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ARTICLE

Field Evaluation and Simulation Modeling of Length Limits and their Effects on Fishery Quality for Muskellunge in the New River, Virginia

Sasha S. Doss,* Brian R. Murphy, and Leandro Castello
Department of Fish and Wildlife Conservation, Virginia Polytechnic and State University, Blacksburg, Virginia 24061, USA

Joseph A. Williams and John Copeland
Virginia Department of Game and Inland Fisheries, 2206 South Main Street, Suite C, Blacksburg, Virginia 24060, USA

Victor J. DiCenzo
SOLitude Lake Management, Post Office Box 969, Virginia Beach, Virginia 23451, USA

Abstract
The trophy fisheries for Muskellunge *Esox masquinongy* in the northern U.S.A. and Canada often are developed and maintained by using high minimum-length limits (MLLs). However, the effectiveness of using such MLLs on southern-latitude Muskellunge populations, which have different rates of growth and mortality, warrants further research. The Muskellunge fishery in the New River, Virginia, was managed under a 30-in (75 cm) MLL until 2006 when the MLL was increased to 42 in (105 cm) to increase the abundance of large Muskellunge. We measured fishery quality before and after the institution of the 42-in MLL using size structure, average individual condition, rates of growth and mortality, and CPUE. We also assessed the potential of alternative length regulations (other MLLs and a 40–48-in protected-slot limit) to improve the population's size structure and trophy production using simulation models in the Fisheries Analyses and Modeling Simulator (FAMS) program. Following the institution of the 42-in MLL, we observed a 5-in increase in the average size of Muskellunge, an increase in the population's size structure with greater proportions of memorable-size individuals (≥42 in) and an increase in the abundance of memorable-size Muskellunge. However, declines in the average condition, i.e., relative weight (W_r), of large Muskellunge (≥38 in) suggest there is possible stockpiling of individuals just below the 42-in length limit. Higher MLLs (e.g., 48-in MLL) could further improve fishery quality by increasing the survival of Muskellunge to large trophy sizes (≥50 in). However, managers should be wary of stockpiling under alternative MLLs as well. Furthermore, a higher MLL is unlikely to garner broad angler support in this system. Conversely, a protected-slot limit that allows the production of some trophy-sized Muskellunge while reducing the overall number of individuals, and that limits potential for stockpiling, may be a more agreeable regulatory option for New River fishery managers. These findings and the methods described within this study may be useful for fisheries managers working on other Muskellunge fisheries in southern systems.

Large predatory fishes are some of the most sought-after sport fishes, particularly in North America (Arlinghaus 2006; McCormick and Porter 2014). Fisheries managers commonly introduce, stock, and regulate them to maintain fisheries with high trophy production (Trushenski et al. 2010). The most common management strategy used to improve trophy production has been the regulation of harvest by size limits, most notably minimum-length limits

*Corresponding author: sasha.s.doss@gmail.com
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(MLLs; Isermann and Paukert 2010). Although the use of MLLs can increase the size structure of populations and the abundance of trophy-sized individuals (e.g., Lyons et al. 1996; Cornelius and Margenau 1999), the ability of an MLL to produce and increase the abundance of large individuals is dependent upon a population's dynamic rates (i.e., growth, recruitment, and mortality; Allen et al. 2002; Isermann et al. 2002; Faust et al. 2015). An MLL is most successful on a population with low recruitment and natural mortality, a relatively fast growth rate, and a high potential for fishing mortality (Wilde 1997). In the absence of these conditions, an MLL may not be effective. For example, if there is high natural mortality before fish reach an MLL, few individuals will approach harvestable size regardless of fishing mortality. In some cases, MLLs can yield undesired consequences, including an accumulation of fish just below the minimum size, known as "stockpiling" (Wilde 1997). Stockpiling occurs when intraspecific competition among fish below the minimum size increases, individual growth is stunted within the abundant size-class, and the condition of fish and quality of the fishery declines. Stockpiling has been documented in a variety of sport fishes (e.g., Largemouth Bass *Micropterus salmoides*: Carline et al. 1984; Walleye *Sander vitreus*: Serns 1978; and Muskellunge *Esox masquinongy*: Cornelius and Margenau 1999). A common management strategy used to remedy stockpiling and restore fishery quality is the institution of a protected-slot limit (PSL). A PSL prevents stockpiling by allowing the harvest of subslot individuals, which reduces intraspecific competition between those individuals and allows healthy fish to grow larger (Anderson 1976; Wilde 1997; Fayram 2003). Ultimately, the effectiveness of all length-limit regulations is dependent upon a population's dynamic rates. Dynamic rates can differ widely over a species' range (Young et al. 2006). Thus, a particular length-limit regulation may not be an effective management solution for every population of a species, particularly when there are known differences in these dynamic rates, as is the case for Muskellunge.

Muskellunge are long-lived, slow-growing, and large predatory fish. Although Muskellunge are indigenous to a few southern systems, such as the Tennessee River, the presence of Muskellunge in many southern systems in southern Illinois, North Carolina, South Carolina, Tennessee, Kentucky, Maryland, Virginia, and West Virginia is the result of extensive stocking (Kerr 2011). Because of differences in population genetics, climate, and prey availability, these southern populations exhibit different dynamic rates than those of their northern counterparts (Harrison and Hadley 1979; Brenden et al. 2007; Miller et al. 2017; Perrion and Koupal 2017). Furthermore, northern Muskellunge fisheries are dominated by a strong catch-and-release ethic, and in some places release rates are as high as 99% (Fayram 2003; Simonson 2017). While the catch-and-release ethic is present and growing in many southern-latitude Muskellunge fisheries, it still lags behind that of northern Muskellunge fisheries. For instance, only 40% of anglers surveyed on the New River, Virginia, indicated that all Muskellunge would be released (Brenden et al. 2007). The low release rates of Muskellunge in some southern systems are further compounded by liberal harvest regulations (low length limits and high bag limits). This is particularly important as recent findings suggest that even relatively low levels of harvest can affect Muskellunge populations (Simonson 2017).

As southern Muskellunge fisheries increase in popularity and attract more anglers, managers are acknowledging that current, liberal harvest regulations may not produce trophy fisheries. Many trophy Muskellunge fisheries in the northern United States and Canada are developed and maintained with regionally specific, high MLLs. For instance, the abundance of adult Muskellunge (>30 in) in Bone Lake, Wisconsin, increased five-fold after the MLL was increased from 30 in (75 cm) to 40 in (100 cm) (Cornelius and Margenau 1999). Similarly, in the St. Lawrence River, the average length of Muskellunge increased 2.5 in after a 48-in MLL was implemented (Farrell et al. 2006). More recently, there has been a push for waterbody-specific regulations based on the waterbody's individual potential (Faust et al. 2015; Rude et al. 2017). Unfortunately, little research has been conducted to determine whether high MLLs would prove a successful management strategy for southern Muskellunge fisheries with different dynamic rates (e.g., Brenden et al. 2007).

