.84	0.62	0.74	0.86	0.94
SE_c	0.19	0.09	0.11	0.10	0.05	0.09	0.09	0.13	0.10	0.10	0.12	0.06	0.15	0.10	0.37	0.13	0.12	0.18	0.08	0.07	0.10	0.10
Z LCL	0.77	0.58	0.67	0.44	0.37	0.61	0.31	0.32	0.19	0.49	0.59	0.34	0.29	0.46	0.37	0.63	0.75	0.54	0.49	0.62	0.70	0.78
Z UCL	1.39	0.88	1.03	0.77	0.53	0.90	0.60	0.73	0.53	0.82	0.97	0.54	0.77	0.80	1.59	1.05	1.13	1.14	0.75	0.87	1.02	1.11
RSE	17%	12%	13%	17%	11%	12%	20%	24%	29%	15%	15%	14%	28%	16%	38%	15%	12%	22%	12%	10%	11%	11%
A	0.66	0.52	0.57	0.45	0.36	0.53	0.36	0.41	0.30	0.48	0.54	0.36	0.41	0.47	0.62	0.57	0.61	0.57	0.46	0.53	0.58	0.61
A LCL	0.54	0.44	0.49	0.35	0.31	0.45	0.26	0.27	0.17	0.39	0.44	0.29	0.25	0.37	0.31	0.47	0.53	0.42	0.39	0.46	0.50	0.54
A UCL	0.75	0.58	0.64	0.54	0.41	0.59	0.45	0.52	0.41	0.56	0.62	0.42	0.53	0.55	0.80	0.65	0.68	0.68	0.53	0.58	0.64	0.67
F	0.84	0.48	0.61	0.36	0.21	0.51	0.21	0.28	0.11	0.41	0.53	0.20	0.28	0.38	0.73	0.59	0.69	0.59	0.37	0.50	0.61	0.70
F LCL	0.49	0.23	0.34	0.10	-0.02	0.25	-0.04	-0.01	-0.15	0.15	0.26	-0.03	0.02	0.11	0.17	0.31	0.43	0.25	0.12	0.26	0.36	0.44
F UCL	1.20	0.71	0.86	0.60	0.38	0.73	0.43	0.55	0.36	0.64	0.79	0.39	0.59	0.61	1.44	0.86	0.95	0.96	0.58	0.70	0.84	0.93
u (Type II)	0.51	0.34	0.41	0.27	0.17	0.36	0.17	0.22	0.10	0.30	0.37	0.16	0.22	0.28	0.47	0.40	0.45	0.40	0.28	0.35	0.41	0.45

[a] N = total catch; N_c = number in catch curve; T_c = age at recruitment to catch curve (Peak Plus); $\hat{c}$ = overdispersion parameter; LCL = lower 90% confidence bound; UCL = Upper 90% confidence bound

TABLE A.3. Linear models exploring the effect of environmental and exploitation factors on Striped Bass spawning stock discrete annual mortality. Results differ from Table 1 in that runaround gill net trips were removed from gill net effort.

Model [a]	*K*	AIC_c	Δ_i	ω_i	R^2
EFFORT, HARV	3	-40.55	0.00	0.74	0.47
EFFORT, HARV, DO, TEMP	5	-36.20	4.34	0.08	0.47
EFFORT	2	-35.86	4.69	0.07	0.26
EFFORT, DO, TEMP	4	-33.97	6.58	0.03	0.33
EFFORT, DO	3	-33.88	6.67	0.03	0.25
EFFORT, TEMP	3	-33.46	7.09	0.02	0.24
HARV	2	-31.68	8.87	0.01	0.09
DO	2	-30.67	9.88	0.01	0.05
HARV, DO	3	-30.38	10.16	0.00	0.11
HARV, TEMP	3	-29.83	10.72	0.00	0.09
DO, TEMP	3	-27.98	12.56	0.00	0.00
HARV, DO, TEMP	4	-27.23	13.32	0.00	0.06

