Muskellunge of the New River, Virginia: The Effects of Restrictive Harvest Regulations on Population Demographics and Predation on Sympatric Smallmouth Bass

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Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Master of Science
In
Fish and Wildlife Conservation

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January 20th, 2017
Blacksburg, VA

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ABSTRACT (Academic)

Potential predation between fishes of recreational interest has incited many bitter conflicts between angler groups. Large predators, such as esocids, are often at the center of these conflicts because of their capacity to alter fish populations. Such a conflict certainly exists between the Muskellunge *Esox masquinongy* and Smallmouth Bass *Micropterus dolomieu* fisheries of the New River, Virginia. Following the institution of a 42-in minimum-length limit (MLL) on Muskellunge, bass anglers feared that increased Muskellunge abundance might be negatively affecting Smallmouth Bass via increased predation. In order to ascertain the impacts of the 42-in MLL, I estimated the demographics, abundance, and food habits of Muskellunge combined with bioenergetics modeling to assess changes (i) in the quality of the Muskellunge fishery and (ii) in Muskellunge predation on Smallmouth Bass. Additionally, given the likelihood of future regulations to incite similar concerns from bass anglers, I modeled alternative length-limit regulations (iii) to assess their potential to improve fishery quality, thereby laying the groundwork for managers to address angler concerns before they arise. I found substantial increases in population size structure and in average adult density of Muskellunge since the institution of the 42-in MLL, but bioenergetics modeling did not indicate a notable increase in the consumption of Smallmouth Bass. I also found that high MLLs (e.g., 48-in) were likely to promote the largest increases in trophy production of Muskellunge compared to low MLLs or protected-slot limits (PSLs). This study suggests

that the current Muskellunge population likely plays a small role in shaping Smallmouth Bass population dynamics and production in the New River; and lays the groundwork for predicting how the impact of Muskellunge on Smallmouth Bass might change under alternative regulations.

ABSTRACT (Public)

Management of fish for recreation can be challenging when multiple species are of interest, particularly when potential exists for one species to negatively influence another and stimulates conflict between users. Large predators are often at the center of these conflicts because of their ability to change fish populations via predation. This type of conflict certainly exists between the Muskellunge *Esox masquinongy* and Smallmouth Bass *Micropterus dolomieu* fisheries of the New River, Virginia. The perceived influence of increased Muskellunge predation on Smallmouth Bass and the bass fishery following the institution of a 42-in minimum-length limit (MLL), has created tension between users. In order to ascertain the impacts of the 42-in MLL, I estimated Muskellunge population structure, abundance, and food habits and combined them with diet modeling to assess changes (i) in the number and size of Muskellunge and (ii) in Muskellunge predation on Smallmouth Bass. Additionally, given the likelihood of future regulations to incite similar concerns from bass anglers, I also used regulation modeling to assess (iii) the potential of other regulations to change the number and size of Muskellunge. I found that the size structure (i.e., the proportion of large Muskellunge in the population) and the number of Muskellunge increased after the 42-in MLL, but I did not find a notable increase in the amount of Smallmouth Bass eaten by Muskellunge. I also found that more-restrictive regulations (i.e., a 48-in MLL) could further increase the size structure and number of Muskellunge. My results suggest that the current Muskellunge population probably plays a small role in shaping the Smallmouth Bass population of the New River, and I lay the groundwork for predicting how that role might change under other regulations.

## Acknowledgements

There are so many people, who with their continued help and support, made this project possible. Thank you to my wonderful friends and family, especially my grandmother Dot Doss and my best friend Alison Parker, for always inspiring me to pursue my interests and for providing encouragement at every step. Thank you to my committee members, Don Orth and John Copeland, for your patience and guidance throughout this process. Your insight and support (both moral and academic) has been invaluable. A special thank you to Joe Williams for his mentorship throughout this thesis and in the field. Your patience and confidence in me—even if misplaced at times—has meant so much to me and has made me a better field biologist. To my advisers, Leandro Castello and Brian Murphy, thank you for taking a chance on me and fostering an environment that allowed me to really grow as a member of the fisheries profession and to hone my skills as a writer, a student, and as a donut and coffee connoisseur. I am forever grateful for your faith in me throughout this project, and I will always look to you both for professional advice in the future. Thank you to my labmates Jordan Richard, Jesse Olsen, and Gretchen Stokes, and pseudo-labmate Vic DiCenzo for "lightening the mood" and for acting as my sounding board whenever I needed one.

And in the words of Dr. Murphy, "Back on your heads [Back to work]."

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**Introduction**

Because predatory fishes are often the most-sought-after sport fishes in North America, fisheries managers commonly stock, introduce, and regulate them to create and maintain successful recreational sport fisheries (Murphy and Kelso 1986; Trushenski et al. 2010). Millions of predatory fishes are regularly stocked in North America, including trout and salmon (Salmonidae), black basses *Micropterus spp.*, pikes *Esox spp.*, and several catfish species (Ictaluridae) (Murphy and Kelso 1986; Halverson 2008; Kolar et al. 2010). Frequently, these introductions and stockings create systems with multiple fisheries supported by top-level predators.

Large predatory fishes have the potential to alter the size structure and dynamics of prey fish populations, eliminate species, and drastically change aquatic communities (He and Kitchell 1990). The ability of predatory fishes to wield such ecological influence often generates fear—and sometimes hatred—towards predator populations and the fisheries they support. In particular, the perception of predatory interaction between two predators of interest can incite bitter conflict between angler groups and between anglers and fisheries management (Churchill et al. 2002). Arlinghaus (2005) deemed these types of conflict "intrasectoral conflicts," wherein disagreement exists between entities within the fishery (i.e., angler versus angler or angler versus management). These conflicts are often driven by diverging values, perceptions, and attitudes and require an understanding of many biological, institutional, and human dimensions factors for their effective resolution (Arlinghaus 2005). Intrasectoral conflicts may be best resolved by involving users in the regulatory process and/or by using "soft paths" (e.g., information, persuasive communications, and education). These soft paths are not limited to but should include

biological evidence that addresses angler concerns. In the specific case of perceived predation between two fishes of interest, this means evidence describing the extent of predatory interaction between the two species.

Introduced populations of Muskellunge *Esox masquinongy* and Smallmouth Bass *Micropterus dolomieu* in the New River, Virginia, are a contemporary example of such conflict and how an understanding of the predatory interaction between two predators of interest could help resolve conflict and improve fisheries management. The Virginia Department of Game and Inland Fisheries (VDGIF) first introduced Muskellunge into the New River in 1968 to diversify local recreational angling opportunities. The agency stocked the predator annually from 1982 to 2003 with the goal of creating a trophy fishery (Brenden et al. 2007). During this period the Muskellunge fishery began to develop, and was managed with a 30-in minimum length limit (MLL) and a bag limit of two fish per day (Brenden et al. 2007). As the Muskellunge fishery grew, anglers supporting the New River's most-popular sport fishery—Smallmouth Bass—complained that large Muskellunge were preying on Smallmouth Bass and reducing their catch. The complaints culminated in a 3-year diet study conducted by the VDGIF, which found that Smallmouth Bass represented only 4% of prey consumed by Muskellunge (based on average percent wet weight per individual). Bioenergetics modeling concluded that annual consumption of Smallmouth Bass was only 0.9 kg·ha$^{-1}$·yr$^{-1}$ (compared to an estimated annual production of 32.1 kg·ha$^{-1}$·yr$^{-1}$ [Roell and Orth 1993]). Therefore, Muskellunge predation was unlikely to exert a significant effect on the Smallmouth Bass population (Brenden et al. 2004).

Several other changes on the lower New River at that time, including a change in the operation of Claytor Dam and changes to regulations on the Smallmouth Bass fishery, likely played a role in shaping the Smallmouth Bass population and angler catch rates. Appalachian Power Company (AEP), the company responsible for the operation of Claytor Dam, switched in 1991 from a daily peak-power-production regime throughout the year, to a "levelized" flow regime between 15 April and 15 October (Federal Energy Regulatory Commission [FERC] 2011). Those months span the majority of the Smallmouth Bass spawning season on the New River (Graham and Orth 1986). While the "levelized" flow regime required AEP to maintain an average minimum daily flow (i.e., 750 cfs), daily fluctuations in flow still likely influenced Smallmouth Bass recruitment (Lukas and Orth 1995; Copeland 2006). Additionally, an 11 to 14-in PSL was instituted on Smallmouth Bass in 1987 and was increased to a 14 to 20-in PSL in 2003. PSLs instituted on bass populations in other systems have resulted in improvements in growth and size structure, but overall reductions in density (Eder 1984)—which may partially explain perceived declines in angler catch rates. Unfortunately, the effects of these changes on angler catch rates of Smallmouth Bass in the lower New River were never explicitly examined.