The New River's Muskellunge fishery in Virginia represents a useful case study for examining whether length limits are capable of producing trophy Muskellunge fisheries in southern riverine systems. The New River Muskellunge fishery was managed under a 30-in MLL until 2006 when the Virginia Department of Game and Inland Fisheries (VDGIF) increased the MLL to 42 in to increase the abundance of large Muskellunge. A previous study on New River Muskellunge predicted that under a 45-in MLL, the abundance of memorable-size Muskellunge could nearly double (Brenden et al. 2007). Thus, the first objective of this research was to determine whether the quality of the New River Muskellunge fishery improved following the institution of the 42-in MLL. We hypothesized that following the institution of the 42-in MLL both the average size of Muskellunge and the abundance of large individuals in the New River would increase. Our second objective was to assess whether other length-limit regulations might be viable options for improving the quality of the Muskellunge fishery. These objectives have important implications for the use of length-limit regulations to manage the New River Muskellunge fishery and other trophy Muskellunge fisheries in southern riverine systems.

METHODS

Study site.— The New River originates in North Carolina and flows northward through Virginia and into West Virginia. We conducted this project on the Virginia portion of the New River, with a focus on the lower section of the New River from Claytor Dam to the West Virginia–Virginia state line (Figure 1). Muskellunge were introduced in the New River in 1968 by the VDGIF. The VDGIF stocked Muskellunge every other year and managed the fishery under a 30-in MLL until 2006, when the MLL was increased to 42 in to increase the abundance of trophy-sized (i.e., ≥50 in) and citation-sized Muskellunge (i.e., ≥40 in; a statewide trophy standard set by the VDGIF as part of Virginia's Angler Recognition Program) (VDGIF 2004, 2015). Release rates of Muskellunge in the New River have been estimated at 86% for all Muskellunge and 46% for Muskellunge ≥40 in (Brenden et al. 2007).

We assessed Muskellunge demographics and abundance at seven fixed sites (Figure 1). All sites were selected based on knowledge of the existing Muskellunge population, boat access, boat maneuverability, and whether the site was sampled in the previous Muskellunge study in 2000–2003 (to allow direct comparison to results of Brenden et al. [2007]).

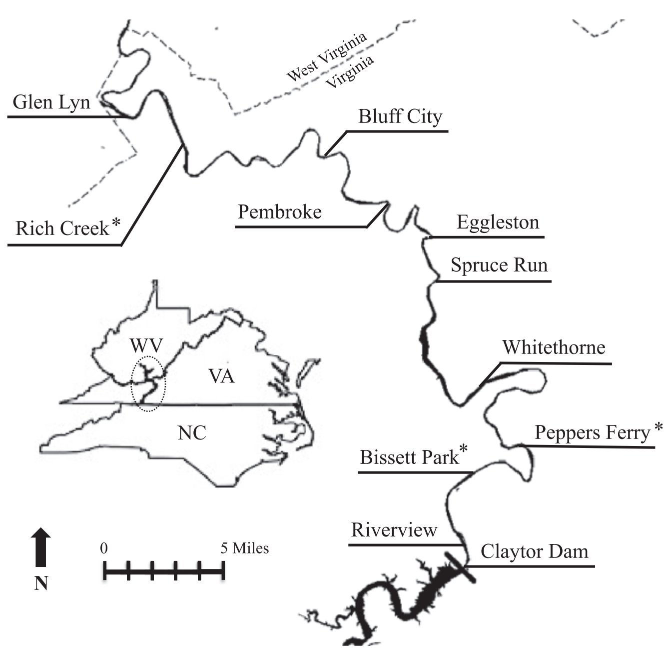

FIGURE 1. Study area and study sites in the New River, Virginia. An asterisk (*) indicates sites sampled on an irregular basis for Muskellunge length and age data.

Muskellunge sampling and data collection.— Our sampling periodicity and methods duplicated previous electrofishing surveys targeting Muskellunge in 2000–2003 conducted by Brenden et al. (2007) and those conducted on a less frequent basis by the VDGIF in 2005–2012. From 2013 to 2015, we conducted 121 single-pass boat electrofishing surveys targeting Muskellunge at each fixed site every 1 to 2 weeks during daylight hours from December through June. Water levels, accessibility, and boat mobility were best during these months due to higher flows, decreased angler activity, and reduced vegetation. Durations of surveys were based on the amount of shoreline suitable for electrofishing at the site and varied between 16 min and 3 h, 10 min. Larger sites were broken down into smaller 15–20-min transects. The length of actual electrofishing time (i.e., unit was on and active) and the number of fish caught for each transect were summed and combined when calculating the CPUE (number caught per hour electrofished). The amount of fishable shoreline at each site was generally consistent with that of Brenden et al. (2007). The electrofishing system was composed of two drop-wire, boom-mounted anodes and a Type VI-A electrofisher (Smith Root, Vancouver, Washington) with one netter. We used pulsed-DC output at approximately 4 A and 60 Hz, and sampled along the 3-ft (91 cm) depth contour of the river where Muskellunge could effectively be netted.

All captured Muskellunge were measured to the nearest millimeter TL and weighed to the nearest 5 g using a hanging scale. The leading left pelvic fin ray from each Muskellunge was clipped with wire cutters as close to the body as possible and stored in a coin envelope for aging (Johnson 1971; Brenden et al. 2006). If possible, sex was determined for each fish using the urogenital papilla and surrounding tissue (Lebeau and Pageau 1989). We also obtained additional fin rays and associated length data from a local Muskellunge angler to increase our sample size of large individuals for age-and-growth analyses.

Lab processing.— Growth measurements were estimated from sectioned pelvic fin rays (Brenden et al. 2007; Koch and Quist 2007). After each fin ray was mounted (see Koch and Quist 2007), a thin section (0.5–0.75 mm) was cut using an Isomet low-speed saw (Buehler, Illinois), and each section was then mounted to a glass microscope slide using a thermo-adhesive crystal bond. The section was then polished using wetted 300-, 400-, 600-, and 1,500-grit sandpapers and lastly with an alumina slurry on a Buehler polishing cloth. The polished sections were photographed using a digital camera attached to a SZ60 stereo-zoom microscope (Olympus America, Melville, New York). Three readers independently aged each fish from the photograph (and through the microscope when needed), and age assignments were based on majority rule. When there was not a majority agreement and readers together could not reach a consensus on an individual's age, that individual was excluded from age-and-growth analyses (see Doss 2017 for further details). Fractional ages were then calculated for each fish based on the month the individual was captured.

Data analysis.— We assessed changes in Muskellunge population demographics and abundance to evaluate changes in fishery quality. We estimated and compared the size structure, average individual condition, rates of growth and mortality, and CPUE, an index of relative abundance, before (2000–2003) and after (2013–2015) institution of the 42-in MLL in 2006. All statistical tests were conducted with a type-I error rate of 0.05.

We compared the pooled length-frequency distributions and mean length of individuals in 2000–2003 with those in 2013–2015 via the Kolmogorov–Smirnov test and a two-sample *t*-test, respectively. We also calculated size-distribution indices for both data sets (i.e., proportional size distribution [PSD], PSD-Q, PSD-P, PSD-M, and PSD-T) using equation 1 below (Gabelhouse 1984; Neumann et al. 2012) (the letters Q, P, M, and T following PSD stand for quality, preferred, memorable, and trophy, respectively).

$$\text{PSD} - X = \frac{\text{Number of fish} \geq \text{specified length}}{\text{Number of fish} \geq \text{minimum stock length}} \times 100 \tag{1}$$

Length categories for PSD calculations can be found in Table 1. We then compared the resulting size-distribution indices using the confidence-interval approach described by Gustafson (1988).