[a] EFFORT = gill net effort, DO = dissolved oxygen, HARV = commercial harvest, TEMP = surface water temperature

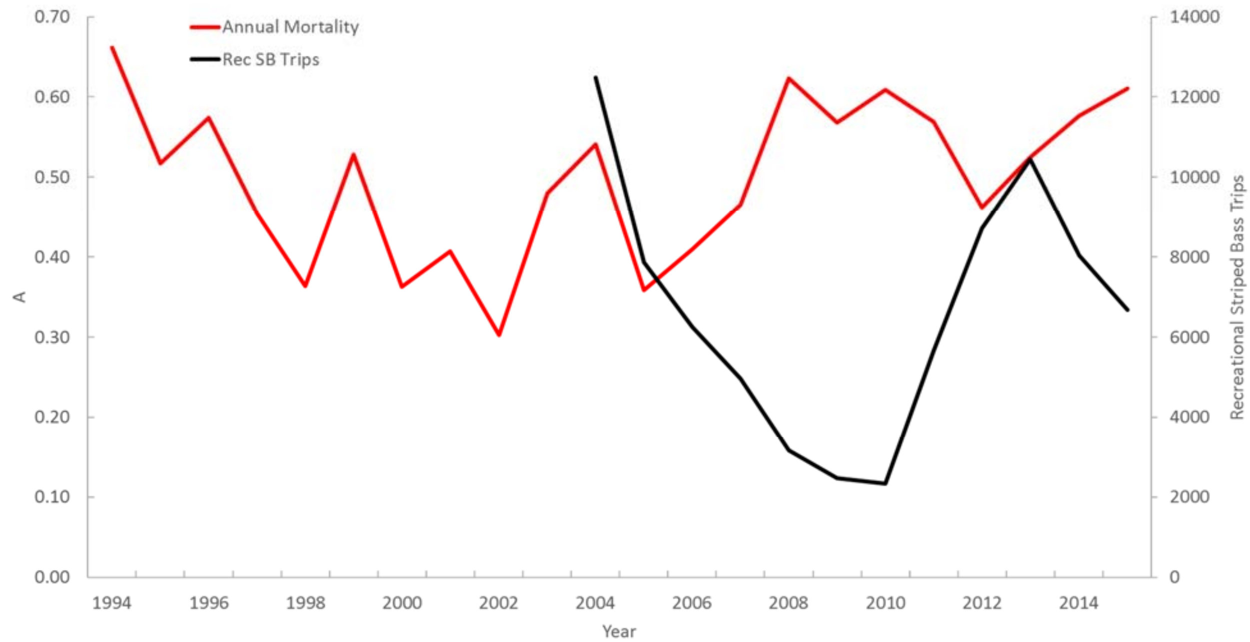

FIGURE A.1. Striped Bass spawning stock discrete annual mortality (*A*) and estimated recreational trips targeting Striped Bass in the Neuse River, 1994-2015 (NCDMF unpublished data).