The VDGIF decided to skip Muskellunge stocking in 2004 to initiate a biennial schedule that would allow assessment of Muskellunge natural reproduction. The agency also switched to fall stockings of 9-12 in advanced fingerlings in 2007 instead of summer stockings of smaller 4-6 in fingerlings in an attempt to boost survival of stocked young-of-the-year (YOY). The agency eventually discontinued stocking in 2012, as evident natural reproduction was deemed sufficient to sustain the Muskellunge population. In

2006, the VDGIF increased the MLL for Muskellunge from 30 to 42 in and decreased the

bag limit from two to one fish per day to promote the production of trophy- (≥50 in) and

citation-sized Muskellunge (≥40 in; a statewide trophy standard set by the VDGIF as part

of Virginia's Angler Recognition Program [VARP]). In the years following the regulation

change, Smallmouth Bass anglers again complained that the growing number of large

Muskellunge was lowering their catch rates and reducing the quality of the Smallmouth

Bass fishery. These declines were corroborated by some site-specific biological data on

the biomass of Smallmouth Bass, which demonstrated substantial declines from 2005 to

2010. For example, Smallmouth Bass biomass at the Whitethorne site (Figure 1)

exhibited a 40% decrease from 27.2 kg·ha$^{-1}$ (95% CI: 25.9 – 28.7) in 2005 to 16.3 kg·ha$^{-1}$

(95% CI: 14.4 – 18.9) in 2010. Furthermore, there was a steady decrease in the number of

Smallmouth Bass citations submitted after 2010 (Figure 2; anglers can submit a citation

for any Smallmouth Bass caught that is ≥20 in or ≥5 lbs as part of the VARP). Although

the previous diet study (Brenden et al. 2004) had found that Smallmouth Bass were only

a minor component of Muskellunge diet, managers realized that a substantial increase in

Muskellunge abundance as result of the 42-in MLL might cause or increase intra- and

interspecific competition and force Muskellunge to prey on less-preferred items, such as

Smallmouth Bass.

While it seems unequivocal that high MLLs would lead to an increase in the

abundance of large Muskellunge, there are cases in which high MLLs have proven

ineffective (e.g., Margenau and AveLallemant 2000). 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; Faust et al.
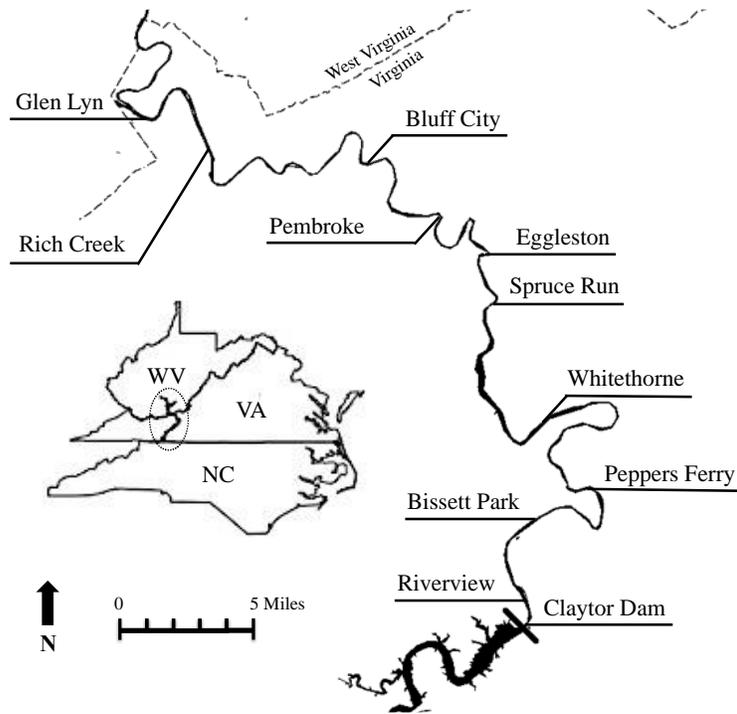
**Figure 1.** Map of the study area and study sites in the New River, Virginia.
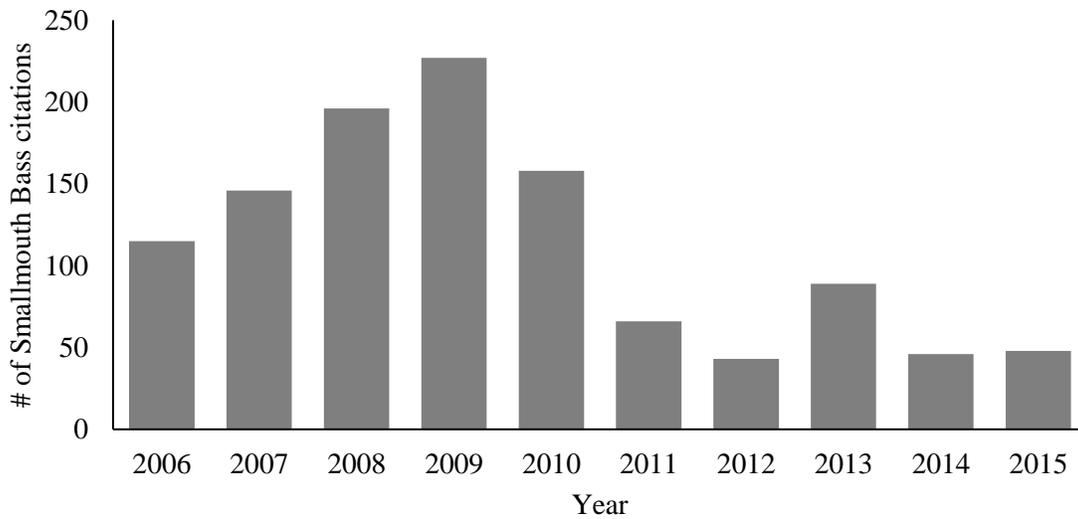


**Figure 2.** The number of Smallmouth Bass citations reported by anglers from 2006 to 2015 to the VDGIF (https://www.dgif.virginia.gov/fishing/trophy-fish/citations, VDGIF 2017). Any Smallmouth Bass caught ≥20 in or 5 lbs can be reported as a citation as part of Virginia's Angler Recognition Program (VARP).

2015). An MLL works best on a population with low recruitment and natural mortality, but a fast growth rate and high fishing mortality (Wilde 1997). For instance, high natural mortality before fish reach an MLL may render the regulation ineffective as few individuals approach harvestable size regardless of fishing mortality. Likewise, few slow-growing fish may ever exceed an MLL, particularly when fishing pressure is high.

Because of differences in population genetics, climate, and prey availability, southern-latitude populations of Muskellunge sometimes exhibit different life histories (i.e., different rates of growth and mortality) than their northern counterparts (Harrison and Hadley 1979; Brenden et al. 2007). Although many trophy Muskellunge fisheries in the northern US and Canada have been successfully developed and maintained using minimum length limits (MLLs), little research has been conducted to determine whether MLLs have the same effectiveness on southern Muskellunge populations that experience different rates of growth and mortality. Furthermore, there have been documented differences in the growth and mortality rates of riverine versus lake populations of Muskellunge, likely due to the availability of forage (Harrison and Hadley 1979).

In addition to providing a case study on predatory interactions and improving fisheries management, Muskellunge in the New River, Virginia, also offer an opportunity for examining whether size-limits are capable of producing trophy Muskellunge fisheries in southern, riverine systems. Lastly, because any future regulatory changes to the Muskellunge fishery will likely raise similar complaints from Smallmouth Bass anglers, understanding how alternative regulations might influence the Muskellunge population and their predation on Smallmouth Bass could help the VDGIF address those complaints before they arise.

Thus, this study consisted of the following objectives:

1. To assess whether the 42-in MLL changed the quality of the New River Muskellunge fishery (i.e., the length, condition, and number of Muskellunge available to anglers);

2. To determine if other size-limit regulations, like a protected-slot limit, might be options for improving quality of the Muskellunge fishery;

3. To assess whether the 42-in MLL altered Muskellunge predation on Smallmouth Bass.

Ultimately, this study describes the current state of Muskellunge and their predation on Smallmouth Bass in the New River, Virginia, and lays the groundwork for making future predictions on how alternative regulations could influence the Muskellunge population and their predation on Smallmouth Bass. I hope that this work will enable the VDGIF and agencies managing similar fisheries to make regulatory decisions regarding the trade-offs between benefits to the target fishery and potential negative consequences on other important fishery species.