We characterized changes in average individual condition by comparing the average relative weight (W_r; Wege and Anderson 1978) of Muskellunge within each size-distribution category in 2000–2003 to that in 2013–2015 using ANOVA. Average W_r was compared by size category because of a significant length-based trend in the 2013–2015 data set (Murphy et al. 1991). Relative weight for each individual was calculated as

TABLE 1. Proportional size distribution (PSD) length categories (inches) for Muskellunge as defined in Neumann et al. (2012).

Length category	Length (in)
Stock (S)	20
Quality (Q)	30
Preferred (P)	38
Memorable (M)	42
Trophy (T)	50

$$W_r = \left(\frac{W}{W_s}\right) \times 100 \tag{2}$$

in which W is the weight of the individual and W_s is a standard weight for a specific length (L) predicted by a length–weight regression. We used sex-specific length–weight regressions if the sex of the fish was known (equations 3 and 4 for male and female Muskellunge, respectively), or the nonsex-specific equation if the sex of the fish was unknown (equation 5) as defined by Neumann et al. (2012).

$$\log_{10}(W_s) = -3.921 + 3.245 \times \log_{10}(L) \tag{3}$$

$$\log_{10}(W_s) = -4.070 + 3.340 \times \log_{10}(L) \tag{4}$$

$$\log_{10}(W_s) = -4.052 + 3.325 \times \log_{10}(L) \tag{5}$$

We compared growth rates before and after the institution of the 42-in MLL. We fit von Bertalanffy growth curves (equation 6) to the male and female Muskellunge length-at-age data from 2013–2015 using nonlinear regression (Isely and Grabowski 2007; Ogle 2016). The von Bertalanffy growth curve is represented by

$$L(t) = L_\infty\left(1 - e^{-k(t-t_0)}\right) \tag{6}$$

where $L(t)$ is the expected length at time t, L_∞ is the asymptotic average length, k is the Brody growth rate coefficient, and t_0 represents the age at which average length is zero. Due to the lack of data for known-sex fish >8 years of age, growth models only refer to individuals between 2 and 8 years of age. We calculated 95% CIs for the growth models using the bootstrap methods described by Ogle (2016) and Ritz and Streibig (2008). Comparisons of growth models (male versus female Muskellunge and before and after the 42-in MLL) were made using likelihood ratio tests (Kimura 1980) and extra sums-of-squares tests (Chen et al. 1992; Ritz and Streibig 2008). Likelihood ratio and extra sums-of-squares tests assess differences in the fit of growth models. By comparing the most complicated model first with a model where no parameters differ between groups and then with simpler, nested models, the tests are able to isolate which parameters differ between groups. In order to model the Muskellunge population under alternative length-limit regulations, we re-estimated each growth model (i.e., one for male and one for female Muskellunge) with a set L_∞, and only estimated parameters k and t_0. We calculated L_∞ using an equation based on the maximum length observed (Froese and Binohlan 2000) and estimated k and t_0 by fitting the von Bertalanffy growth curve using nonlinear regression.

Total mortality was estimated by using weighted catch-curve regression whereby the natural logarithm of pooled

(2013–2015) catch at age was plotted against age, and the slope of the regression line represented total instantaneous mortality Z (Miranda and Bettoli 2007). We calculated 95% CIs around the 2013–2015 estimates of total mortality and compared those intervals with the 95% CIs of estimates in 2000–2003 (Ogle 2016). We pooled the 2013–2015 catch-at-age data to reduce the influence of any variability in recruitment on mortality estimates (Miranda and Bettoli 2007). There was a change in mortality in the 2013–2015 population once Muskellunge reached harvestable length (42 in), effectively violating the constant-mortality assumption required by catch-curve regression. Thus, we elected to fit two catch curves as suggested by Miranda and Bettoli (2007). One curve was fitted to data for unexploited fish ages 4–7 and another to data for exploited fish ages 7–11. New River Muskellunge only reach harvestable lengths at ages 7+. Thus, we assumed that the catch-curve regression for fish ages 4–7 represented mortality primarily from natural causes, while the second catch curve fit to fish ages 7–11 encompassed both natural and fishing mortality (Miranda and Bettoli 2007). The two catch curves were fit only to the descending limb of the catch-at-age data, based on the assumption that the descending arm represents fish that had become fully vulnerable to the electrofishing gear (Miranda and Bettoli 2007; Ogle 2016). The sample size and corresponding degrees of freedom were small after splitting the catch curve, so we also calculated mortality using the Robson–Chapman maximum-likelihood method (Robson and Chapman 1961) for comparison with both 2013–2015 mortalities calculated from catch curves and mortalities estimated in 2000–2003.

We characterized changes in the relative abundance of Muskellunge by analyzing the CPUE data of all individuals from regular electrofishing surveys in 2000–2015 by using negative binomial regression. We also fit a separate negative binomial regression on the CPUE data for Muskellunge ≥42 in to investigate potential changes in the relative abundance of large Muskellunge.

Population modeling under alternative fishery regulations.— Using the dynamic pool model in the Fisheries Analysis and Modeling Simulator (FAMS; Slipke and Maceina 2014), we modeled the population under the current 42-in MLL, a lower 38-in MLL, a higher 48-in MLL, and a 40- to 48-in PSL. These regulations were selected based on evidence from other systems of the ability of the regulations to increase the size and abundance of large sport fish (e.g., Luecke et al. 1994; Cornelius and Margenau 1999), as well as what might be feasibly implemented by the managing agency. Sex-specific growth estimates (L_∞, k, t_0) and length–weight relationships from 2013–2015 were used as inputs to FAMS. To account for changes in mortality under alternative regulations and the increasing popularity of the New River Muskellunge fishery, each regulation was modeled under a range of conditional fishing mortalities from 0.1 to 0.5. Conditional natural mortality was based on our estimate of natural mortality (i.e., total mortality of sublegal-size fish ages 4–7) and was set at 0.1. This mortality estimate was similar to mortality estimates calculated in FAMS. Each model was run for 100 years to represent a population in steady-state condition. Female and male Muskellunge were modeled separately due to differences in growth and the age-related onset of fishing mortality. We combined model results for male and female Muskellunge in the final result for each regulation to give an overall view of the fishery. Models were conducted with an initial population size of 1,000 fish per sex and with variable recruitment, with every other year considered a “strong” year (i.e., twice the average of 1,000 recruits). The variable recruitment option was selected based on field observations of alternate strong and weak years of natural recruitment in the New River (i.e., VDGIF were no longer stocking Muskellunge). We evaluated each regulation by estimating population PSD-T, total yield (kg), and number of Muskellunge harvested by anglers (based on fishing mortality). These metrics were then compared across regulations to assess which regulations would best increase fishery quality.

RESULTS

We captured a total of 528 Muskellunge from the New River in 2013–2015. Fish ranged 10–49 in (25–122.5 cm) in length and 1–11 years of age (Table 2). The sex ratio was nearly equal (female, 51%; male, 49%). Additional information on 48 individuals was received from a

TABLE 2. Age distribution of Muskellunge captured during boat electrofishing surveys and by angling Muskellunge in the New River, Virginia, 2014–2015; Muskellunge captured in 2013 were not aged.