APPENDIX B

Sample R code for constructing global model and best linear model. Code for both intercept and regression through origin models (RTO) is given, RTO models were used for final model results. R code was constructed using R version 3.2.5 (2016-04-14) "Very, Very Secure Dishes"

```
install.packages("stats")
install.packages("dynlm")
install.packages("car")
install.packages("relaimpo")
install.packages("tseries")

library(stats)
library(dynlm)
library(car)
library(relaimpo)
library(tseries)

# Spawning stock discrete annual mortality
A<-c(0.66, 0.52, 0.57, 0.45, 0.36, 0.53, 0.36, 0.41, 0.30, 0.48, 0.54,
    0.36, 0.41, 0.47, 0.62, 0.57, 0.61, 0.57, 0.46, 0.53, 0.58, 0.61)

# Total gill net trips
NET<-c(2531, 2601, 3018, 3084, 3209, 2527, 3030, 2619, 3317, 3196, 2159,
    2305, 2777, 2893, 1980, 2464, 1583, 1485, 1577, 2206, 1603, 1091)

# Mean summer surface water temperature (°C)
MODTEMP<-c(27.5, 26.9, 28.0, 27.8, 27.9, 28.9, 27.3, 27.7, 29.1, 28.1, 28.5,
    29.9, 28.1, 28.8, 29.6, 28.2, 30.1, 29.1, 27.8, 27.0, 28.2, 27.8)

# Mean summer surface dissolved oxygen (mg/L)
MODSDO<-c(7.12, 6.71, 6.45, 8.57, 6.31, 9.04, 6.64, 6.84, 9.47, 6.43, 7.31,
    9.14, 7.65, 8.84, 9.75, 7.90, 8.04, 7.84, 6.23, 5.92, 6.71, 6.12)

# Commercial Striped Bass harvest (kg)
CHARVkg<-c(3760, 1792, 3159, 2424, 2511, 2764, 2181, 3149, 1869, 2621, 3547,
    2346, 3216, 3053, 2190, 3758, 5092, 7081, 1946, 5328, 2801, 3793)

# Total gill net trips with runaround gill nets removed
noRAN<-c(2438, 2211, 2336, 2427, 2608, 2154, 2651, 2269, 2833, 2708, 1896,
    1913, 2227, 2237, 1559, 1899, 1043, 1067, 1012, 1605, 1160, 668)

#Merge data & format as time series
G1<-as.zoo(cbind(A, NET, MODTEMP, MODSDO, CHARVkg, noRAN ))
#remove 1994 value for CHARVkg to equalize sample sizes since variable is not lagged
G1[1,5]<- NA
#PACF to determine if mortality is autocorrelated
```

```
pacf(A, plot=F, ci.type="white")
#Augmented Dickey-Fuller Test to assess stationarity
adf.test(A)

# Global model
dfmNCDT<-dynlm(d(A) ~ L(d(NET)) + d(CHARVkg) + L(d(MODSDO)) + L(d(MODTEMP)),
  data=G1, model=TRUE)
summary(dfmNCDT) # Model summary & estimated parameters
AIC(dfmNCDT, k=2) # AIC (requires AICc correction)
vif(dfmNCDT) # Calculate Variance Inflation Factors
calc.relimp(dfmNCDT, rela=TRUE, type=c("lmg", "betasq","genizi" , "car")) # Relative importance

# Best linear model
dfmNCI<-dynlm(d(A) ~ L(d(NET)) + d(CHARVkg) , data=G1, model=TRUE)
summary(dfmNCI)
AIC(dfmNCI, k=2)

#Regression through origin global model
dfmNCDT1<-dynlm(d(A) ~ 0 + L(d(NET)) + d(CHARVkg) + L(d(MODSDO)) + L(d(MODTEMP)),
  data=G1, model=TRUE)
summary(dfmNCDT1)
AIC(dfmNCDT1, k=2)

# Regression through origin, best linear model
dfmNC1<-dynlm(d(A) ~ 0 + L(d(NET)) + d(CHARVkg), data=G1, model=TRUE)
summary(dfmNC1)
AIC(dfmNC1, k=2)

#Global model, no runaround nets
dfmNCDT2<-dynlm(d(A) ~ L(d(noRAN)) + d(CHARVkg) + L(d(MODSDO)) + L(d(MODTEMP)),
  data=G1, model=TRUE)
summary(dfmNCDT2)
AIC(dfmNCDT2, k=2)
vif(dfmNCDT2)
calc.relimp(dfmNCDT2, rela=TRUE, type=c("lmg", "betasq","genizi" , "car"))

# Regression through origin, best linear model, no runaround nets
dfmNC2<-dynlm(d(A) ~  0 + L(d(noRAN)) + d(CHARVkg), data=G1, model=TRUE)
summary(dfmNC2)
AIC(dfmNC2, k=2)
```