# Chapter 1

## Effects of size-limits on fishery quality for a riverine Muskellunge population in the southern US

### Abstract

Although many trophy Muskellunge *Esox masquinongy* fisheries in the northern US and Canada have been successfully developed and maintained using minimum length limits (MLLs), little research has been conducted to determine whether MLLs have the same effect on southern-latitude Muskellunge populations that experience different rates of growth and mortality. Another size-limit regulation, a protected-slot limit (PSL), is a management strategy of growing interest to fisheries managers working with Muskellunge and other large sport fish who have found MLLs unsatisfactory, particularly when MLLs result in 'stockpiled' populations. The use of PSLs on Muskellunge fisheries is still a novel management strategy and little is known about the regulations' performance for Esocids. I investigated the potential of size limits to increase the fishery quality of a southern riverine Muskellunge fishery. The Muskellunge fishery of the New River, Virginia, was managed under a 30-in MLL until 2006, when the MLL was increased to 42 in to increase the abundance of large Muskellunge. To ascertain whether the 42-in MLL improved fishery quality (i.e., the length, condition, and number of Muskellunge available to anglers), I compared size structure, average individual condition, rates of growth and mortality, and catch-per-unit-effort, before (2000-2003) and after (2013-2015) the enactment of the 42-in MLL. I also evaluated the potential of other size-limit regulations to improve fishery quality by modeling the population's size

structure and trophy production under three alternative regulations, including a 40- to 48-in PSL. I found that the 42-in MLL substantially improved the quality of the Muskellunge fishery by increasing both the average size of Muskellunge and the abundance of large individuals. Higher MLLs could further improve fishery quality via trophy production by increasing the survival of Muskellunge to large sizes (i.e., ≥50 in); however, the implementation of such a regulation is unlikely to garner broad angler support in this system. A PSL that results in a somewhat similar size structure to the current (2013-2015) population, while allowing the production of some trophy-sized Muskellunge and reducing the overall number of Muskellunge, may be a more agreeable regulatory option for New River fishery managers.

**Introduction**

Because large predatory fishes are some of the most sought-after sport fishes (Arlinghaus 2006), particularly in North America (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 regulation of harvest by size limits, most notably minimum-length limits (MLLs) (Isermann and Paukert 2010). Under an MLL, fish below the designated minimum size must be released, while fish above the minimum size may be harvested. Although MLLs have been shown to 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; Faust et al. 2015). An MLL works

best on a population with low recruitment and natural mortality, but a fast growth rate

and high fishing mortality (Wilde 1997). For instance, high natural mortality before fish

reach an MLL may render the regulation ineffective as few individuals approach

harvestable size regardless of fishing mortality.  Likewise, few slow-growing fish may

ever exceed an MLL, particularly when fishing pressure is high.

　　Sometimes MLLs result in populations that do not meet management objectives. One

of the most common undesired consequences is an accumulation of fish just below the

minimum size, known as 'stockpiling' (Wilde 1997). Intraspecific competition among

fish below the minimum size increases, growth becomes stunted within the abundant size

class, and condition of fish and quality of the fishery declines. Stockpiling has been

documented in a variety of sportfish (e.g., Largemouth Bass *Micropterus salmoides*,

Carline et al. 1984; Walleyes, 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).

Under a PSL, fish smaller than the specified lower limit and larger than the specified

upper limit may be harvested, while fish within the limits must be released. Similar to an

MLL, the effect of a PSL is dependent on the population's dynamic rates, particularly on

fishing mortality of sub-slot fish (Fayram 2003). A PSL increases the abundance of

protected-size fish by promoting growth of smaller fish (i.e., the stockpiled segment of

the population). This is accomplished by reducing intraspecific competition via angler

harvest of sub-slot individuals (Anderson 1976; Wilde 1997). If voluntary release of sub-

slot fish substantially decreases the number of fish harvested, growth rates may not

increase as anticipated (Fayram 2003). Finally, PSLs tend to perform best on populations with high recruitment and slow growth. Recruitment, growth, and mortality can differ drastically over a species' range; thus, the effect of size-limit regulations (both MLLs and PSLs) will likely also differ (Young et al. 2006). Understanding how population dynamics vary across geographic gradients, and in turn how regulation performance varies, is crucial to effective fisheries management.

Although Muskellunge are indigenous to a few southern systems, such as the Tennessee River, the presence of Muskellunge in many southern systems in 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 sometimes exhibit different life histories (i.e., different rates of growth and mortality) than their northern counterparts (Harrison and Hadley 1979; Brenden et al. 2007). Additionally, in comparison to northern Muskellunge fisheries, southern Muskellunge fisheries tend to have more-liberal harvest regulations (low length limits and high bag limits) (Brenden et al. 2007). As southern Muskellunge fisheries increase in popularity and attract more anglers, managers are acknowledging that such liberal regulations may not produce trophy fisheries. Many trophy Muskellunge fisheries in the northern US and Canada have been successfully developed and maintained with waterbody-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 to 40 in (Cornelius and Margenau 1999). Similarly, in the St. Lawrence River, the average length of Muskellunge increased at least 2.5 inches after a 48-in MLL was implemented (Farrell et al. 2006).

Unfortunately, little research has been conducted to determine whether MLLs would have similar effects on southern Muskellunge fisheries that may function under different rates of growth and mortality than northern Muskellunge fisheries (e.g., Brenden et al. 2007). Additionally, there have been documented differences in the growth and mortality rates of riverine versus lake populations of Muskellunge, likely due to the availability of forage (Harrison and Hadley 1979), and more-extensive research on regulation performance in riverine Muskellunge fisheries may aid managers in selecting effective size-limit regulations.

The New River's Muskellunge fishery in Virginia represents a useful case study for examining whether size limits are capable of producing trophy Muskellunge fisheries in southern, riverine systems. Muskellunge were introduced into the New River in 1968 by the Virginia Department of Game and Inland Fisheries (VDGIF). The VDGIF stocked Muskellunge regularly 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 (i.e., $\geq$50 in) and citation-sized Muskellunge (i.e., $\geq$40 in; a statewide trophy standard set by the VDGIF as part of Virginia's Angler Recognition Program [VARP]) (VDGIF 2004, 2015). Brenden et al. (2007) predicted that under a 45-in MLL, the abundance of memorable-size Muskellunge could nearly double. I hypothesized that the new 42-in MLL improved the quality of the Muskellunge fishery by increasing both the average size of Muskellunge and the abundance of large individuals in the New River. Although fishery quality is also influenced by many non-catch-related factors (e.g., weather and companionship), catch-related factors, such as the size, number, condition, and species of fish caught (in this case Muskellunge), are the aspects of quality that managers can most easily influence and

are the aspects of quality that most management strategies, such as an MLL, aim to change (Anderson 1976; Weithman and Anderson 1978).

Thus, the first objective of this research was to determine whether the 42-in MLL changed the quality of the New River Muskellunge fishery (i.e., the length, condition, and number of Muskellunge available to anglers). To characterize changes in fishery quality I estimated and compared the size structure, average individual condition, rates of growth and mortality, and catch-per-unit-effort before (2000-2003) and after (2013-2015) the enactment of the 42-in MLL. My second objective was to determine if other size-limit regulations might be viable options for improving quality of the Muskellunge fishery. To do this I modeled the Muskellunge population and its trophy production under two alternative MLLs and one alternative PSL.

While other changes to the New River may have also shaped the Muskellunge population—most notably changes in flow management and stocking procedures—we expect the institution of a 42-in MLL to play the largest role. Since the first licensing of Claytor Dam in 1943, there have only been two changes in flow management on the lower New River. The first change was in 1991 when Appalachian Power Company (AEP), the entity responsible for the operation of Claytor Dam, switched from a daily peak-power-production regime throughout the year, to a "levelized" flow regime between 15 April and 15 October (Federal Energy Regulatory Commission [FERC] 2011). Starting in 1991, AEP was also required to meet an average daily flow of at least 750 cfs. Generally, these changes in flow should have provided more consistent habitat availability and may have subsequently influenced the Muskellunge population. Data from the previous study were collected in 2000-2003, giving the Muskellunge population

nine years to adapt to changes in the flow regime. Fish collected during the 2000-2003 sampling period could have gone through an entire life cycle since the change based on maximum ages in Brenden et al. (2007) and in the current study. Thus, these data should be representative of the New River Muskellunge population under a 30-in MLL. The second change in flow management in 2011 was marked by a shift to an average *hourly* flow requirement of 750 cfs in April-November, an average hourly flow requirement of 1000 cfs in December-January, and 1200 cfs in February-March. Additionally, the period of "levelized" flow was expanded to 1 April and 30 November. Overall, these changes provided more consistency in flow and habitat availability. They also provided higher flows in winter months, which better mimicked the river's natural, long-term hydrograph and provided a better base flow for resident fishes (FERC 2011). These 2011 flow management changes may have substantially improved the success of Muskellunge spawning, which typically occurs in March or early April (Parsons 1959). However, these changes have only been in place since the beginning of 2012. Data for this study were collected in 2013-2015, meaning substantial increases in population size structure, as a result of improved spawning, would not be observable until approximately 2017 or 2018 when individuals reached preferred or memorable size (i.e., 38 and 42 in respectively) (based on growth rates from Brenden et al. [2007] and the current study). Additionally, the VDGIF switched to fall stockings of 9-12 in advanced fingerlings in 2007 instead of summer stockings of smaller 4-6 in fingerlings in an attempt to boost survival of stocked young-of-the-year (YOY). 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 stocked fish under the modified stocking procedures would have made it to legal size at the time my data were collected (i.e., 2013-2015) based on the growth rates reported in the Brenden et al. (2007) and those found in the current study. Thus, any positive shifts in size structure or adult Muskellunge density were most likely attributable to the institution of the 42-in MLL.