Age (years)	Collection method: Boat electrofishing surveys	Collection method: Angling
1	35	0
2	24	0
3	39	0
4	55	4
5	48	8
6	51	15
7	39	17
8	9	2
9	1	0
10	1	0
11	3	0
12	0	1

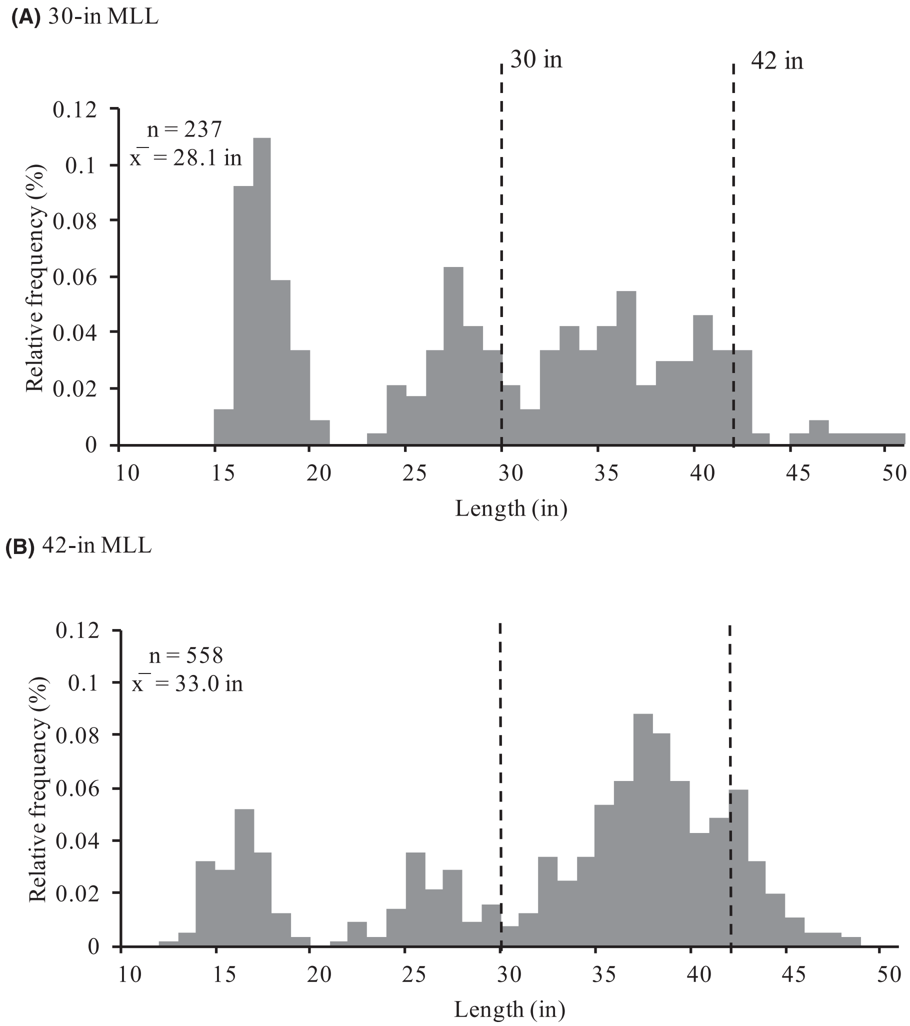

FIGURE 2. Length-frequency distributions for the New River Muskellunge population under **(A)** the 30-in MLL sampled from 2000 through 2003 and **(B)** the 42-in MLL sampled from 2013 through 2015. Dashed lines mark the 30- and 42-in MLLs. Data are (A) from Brenden et al. (2007) and (B) this study.

TABLE 3. Proportional size distribution (Neumann et al. 2012) values (and 90% CIs) for the New River, Virginia, Muskellunge population sampled under two different harvest regulations (MLL = minimum length limit, P = preferred, M = memorable).

Harvest regulation (dates instituted)	Years sampled	PSD	PSD-P	PSD-M
MLL (1980–2006)	2000–2003	65 (58–72)	26 (20–32)	5 (2–8)
MLL (2006–2016)	2013–2015	84 (81–87)	42 (38–46)	16 (13–19)

cooperating angler, and those individuals ranged 40–52 in (100–130 cm) in length and 4–12 years of age (Table 2).

The length-frequency distribution of Muskellunge in 2013–2015 was significantly different than that in 2000–2003 (Kolmogorov–Smirnov test: $D = 0.30661$, $P < 0.0001$; Figure 2) with greater proportions of individuals ≥42 in in 2013–2015. The average length of Muskellunge also increased from 28.1 to 33.0 in (70.3 to 82.5 cm) (Welch's two sample *t*-test: $t = -6.776$, df = 442.87, $P < 0.0001$). This positive shift in size structure was also evident in the size-distribution indices for the current (2013–2015) population (i.e., PSD, PSD-P, and PSD-M)

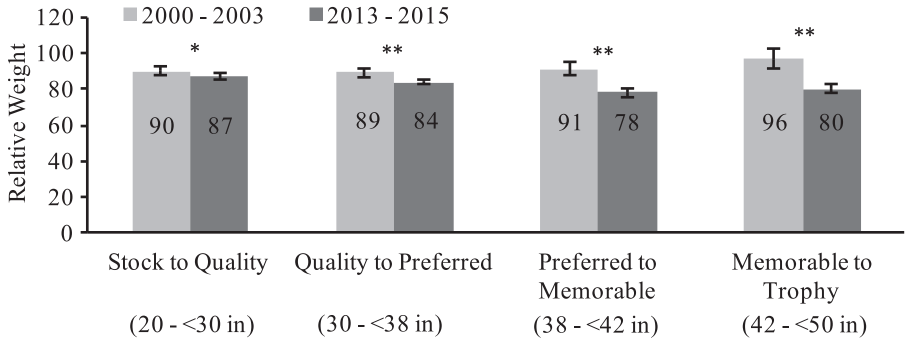

FIGURE 3. Average W_r by size-distribution length category for New River Muskellunge captured by means of boat electrofishing surveys before (2000–2003; light gray) and after (2013–2015; dark gray) the 42-in MLL. Numbers in the bar are the average W_r. Error bars are 95% CIs calculated using methods by Murphy et al. (1990). Average condition in 2013–2015 was significantly lower than the corresponding average condition in 2000–2003 regardless of size (ANOVA: $P \leq 0.05$*, $P \leq 0.0001$**).

all of which increased significantly since the systematic sampling performed in 2000–2003 (Table 3). The average condition of Muskellunge decreased significantly between the 2000–2003 sampling and that of 2013–2015 across all size-classes (Figure 3; ANOVA: $P \leq 0.05$). Reduced condition was especially noticeable for preferred-size (≥38 in) and memorable-size (≥42 in) Muskellunge (Figure 3; ANOVA: $P \leq 0.0001$). Likelihood ratio and extra sums-of-squares tests found a significant difference in the fit of growth models in which k and L_∞ differed between female and male Muskellunge. Female Muskellunge had a 6-in (15 cm) higher L_∞, but approached L_∞ (k) more slowly than male Muskellunge in 2013–2015. This was also true of Muskellunge in 2000–2003; female Muskellunge had a 5-in (12.5 cm) higher L_∞ and approached L_∞ (k) more slowly than did male Muskellunge. The von Bertalanffy parameter k for female Muskellunge was significantly lower in 2013–2015 than in 2000–2003, and L_∞ for male Muskellunge was significantly lower (Figure 4; Table 4; additional supplementary material [statistical results for likelihood ratio and extra sums-of-squares tests for comparisons of von Bertalanffy growth models between male and female Muskellunge and between the 2000–2003 and 2013–2015 sampling periods] is available online). Both male and female Muskellunge in 2013–2015 generally needed an additional year of growth to reach citation (40 in) and memorable sizes (42 in) than Muskellunge in 2000–2003.

Estimated annual mortality of Muskellunge below the length limit during 2013–2015 (i.e., ages 4–7 under the 42-in MLL) was similar to that estimated for sublegal fish in 2000–2003 based on both the Robson–Chapman method (42% versus 46%) and catch-curve regression (9% versus 22%; 95% CIs in Table 5; Figure 5). Estimates of annual mortality for legal-size fish demonstrated a significant increase from 38% in 2000–2003 to 67% in 2013–2016 based on the Robson–Chapman method or 32% to 77% based on catch-curve regression (95% CIs in Table 5; Figure 5). Generally, the Robson–Chapman method produced more precise estimates of mortality than those produced from catch curves. Estimates of annual mortality were similar between the two methods for legal-size fish, but the Robson–Chapman method estimated much higher annual mortality for sublegal-size Muskellunge. Despite absolute differences in the estimates the general trend of increased mortality of legal-size fish was the same among both mortality estimation techniques.

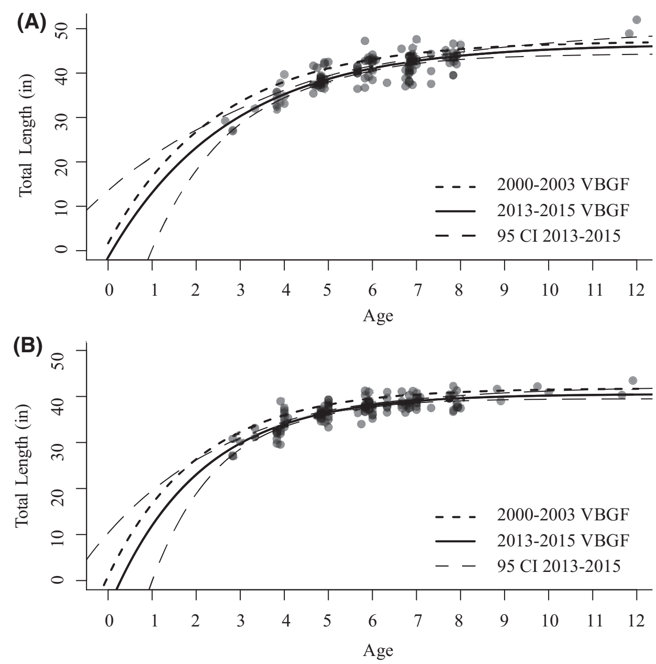

FIGURE 4. Fitted von Bertalanffy growth curves (and 95% CIs) for **(A)** female and **(B)** male Muskellunge in 2000–2003 and 2013–2015. Data shown are for Muskellunge sampled in 2013–2015 under the 42-in MLL. Data points are partially transparent so data of similar values can be seen.

Catch-per-unit-effort data for 2000–2015 revealed a significant increase in the total relative abundance of all

TABLE 4. Estimates for von Bertalanffy parameters (L_∞, k, t_0) and 95% confidence intervals for female and male New River Muskellunge under a 30-in MLL (Brenden et al. 2007) and under a 42-in MLL (and years sampled).

von Bertalanffy parameter	30-in MLL (2000–2003)	42-in MLL (2013–2015)
	Females	
L_∞	47.3 (45.4–49.4)	46.6 (43.9–53.7)
k	0.40 (0.35–0.46)	0.36 (0.17–0.57)
t_0	−0.09 (−0.24–0.04)	0.09 (−2.3–1.16)
	Males	
L_∞	41.8 (40.7–42.9)	40.5 (39.4–42.4)
k	0.49 (0.43–0.55)	0.49 (0.32–0.69)
t_0	−0.47 (−0.18–0.07)	0.29 (−1.10–1.09)

Muskellunge (negative binomial regression: regression coefficient = 0.07975, df = 354, $P < 0.0001$; Figure 6A) and of large Muskellunge (≥42 in) (negative binomial regression: regression coefficient = 0.16130, df = 354, $P < 0.0001$; Figure 6B).

Simulation Modeling of Alternative Regulations

Of the four regulatory scenarios evaluated, a 48-in MLL increased PSD-T the most, regardless of fishing mortality (Figure 7A). The 42-in MLL and the 40- to 48-in PSL performed similarly across different levels of fishing mortality for the production of trophy fish as measured by PSD-T. The 38-in MLL was least likely to produce trophy fish, especially at higher fishing mortalities. Yield (kilograms harvested by anglers) was highest under the 38- and 42-in MLLs under high rates of fishing mortality (Figure 7B). Yield was lowest under the 48-in MLL, but the 48-in MLL surpassed the 40–48-in PSL in yield under conditional fishing mortalities >0.4 (Figure 7B). At high conditional fishing mortalities under the 40–48-in PSL, yield declined, indicating potential for growth overfishing. The 38-in and 42-in MLLs and the 40–48-in PSL performed similarly on the number of fish harvested, and the 48-in MLL, as expected, showed the lowest number of fish harvested (Figure 7C).

DISCUSSION

The New River Muskellunge Population under Current Regulations

Following the institution of the 42-in MLL, we observed a 5-in increase in the average size of Muskellunge, an increase in the population's size structure with greater proportions of memorable-size individuals (≥42 in), and an increase in the abundance of memorable-size Muskellunge. These findings corroborate the positive effects of high MLLs observed in Muskellunge fisheries in northern latitudes (Cornelius and Margenau 1999; Farrell et al. 2006) and demonstrate similar positive effects on a Muskellunge fishery in a southern-latitude system. Our findings also corroborate earlier predictions regarding the New River's Muskellunge population under a higher MLL (Brenden et al. 2007).

The 42-in MLL eliminated the legal harvest of Muskellunge ages 3–7 years, which had previously been vulnerable to harvest under the 30-in MLL. Reduced mortality for these young individuals increased the recruitment of Muskellunge to large size-classes and provided individual Muskellunge more time to reach sexual maturity, spawn, and contribute to the overall standing stock of Muskellunge. Muskellunge typically reach sexual maturity at ages 3–4 in males and ages 4–5 in females (Cook and Solomon 1987). Under the 30-in MLL, the potential existed for Muskellunge to be harvested before reaching sexual maturity. The average minimum harvestable length identified by the majority of New River anglers in 2000–2003 was 33 in (82.5 cm), equivalent to a Muskellunge that is 3–4 years old based on growth models in Brenden et al. (2007) and this study. The delay of mortality under the 42-in MLL played an important role in shaping the current New River Muskellunge population.