**Methods**

*Study Site*

The New River originates in North Carolina, and flows northward through Virginia and into West Virginia. There the river joins the Gauley River to form the Kanawha River, which then flows into the Ohio River. I conducted this project on the Virginia portion of the New River, with focus on the lower section of the New River from Claytor Dam to the West Virginia-Virginia state line (Figure 1.1).

I assessed Muskellunge demographics and abundance at seven fixed sites (Figure 1.1). I also sampled several other sites on a less-regular basis for length and age data (i.e., Bissett Park, Peppers Ferry, and Rich Creek, indicated with asterisks in Figure 1.1). 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).
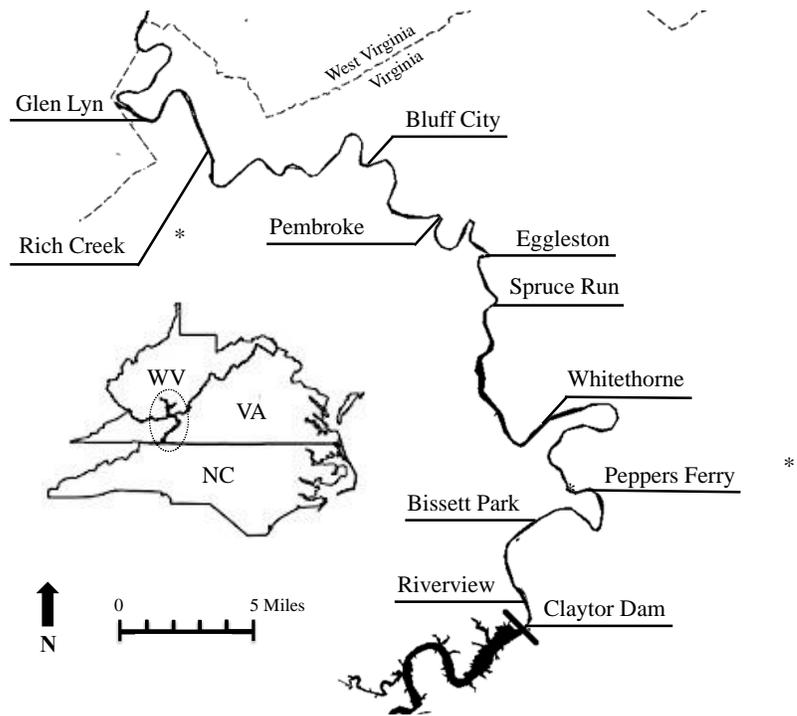
**Figure 1.1.** Map of the study area and study sites in the New River, Virginia. * indicates sites sampled on an irregular basis for length and age data.

*Muskellunge Sampling and Data Collection*

From 2013 to 2015, I conducted a single-pass boat electrofishing survey targeting Muskellunge at each fixed site every one to two weeks during daylight hours from December through June (for a total of 121 surveys). Water levels, accessibility, and boat mobility were best during these months due to higher flows, decreased angler activity, and less vegetation. Duration of surveys were based on the amount of shockable shoreline at the site and varied between 16 minutes and 3 hours, 10 minutes. The electrofishing system was composed of two drop-wire boom-mounted anodes and a Type VI-A electrofisher (Smith Root, Vancouver, Washington, USA) with one netter. I used pulsed-DC output at approximately 4-A and 60 Hz, and sampled along the 3-foot depth contour of the river where Muskellunge could be effectively dipped.

All captured Muskellunge were measured (TL) to the nearest mm and weighed to the nearest 5g 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). If possible, each fish was sexed using the urogenital papilla and surrounding tissue (Lebeau and Pageau 1989). I also obtained additional fin rays and associated length data from a local Muskellunge angler to increase my sample size of large individuals for age-and-growth analyses. All 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.

Growth parameters 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 – 0.75mm) was cut using an Isomet low-speed saw, and each section was then adhered to a glass microscope slide using thermo-adhesive crystal bond. The section was then polished using wetted 300-, 400-, 600-, and 1500-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 Inc., Melville, New York, USA). 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.

*Data Analysis*

I assessed changes in Muskellunge population demographics and abundance (to evaluate changes in fishery quality), by estimating and comparing the size structure, average individual condition, rates of growth and mortality, and catch per unit effort before (2000-2003) and after (2013-2015) enactment of the 42-in MLL.

I calculated size-distribution indices for both datasets (i.e., PSD, PSD-Q, PSD-P, PSD-M, and PSD-T) (Gabelhouse 1984; Neumann et al. 2012). I then compared the resulting size-distribution indices using the confidence-interval approach described by Gustafson (1988). I also compared the pooled length-frequency distributions and mean length of individuals in 2000-2003 to that in 2013-2015 via the Kolmogorov-Smirnov and the Wilcoxon Rank Sum tests, respectively.

To characterize changes in average individual condition, I compared the average relative weight (Wege and Anderson 1978) of Muskellunge within each stock-density

size category in 2000-2003 to that in 2013-2015 using analysis of variance (ANOVA).

Average relative weight was compared by size category due to a significant length-based

trend in the 2013-2015 dataset (Murphy et al. 1991). Relative weight for each individual

was calculated using the appropriate sex-specific equation for Muskellunge if the sex of

the fish was known, or the non-sex-specific equation if the sex of the fish was unknown

(Neumann and Willis 1994).

To compare growth rates before and after the enactment of the 42-in MLL, I

attempted to fit von Bertalanffy growth curves to the 2013-2015 male and female

Muskellunge length-at-age data using nonlinear regression (Isely and Grabowski 2007;

Ogle 2016). These estimates were to be compared with von Bertalanffy growth estimates

($L\infty$, $k$, $t_0$) estimated from the 2000-2003 data. However, after examining plots of

predicted versus actual lengths, the lack of data on old (i.e., >8 years) known-sex

individuals precluded me from estimating growth models that accurately predicted length

for older individuals. As a result, comparisons of growth only refer to individuals

between 2 and 8 years of age. In order to model the Muskellunge population under

alternative size-limit regulations, I decided to re-estimate each growth model (i.e., one for

male and one for female Muskellunge) with a set $L\infty$, and I only estimated parameters $k$

and $t_0$. I calculated $L\infty$ 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. I calculated pseudo $r^2$, which is conceptually similar to the $r^2$

for a linear model (i.e., it measures the amount of variance in the data explained by the

model [Myers 1990]), to contextualize the differences in fit between the sets of growth

parameters.

To test for changes in mortality, I calculated 95% confidence intervals around the 2013-2015 estimates of total mortality and compared those intervals to the estimates in 2000-2003 (Ogle 2016). Total mortality was estimated using 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). I pooled the 2013-2015 catch-at-age data to reduce the influence of any variability in recruitment on mortality estimates (Miranda and Bettoli 2007). Because 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—I elected to fit two catch-curves as suggested by Miranda and Bettoli (2007). One curve was fitted to unexploited fish ages 4-7 and another to exploited fish ages 7-11 (Figure 1.6). Because New River Muskellunge only reach harvestable lengths at ages 7+, I assumed that the catch-curve regression for fish ages 4-7 represented mortality primarily from natural causes, while the second catch curve that was 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 represented fish that had become fully vulnerable to the electrofishing gear (Ogle 2016; Miranda and Bettoli 2007). Because the sample size and corresponding degrees of freedom were so few after splitting the catch curve, I also calculated mortality using the Robson and Chapman maximum-likelihood method (Robson and Chapman 1961) for comparison to both 2013-2015 mortalities calculated from catch curves and mortalities estimated in 2000-2003.

To characterize changes in the relative abundance of Muskellunge, I analyzed catch-per-unit-effort (CPUE) data (an index of relative abundance) of all individuals from regular electrofishing surveys in 2000-2015 using negative binomial regression. I also fit a separate negative binomial regression on CPUE data for Muskellunge ≥ 42 in to investigate potential changes in the relative abundance of large Muskellunge.