TABLE 5. Estimates of instantaneous total mortality rate and annual mortality for sublegal-size and legal-size Muskellunge in 2000–2003 and in 2013–2015. Instantaneous total mortality (Z) and annual mortality estimates (and 95% CIs) were calculated using catch-curve regression and the Robson–Chapman method.

Harvest regulation	Sampling period	Size of fish	Method	Z	Annual mortality (95% CI)
30-in MLL	2000–2003	Legal-size fish	Catch-curve	0.38	0.32 (0.18–0.43)
			Robson–Chapman	0.48	0.38 (0.31–0.44)
42-in MLL	2013–2015		Catch-curve	1.47	0.77 (0.25–0.93)
			Robson–Chapman	1.11	0.67 (0.56–0.77)
30-in MLL	2000–2003	Sublegal-size fish	Catch-curve	0.25	0.22 (0–0.43)
			Robson–Chapman	0.61	0.46 (0.42–0.50)
42-in MLL	2013–2015		Catch-curve	0.096	0.09 (0–0.24)
			Robson–Chapman	0.54	0.42 (0.36–0.48)

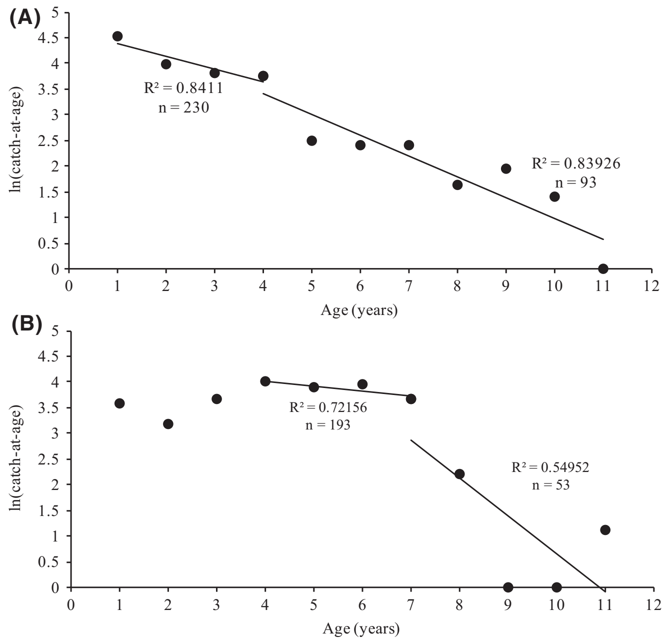

FIGURE 5. Catch curves fit for New River Muskellunge caught by means of boat electrofishing in **(A)** 2000–2003 and **(B)** 2013–2015. Separate catch-curve regressions were fit to catch of sublegal (<30 and <42 in during 2000–2003 and 2013–2015, respectively) and legal-sized fish. Sample size (*n*) and r^2 value are included with each catch curve.

Not all changes to the Muskellunge population following the institution of the 42-in MLL were positive. The average condition of large Muskellunge in the New River decreased, and total mortality for large Muskellunge increased. Declines in average condition (i.e., W_r) along with increases in CPUE of large Muskellunge and a positive shift in the population's length-frequency distribution are evidence of possible stockpiling of New River Muskellunge between 35 and 40 in. This size-class has the lowest average condition, and mortality increases at the larger end of the size-class. Reduced growth and condition of fish immediately below the length limit are common following an increase in the MLL and are usually attributed to increased intraspecific competition and the division of forage and space among more individuals (Anderson 1976; Wilde 1997). With densities estimated in the New River as high as four Muskellunge per hectare in some areas (Doss 2017), a reduction in growth rate as a result of intraspecific competition is feasible, particularly for large Muskellunge. A study in Bone Lake, Wisconsin, attributed reduced condition following the implementation of 34- and 40-in MLLs to intraspecific competition, and found that large Muskellunge (>38 in) had the lowest average condition (Cornelius and Margenau 1999). In the New River, large Muskellunge (≥38 in) also exhibited the lowest average condition. Accordingly, Doss (2017) found evidence of small shifts in the importance of various prey items in the diet of adult Muskellunge—especially catostomids—since the institution of the 42-in MLL, which could be indicative of increased competition for forage.

Estimates of total mortality for older, legal-size Muskellunge were higher than that estimated in 2003 (Brenden et al. 2007). One possible cause for this increase in mortality is that the novelty of a high MLL in a southern-latitude system attracted more anglers and increased fishing pressure on the Muskellunge stock (Brenden et al. 2007). Increased fishing pressure on Muskellunge and other sport fishes following the implementation of a unique regulation, such as a high MLL, has been observed in other systems (Clady et al. 1975; Cornelius and Margenau 1999). Angler survey data collected by the VDGIF showed an increase in the proportion of New River anglers targeting Muskellunge (J. Copeland, VDGIF, unpublished data). However, since the MLL was only changed 7 years before the initiation of our sampling, some fish may have been susceptible to harvest under the 30-in MLL. Thus, the catch curve fit to Muskellunge ages 7+ represents a transition between the 30- and 42-in MLLs. In the future, a catch curve fit to legally harvestable fish ages 7+ might yield a lower estimate of total mortality when older and larger classes of fish have matured exclusively under the 42-in MLL. Furthermore, older fish were the most difficult to age, and underaged fish could lead to increased mortality estimates. In particular, this study and Brenden et al. (2006) had trouble agreeing on ages of fish greater than or equal to 8 years. Difficulty in aging older fish is further complicated by small sample sizes of large, old fish. While Brenden et al. (2006) found that pelvic fin ray aging is a useful, nonlethal method for aging Muskellunge, pelvic fin ray aging—and subsequent estimates of Muskellunge mortality—might be greatly improved by means of an age validation study. Because mortality of Muskellunge will drastically influence the effectiveness of any future fishery regulation, accurately estimating Muskellunge mortality will be critical. Future management should place priority on accurate estimations of mortality and on understanding the inevitable interactions between regulations, mortality, and various measures of fishery quality.

While this study enumerates many changes in the New River Muskellunge population before and after the institution of a 42-in MLL, our study design lacked the statistical security afforded by a before-after-control-impact design. Thus, there are many biotic and abiotic factors that may have also shaped the Muskellunge population, including variation in year-class strength, changes in forage, and changes in habitat. Ultimately, we cannot rule out every possible driver of change to be at least partially responsible for the differences we observed in the Muskellunge population. Thus, we attribute observed changes in the Muskellunge population to the institution of the 42-in

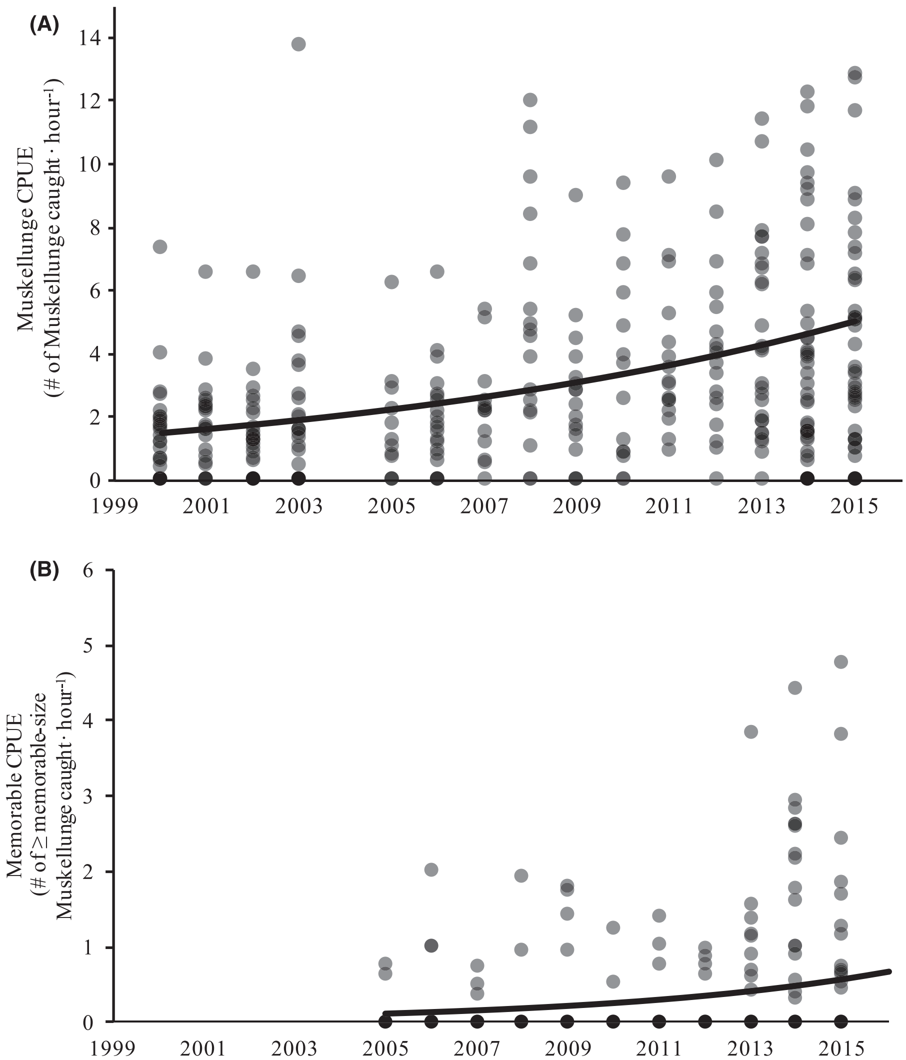

FIGURE 6. The CPUE data for **(A)** all Muskellunge and **(B)** memorable-sized Muskellunge (i.e., ≥42 in) from electrofishing surveys in 2000–2015. No data were collected in 2004, and length-specific CPUE data were only available beginning in 2005. Thus, there are no data on memorable-length CPUE from 2000–2004. Data points are partially transparent so CPUE data of the same value can be seen (e.g., there were multiple days each year with CPUEs of zero Muskellunge caught per hour; thus, those data points appear darker). All CPUE data was analyzed using negative binomial regression.

MLL with the caveat that the current Muskellunge population is obviously the culmination of many factors. However, there are two factors—changes in flow and stocking procedures—that are unlikely to have driven the observed changes in the Muskellunge population. Firstly, variation in flow among years is unlikely to have influenced the Muskellunge population due to the overriding control of dam operations on river flows. Claytor Dam, operated by the Appalachian Power Company (AEP) controls water flow on the lower New River, and there have only been two changes in flow management since it was first licensed in 1943. Neither of these flow management changes should have driven change in the Muskellunge population as AEP generally maintained consistent flows resulting in similar habitat availability throughout the study (for more information on flow management see Doss 2017). Secondly, the VDGIF switched to fall stockings of advanced fingerlings 9–12 in (22.5–30 cm) TL in 2007 instead of summer stockings of smaller 4-6 in (10–15 cm) fingerlings in an attempt to boost survival of stocked young of the year. The agency eventually discontinued stocking in 2012, as evident natural reproduction was deemed sufficient to sustain the Muskellunge population. While changes to the Muskellunge stocking procedures in 2007 likely increased the survival of stocked fish, and thus the overall density of Muskellunge, these changes were not likely to have positively shifted the size structure of the population at the time of this study. Only one group of

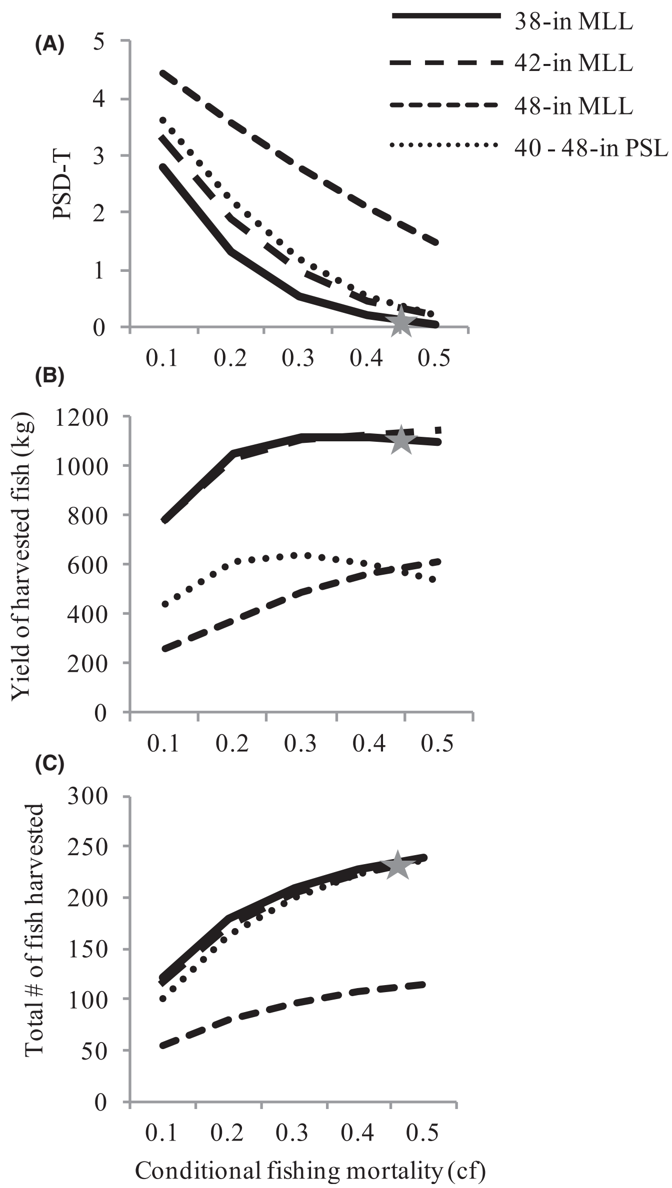

FIGURE 7. The 100-year average of **(A)** PSD-T, **(B)** total yield (kg) of Muskellunge harvested by anglers, and **(C)** total number of Muskellunge harvested by anglers under the four regulatory scenarios (i.e., 38-in, 42-in, and 48-in MLLs and a 40–48-in protected-slot limit [PSL]) modeled in FAMS across various levels of conditional fishing mortality (cf). The star in each panel reflects an approximate estimation of the fishery's current state.

stocked fish under the modified stocking procedures would have made it to legal size by the time our data were collected (i.e., 2013–2015) based on the growth models reported in Brenden et al. (2007) and those found in the current study.