*Population Modeling under Alternative Fishery Regulations*

To determine if alternative regulations could improve the quality of the Muskellunge fishery, sex-specific growth estimates ($L_\infty$, $k$, $t_0$) and length-weight relationships from 2013-2015 were used as inputs to the Fisheries Analyses and Modeling Simulator (FAMS, Slipke and Maceina 2014), and the Muskellunge population was modeled under various alternative size-limit regulations. Using the dynamic pool model in FAMS, I 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 regulations' ability to increase the size and abundance of large sport fish (e.g., Cornelius and Margenau 1999; Luecke et al. 1994), as well as what might be feasibly implemented by the managing agency. In order to account for possible changes in mortality under alternative regulations, 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 fish ages 4-7) and was set at 0.1. Each model was run for 100 years so that the results would represent a population in steady-state condition. The results from those runs were averaged and compared. Female and male Muskellunge were modeled separately due to differences in growth and the age-related onset of fishing mortality, but results were combined in the

final result for each regulation. Models were conducted with an initial population size of 1000 fish per sex and variable recruitment, with every other year considered a "strong" year (i.e., twice the average of 1000 recruits). The variable recruitment option was selected based on alternate year stocking conducted by the VDGIF from 2005-2011. I 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 might best increase fishery quality.

**Results**

In 2013-2015 I captured a total of 528 Muskellunge from the New River (from Claytor Dam to the Virginia-West Virginia state line) for which the sex ratio was nearly equal (female 51%; male 49%). I captured individuals ranging 10-49 in and 1-11 years of age (Table 1.1). I received information on 48 individual Muskellunge from the cooperating angler, and those individuals ranged 40-52 in and 4-12 years of age (Table 1.1).

*Population Changes*

The length-frequency distribution of Muskellunge in 2013-2015 showed greater proportions of large individuals than in 2000-2003, particularly for Muskellunge ≥42 in (Kolmogorov-Smirnov test; $p < 0.0001$; Figure 1.2). The average length of Muskellunge also increased from 28.1 to 33.0 inches (Wilcoxon Rank Sum test; $p < 0.0001$). This positive shift in size structure was also evident in the current (2013-2015) population's

| Age | Collection Method | |
| :-: | :-: | :-: |
| | Boat Electrofishing Surveys | Angled |
| 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 |

**Table 1.1** Age distribution of Muskellunge captured during boat electrofishing surveys and age distribution of angled Muskellunge.

Dates sampled: 2000 - 2003
n = 237
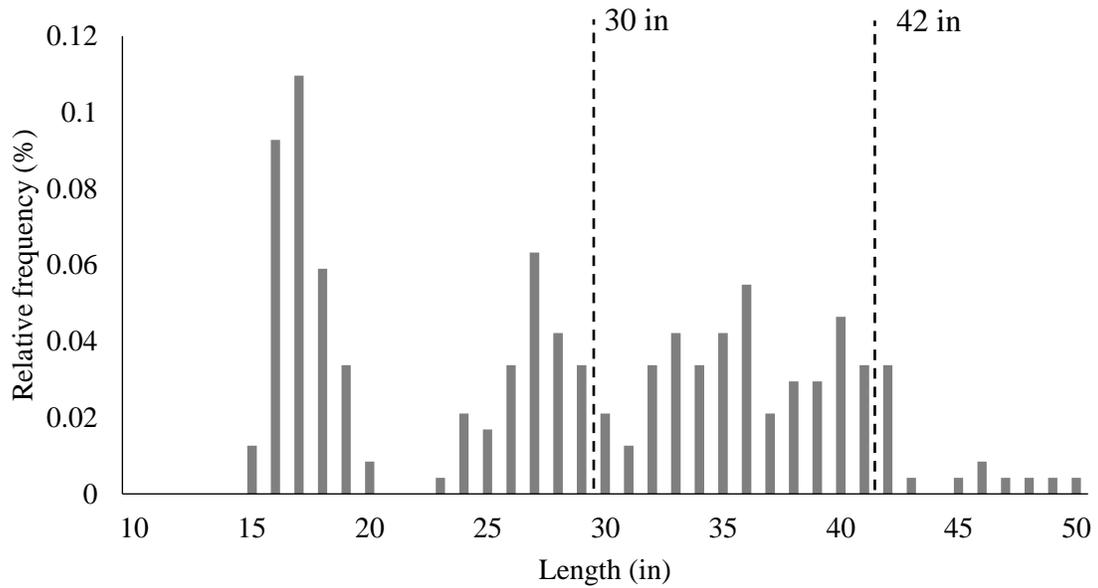
Dates sampled: 2013 - 2015
n = 558
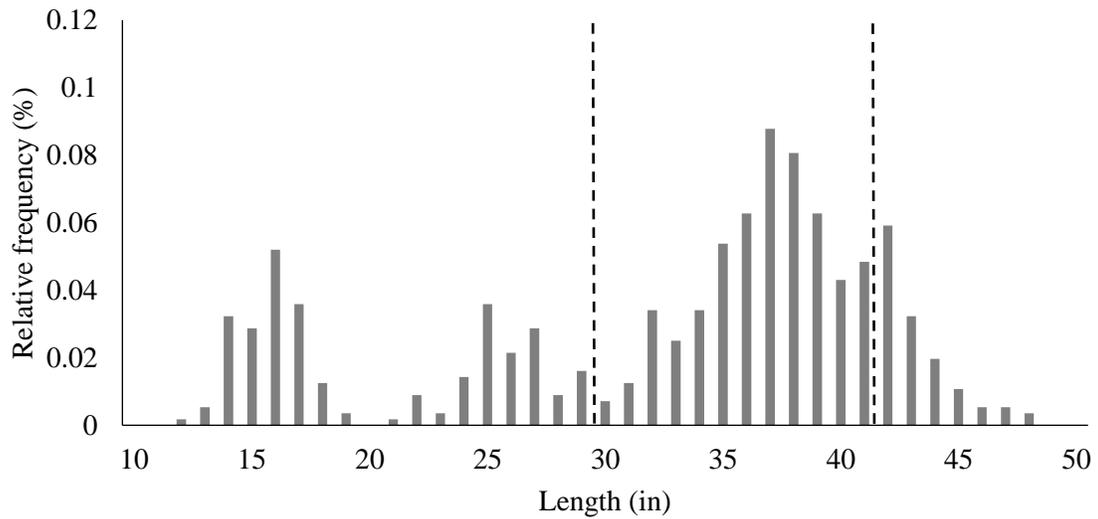
**Figure 1.2**. Length-frequency distributions for the New River Muskellunge population under the 30-in MLL (top) and the 42-in MLL (bottom). Dashed lines mark the 30- and 42-in MLLs. Data are from Brenden et al. (2004; top) and this study (bottom).

mean length and size-distribution indices (i.e., PSD, PSD-P, and PSD-M), all of which increased substantially since the last systematic sampling in 2000-2003 (Table 1.2).

The average condition of Muskellunge, as measured by relative weight, decreased significantly between 2000-2003 and 2013-2015 across all size classes (Figure 1.3). Reduced condition was especially noticeable for preferred- (≥38 in) and memorable-size (≥42 in) Muskellunge.

Growth of fish between 2 and 8 years of age appeared slightly reduced in 2013-2015 compared to that in 2000-2003 (Figure 1.4). Both male and female Muskellunge in 2013-2015 generally needed an additional year to reach citation or memorable size. However, only the $k$ parameter was significantly different between the sampling periods for both male and female Muskellunge.

Estimated annual mortality ($A$) of young Muskellunge below the length limit during 2013-2015 (i.e., ages 4-7 under the 42-in MLL) was similar to that estimated for 'illegal' fish in 2000-2003 (i.e., ages 1-4 under the 30-in MLL) (Figures 1.5 and 1.6). Estimates of annual mortality for legal-size fish demonstrated a substantial increase from 2000-2003 to 2013-2016 (Figures 1.5 and 1.6). Generally, the Robson-Chapman method produced higher and more precise estimates of mortality compared to those produced from catch curves. Estimates of annual mortality were similar between the two methods for older, legal fish, but the Robson-Chapman method estimated much higher annual mortality for younger, sublegal Muskellunge. Despite absolute differences in the estimates (i.e., the actual values), the general trends between the sets of mortality estimates were the same (e.g., mortality of legal fish increased using the both methods).

| Harvest regulation (dates instituted) | Dates sampled | PSD | PSD-P | PSD-M |
|---|---|---|---|---|
| 30-in MLL (1980 – 2006) | 2000 – 2003 | 65 (58 – 72) | 26 (20 – 32) | 5 (2 - 8) |
| 42-in MLL (2006 – 2016) | 2013 – 2015 | 84 (81 – 87) | 42 (38 – 46) | 16 (13 – 19) |

**Table 1.2.** Proportional size distribution (Neumann et al. 2012) values (and 90% confidence intervals) for the New River, Virginia Muskellunge population sampled under two different harvest regulations (MLL = minimum length limit).
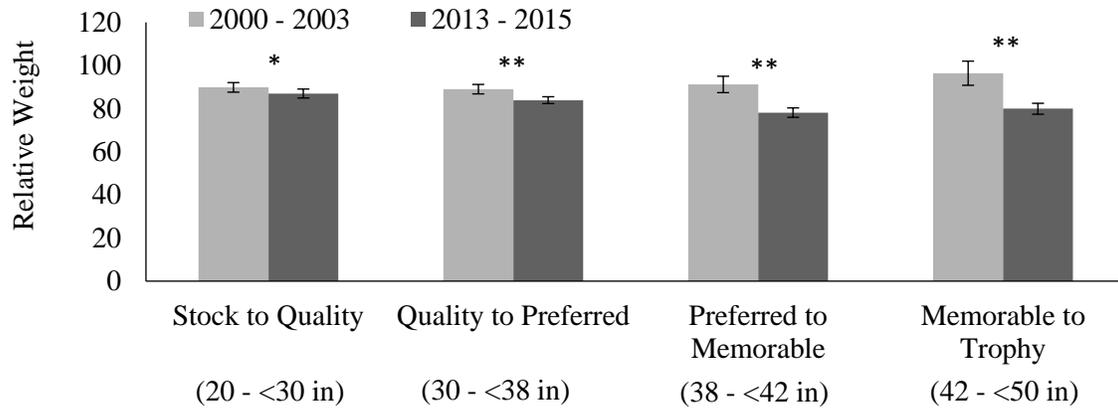
**Figure 1.3.** Average relative weight by stock-density length category for New River Muskellunge captured with boat-electroshocking surveys before (2000-2003) and after (2013-2015) the 42-in MLL. Average condition in 2013-2015 was significantly lower than the corresponding average condition in 2000-2003 regardless of size (ANOVA; $P \leq 0.05^*$, $P \leq 0.0001^{**}$).
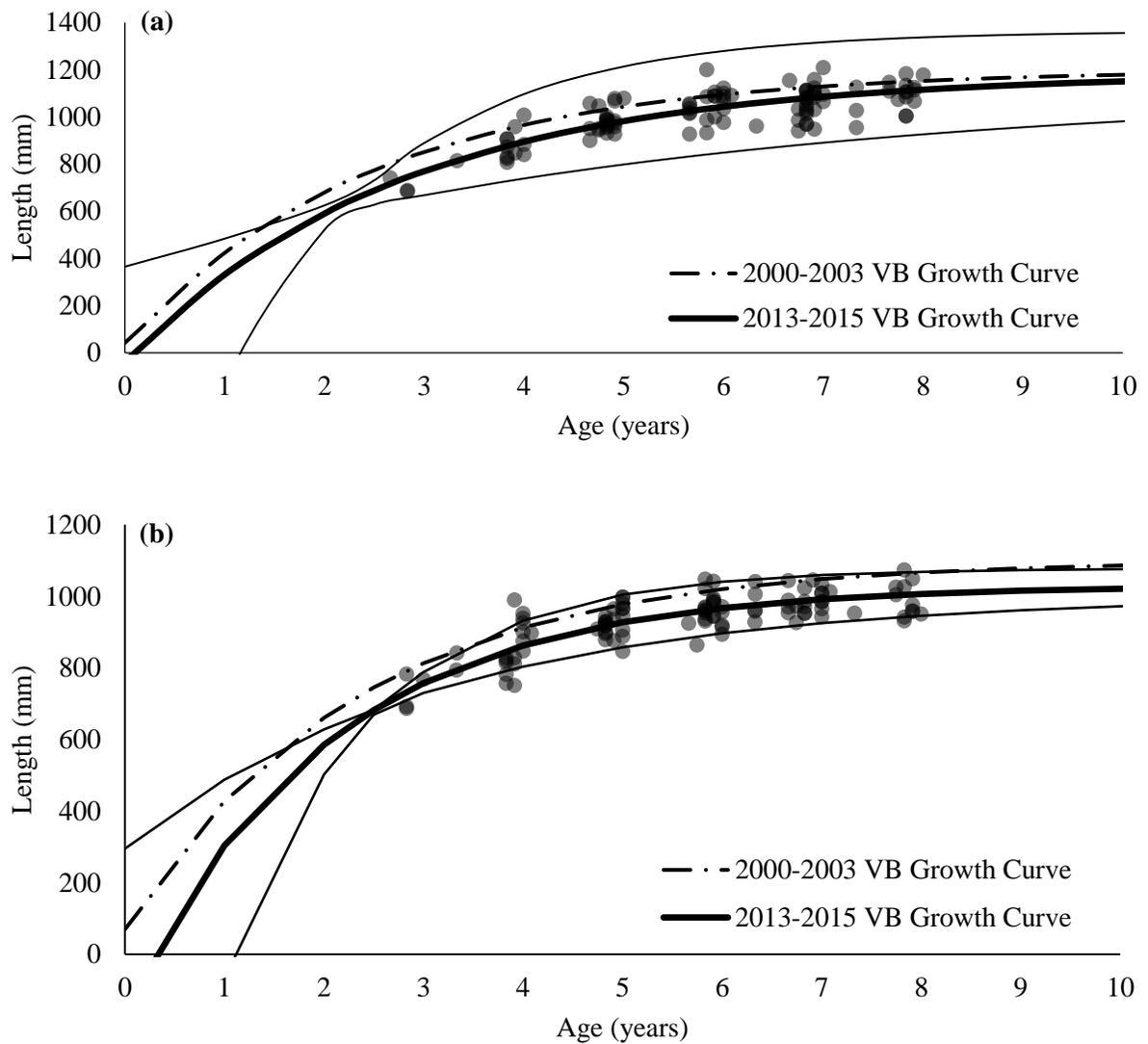
**Figure 1.4.** Fitted von Bertlanffy growth curves (and 95% confidence intervals) for female **(a)** and male **(b)** Muskellunge in 2000-2003 and 2013-2015. Data shown is for Muskellunge sampled in 2013-2015 under the 42-in MLL. Growth curves were fit using nonlinear regression.
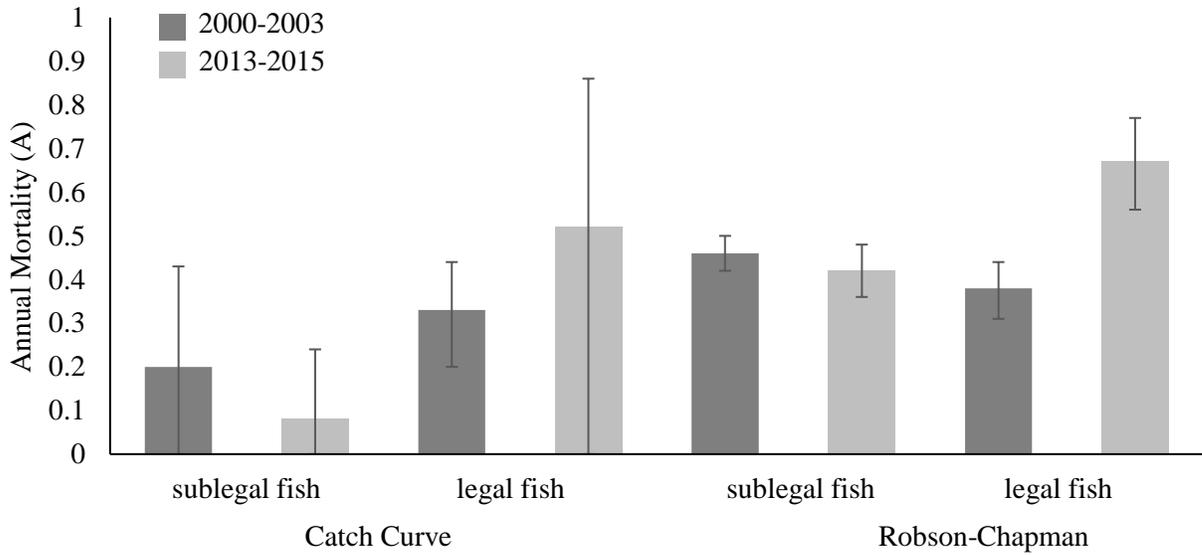
**Figure 1.5** Estimates of annual mortality for sublegal and legal-sized Muskellunge in 2000-2003 (dark grey) and in 2013-2015 (light grey). Annual mortality estimates were calculated using catch-curve regression on the left, and using the Robson-Chapman method on the right.
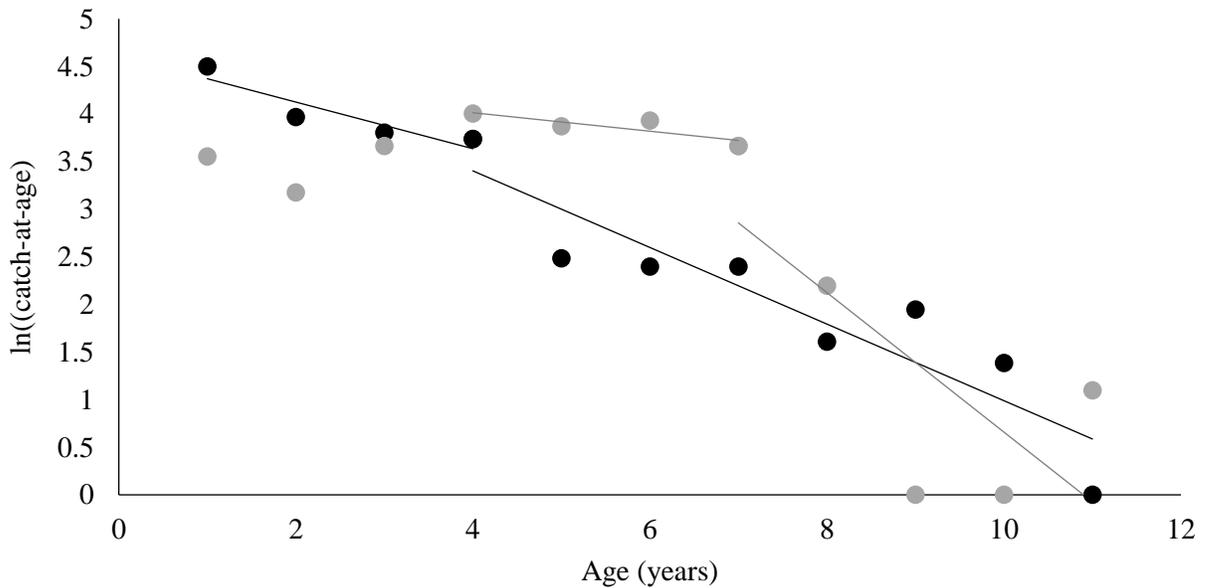