The Muskellunge Fishery under Alternative Regulations

Of the regulations modeled, the 48-in MLL would likely increase the production of the population's trophy-size fish the most; this corroborates other findings regarding the effects of instituting high MLLs on Muskellunge fisheries (Cornelius and Margenau 1999; Kerr 2007). If the production of trophy-size fish is the only or primary goal of the VDGIF, then implementing a high MLL is the most sensible regulatory option. However, fishery quality is defined by many factors in addition to the production of trophy-size fish, including catch rate and individual condition of angled fish. Under the 42-in MLL, the New River Muskellunge population demonstrated symptoms of stockpiling. Thus, while an increase in the MLL will likely increase the production of trophy-size fish, stockpiling and reduced condition may be similarly evident under a new, increased MLL.

The 40- to 48-in PSL did not increase the production of trophy-size fish (i.e., PSD-T) as much as the 48-in MLL and demonstrated only limited production of trophy-size fish under low fishing mortalities (i.e., ≤0.2). The PSL also demonstrated some evidence of growth overfishing. Growth overfishing occurs when yield is reduced because fishing mortality is too high on young or small fish (Allen and Hightower 2010). We found that long-term average yields began to decrease at conditional fishing mortalities as low as 0.2. This has the important management implication that managers must find a delicate balance for mortality of subslot fish. Harvest of subslot individuals must be high enough to reduce intraspecific competition, but low enough to maintain steady recruitment of fish through the slot. Bag limits or seasonal restrictions could help managers find and maintain this level of mortality. Maintaining low natural mortality is also important, as increases in natural mortality of fish would lower yield under all length-limit regulations. The 38-in MLL was least likely to produce trophy fish, especially at high fishing mortalities, and is not likely create a fishery that meets current management objectives.

Management Implications

While the previous shift from a 30-in to a 42-in MLL indeed increased several measures of fishery quality, it also resulted in reduced growth and condition of large Muskellunge (≥38 in). Additionally, the stated goal of achieving trophy-size (≥50 in) Muskellunge has yet to be achieved. A 40–48-in PSL might remedy the current stockpiled size-class (35–40 in) by making them available for harvest, which should promote growth of that size-class as intraspecific competition is reduced (assuming anglers harvest subslot fish). However, fisheries managers should be wary of overharvest of subslot individuals and may avoid growth overfishing by setting bag limits or seasonal restrictions to limit subslot mortality. The PSL regulation also has the potential for a minor increase in the production of trophy-size Muskellunge in the New River under low fishing mortalities. Thus, a PSL could help managers achieve a trophy-oriented goal without sacrificing growth rate or condition, both of which are important to fishery quality and are often considered measures of management effectiveness and efficiency.

Another factor of fishery quality that managers must consider is how amenable a regulation is to the interests of other angler groups. On the New River, many anglers of Smallmouth Bass *M. dolomieu* feel strongly that increasing the number of Muskellunge will reduce the quality of the bass fishery (Brenden et al. 2004). Thus, a higher MLL directly aimed at increasing the abundance of large Muskellunge could be poorly received. A PSL that allows the production of some trophy-sized Muskellunge while reducing the overall number of individuals may be a more agreeable regulatory option that mitigates the fears of Smallmouth Bass anglers.

Protected-slot limits are still a novel approach to managing Muskellunge and esocids in general, and they have only been implemented and studied in a handful of cases, typically with Northern Pike *E. lucius* populations (Paukert et al. 2001; Carlson 2016). Investigations into the effects of those regulations are ongoing, and preliminary results are difficult to interpret. For instance, in Minnesota, Northern Pike populations in three of five lakes with PSLs showed considerable increases in size structure with increased proportions of fish ≥24 in (Pierce 2010). However, the remaining two lakes demonstrated little to no improvement in size structure. Both movement between water bodies and angler noncompliance were cited as possible causes for the failure of the regulations in those lakes (Pierce 2010). Additionally, the preferential harvest of male fish—most male Muskellunge rarely grow larger than 40 in—should also be considered under a PSL. If too many males are removed from the population, a PSL could have the unintended consequence of affecting the reproductive viability of the population. Ultimately, more long-term, empirical research is needed to identify the effects and potential limitations of PSLs on large sport fish such as Muskellunge.

Even under the most restrictive regulations, the New River's Muskellunge fishery may not reach the level of trophy production associated with northern Muskellunge fisheries due to social and environmental constraints. Competing angler interests may dissuade managers from setting regulations with the highest predicted production of trophy-size fish, and excessive harvest of large individuals, as can be common in some southern Muskellunge fisheries (Brenden et al. 2007), may prohibit the New River's Muskellunge fishery from reaching "traditional" trophy status (i.e., notable abundance of Muskellunge ≥50 in). While many Muskellunge fisheries are supported by a strong catch-and-release ethic, the New River still experiences substantial harvest. Only 40% of anglers surveyed in 2007 indicated they would release all caught Muskellunge (Brenden et al. 2007). Release rates for Muskellunge in the New River have been estimated at 86% for all Muskellunge and 46% for Muskellunge ≥40 in (Brenden et al. 2007). However, the catch-and-release ethic is growing among New River anglers. Preliminary creel data collected by VDGIF shows that more anglers are practicing catch-and-release angling regarding caught Muskellunge. In terms of environmental constraints, Muskellunge in southern systems are thought to grow and mature more quickly and experience shorter lifespans than Muskellunge in northern systems, primarily due to differences in temperature and forage (Blanck and Lamouroux 2007; Casselman 2007; Faust et al. 2015; Rude et al. 2017). This has been explicitly documented in Northern Pike (Griffiths et al. 2004; Blanck and Lamouroux 2007; Rypel 2012). The recognition of system-specific constraints on trophy potential for Muskellunge and other sport fishes has led to a growing emphasis on system-specific regulations for individual water bodies and populations (Radomski et al. 2001; Faust et al. 2015; Rude et al. 2017), and entire studies have focused on creating and managing for system-specific trophy standards (Casselman 2007). If the VDGIF continues to manage the New River Muskellunge population for the production of large individuals, we strongly urge that management objectives be constructed with system-specific constraints in mind. Similarly, fishery managers working with other southern-latitude Muskellunge fisheries should consider these constraints.

This study demonstrated a substantial improvement in some measures of Muskellunge fishery quality following the institution of a 42-in MLL and provided evidence that a higher MLL would likely further improve fishery quality and trophy production. A higher MLL may not be a regulatory option available to managers due to social constraints, and our modeling indicated a PSL might be a more agreeable regulatory option that could promote higher production of trophy-size fish than the current regulation. While a high MLL or PSL may accomplish VDGIF objectives for the Muskellunge fishery, their ability to increase the production of trophy-size fish relies on maintaining low mortality (e.g., avoiding overharvest of subslot fish under a PSL) and may require frequent population assessments to ensure the new regulation has its intended effect. Additionally, consideration should be given to how population changes resulting from new regulations might alter the interactions that Muskellunge have with other New River fishes. This study on the New River Muskellunge fishery provides important empirical evidence for fisheries managers working with Muskellunge in other southern riverine systems. In particular, this study demonstrates the positive effects that a high MLL can have on a southern-latitude Muskellunge fishery and highlights some important pitfalls regarding the use of length-limit regulations for managing Muskellunge.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.