**Figure 1.6** Catch curves fit for New River Muskellunge caught boat electrofishing in 2000-2003 (black) and in 2013-2015 (grey). Separate catch-curve regressions were fit to catch of sublegal and legal sized fish (30 and 42 in during 2000-2003 and 2013-2015 respectively).

CPUE for 2000-2015 revealed a significant increase in the total relative abundance of all Muskellunge (negative binomial regression, regression coefficient = 0.07975, $df$ = 354, $p < 0.0001$, Figure 1.7a) and of large Muskellunge ($\geq$42 in) (negative binomial regression, regression coefficient = 0.16130, $df$ = 354, $p < 0.0001$, Figure 1.7b). These increases corroborate increased density estimates for adult Muskellunge calculated from VDGIF depletion catch-and-effort data (Chapter 2).

*Evaluating Alternative Regulations*

Of the four regulatory scenarios evaluated, a 48-in MLL increased PSD-T the most, regardless of fishing mortality (Figure 1.8a). The 42-in MLL and the 40- to 48-in PSL performed similarly across different levels of fishing mortality for 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 (kg harvested by anglers) was highest under the 38- and 42-in MLLs under high rates of fishing mortality (Figure 1.8b) 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 1.8b). 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 1.8c).

**Discussion**

*The New River Muskellunge Population under Current Regulations*

The 42-in MLL substantially increased the quality of the New River's Muskellunge fishery by increasing the average length and abundance of large individuals. Increasing the MLL from 30 to 42 in reduced mortality for sublegal Muskellunge and increased the
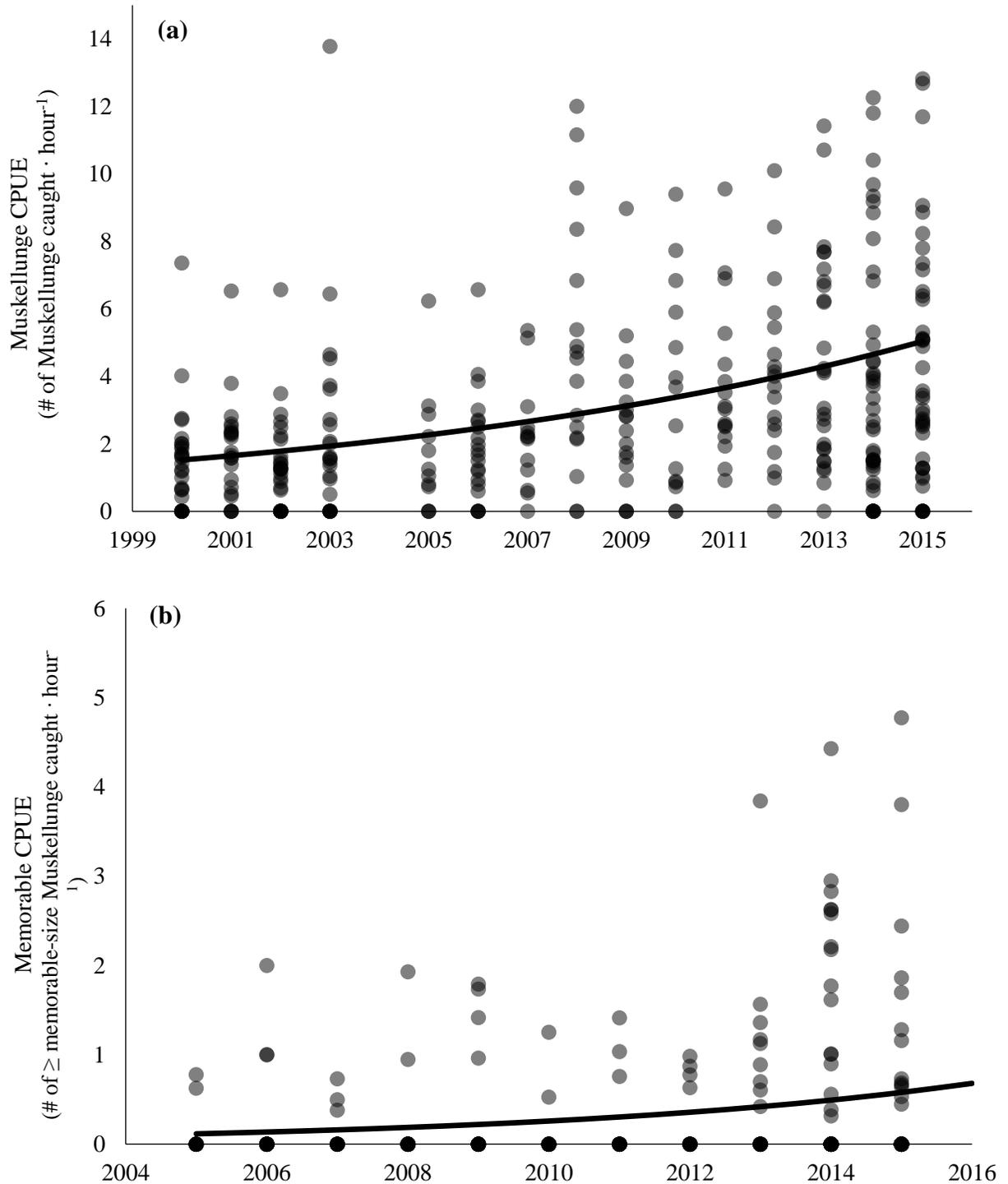
**Figure 1.7.** CPUE data for all Muskellunge **(a)** and for memorable-sized Muskellunge (i.e., $\geq$42 in; **(b)**) from electrofishing surveys in 2000-2015. Length-specific CPUE data was only available beginning in 2005. Data points are partially transparent so CPUE data of the same value can be seen (e.g., there were multiple days each year with CPUEs of zero Muskellunge caught · hour$^{-1}$; thus, those data points appear darker). CPUE data was analyzed using negative binomial regression.
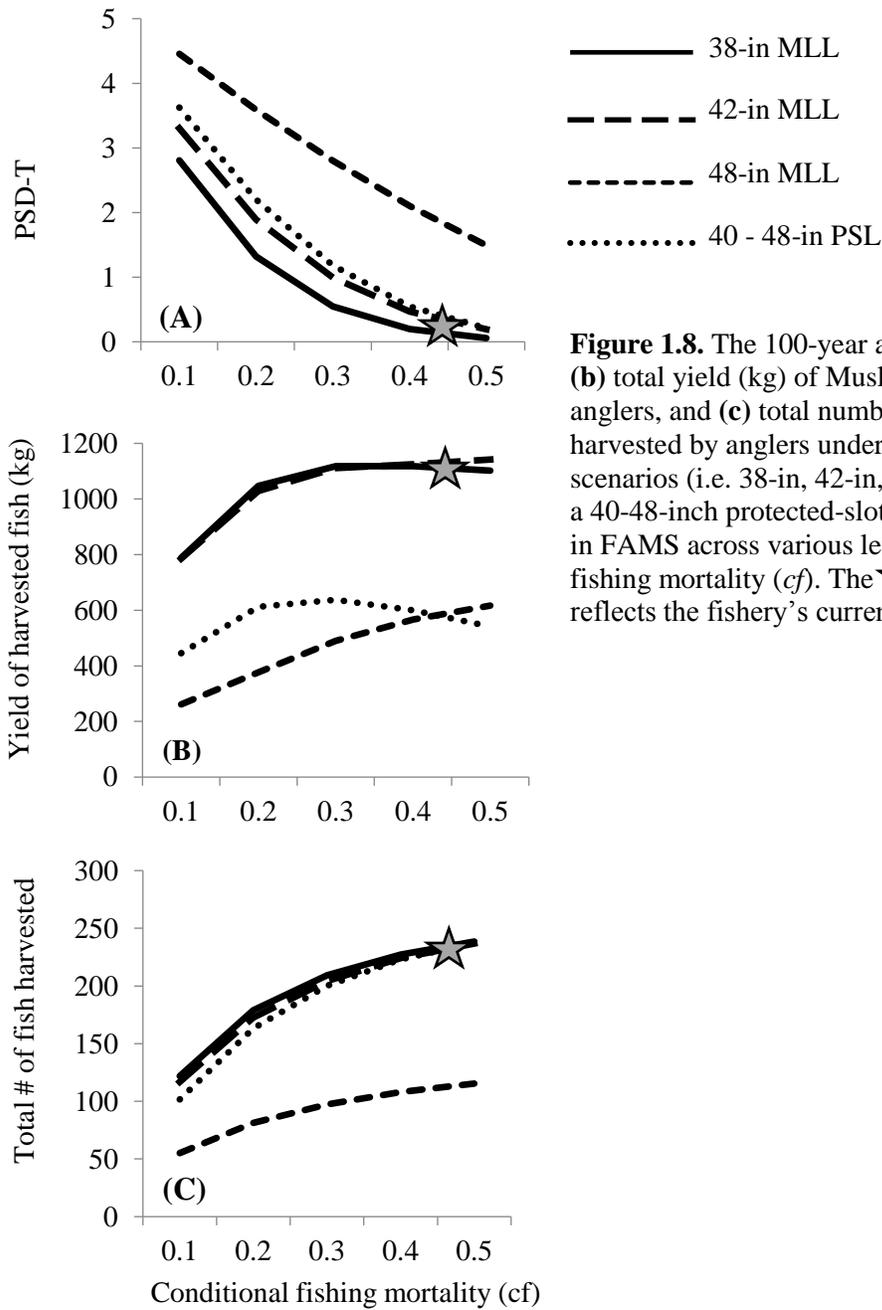
**Figure 1.8.** The 100-year average of **(a)** PSD-T, **(b)** total yield (kg) of Muskellunge harvested by anglers, and **(c)** total number of Muskellunge harvested by anglers under the four regulatory scenarios (i.e. 38-in, 42-in, and 48-in MLLs and a 40-48-inch protected-slot limit (PSL) modeled in FAMS across various levels of conditional fishing mortality (*cf*). The ★ in each panel reflects the fishery's current state.

recruitment of individuals to large size classes as demonstrated by the increase in abundance of individuals ≥42 in. Additionally, lower mortality for sublegal Muskellunge likely increased the number of spawning opportunities for individual 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, many Muskellunge were harvested before reaching sexual maturity. The delay of mortality under the 42-in MLL (Figure 1.6) provided Muskellunge more time to reach sexual maturity, to spawn, and to contribute to the overall standing stock of Muskellunge. The increase in abundance of large individuals and consequent positive shift in population size structure provide evidence for the positive effects of raising MLLs for Muskellunge, and corroborate earlier predictions made regarding the New River's Muskellunge population under a higher MLL (Brenden et al. 2007). The average condition (as measured by relative weight $W_r$) of large Muskellunge in the lower New River has declined. Reduced growth rate and condition as a result of stockpiled fish just below the length limit are common concerns of fisheries managers following the implementation of an MLL (Brousseau and Armstrong 1987; Noble and Jones 1993; Stone and Lott 2002). Estimates of adult Muskellunge density (calculated and discussed in chapter 2), declines in average condition, and visual inspection of the 2013-2015 length-frequency distribution, provide evidence for possible stockpiling of New River Muskellunge between 35 and 40 in. This size class (i.e., preferred) has the lowest average $W_r$, and mortality seems to increase dramatically at the larger end of this size class, likely due to fish becoming vulnerable to harvest. As fisheries biologists refine management of this Muskellunge population, care should be taken to monitor the relative weights of Muskellunge below the current 42-in MLL,

below any alternative MLL, or within any alternative PSL, to avoid stockpiling. Additionally, measures should be taken to increase the condition and survival of these fish if stockpiling continues to diminish those characteristics.

Reduced growth rate ($k$) following an increase in the MLL is not unusual. For instance, Muskellunge growth rate in a northern Wisconsin Lake exhibited a strong negative relationship with male Muskellunge density (Hanson 1986). Declines in the growth rate of large fish under an increased MLL are usually attributed to increased intraspecific competition and the division of forage between more individuals (Anderson 1976; Wilde 1997). With densities estimated in the New River as high as four Muskellunge per ha in some areas (J. Copeland, VDGIF, personal communication), a reduction in growth rate as a result of intraspecific competition is possible, particularly for large Muskellunge. The fact that large Muskellunge (≥42 in) also exhibited the greatest decrease in average condition compared to other size classes of Muskellunge also provides evidence for possible intraspecific competition. Accordingly, a companion study (Chapter 2) found evidence of small shifts in the importance of various prey items in the diet of adult Muskellunge—especially catostomids—which could be indicative of increased competition for forage.

My estimate of total mortality for older, legal Muskellunge was substantially higher than that estimated in 2003. 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), and angler survey data collected by the VDGIF shows 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 my recent sampling, some fish (and related size classes) that I sampled were susceptible to harvest under the 30-in MLL. Thus, the catch curve fit to fish ages 7+ represents a transition between the 30 and 42-in MLLs. In the future, a catch curve fit to fish age 7+ might yield a lower estimate of total mortality when older and larger classes of fish have matured under lifelong influence of the new MLL. Furthermore, older fish were the most difficult to age and the samples on which my aging team was least likely to reach consensus. Thus, my estimate of mortality may be biased higher from the inherent difficulty in aging older fish and my exclusion of some older fish from the analysis. Because mortality can drastically influence a regulation's effectiveness, monitoring Muskellunge mortality will be critical. Future management decisions should take full measure of the inevitable multi-way interactions between regulations, mortality, and various measures of fishery quality.

*The Muskellunge Fishery under Alternative Regulations*

Of the regulations modeled, the 48-in MLL would likely increase the population's trophy production the most, which corroborates other findings regarding the effects of instituting high MLLs on Muskellunge fisheries (Cornelius and Margenau 1999; Kerr 2007). If trophy production is a management agency's only or primary goal, then implementing a high MLL is the most sensible regulatory option. However, fishery quality is defined by many factors in addition to trophy production, including catch rate and individual condition of angled fish. Under the 42-in MLL, the New River

Muskellunge population demonstrated symptoms of stockpiling and mixed changes in measures of fishery quality. While any regulation change that increases the MLL may indeed increase production of fish that reach trophy length (and thus related measures of fishery quality), stockpiling and low condition would likely be similarly evident just below the new MLL. Under the 40- to 48-in PSL, the current stockpiled size class (35-40 in) would be subject to harvest, which should promote growth out of that size class as intraspecific competition is reduced (assuming anglers harvest sub-slot fish). However, the 40- to 48-in PSL did not increase trophy production (i.e., PSD-T) as much as the 48-in MLL. The PSL demonstrated only limited trophy production under low fishing mortalities (i.e., $cf \leq 0.2$). But if fishing mortality under the PSL were to decrease to such low levels (i.e., cf <0.2), PSD-T would still increase compared to the current state due to high fishing mortality under the 42-in MLL.

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 Smallmouth Bass anglers feel strongly that increasing the number of Muskellunge will reduce the quality of the bass fishery, and thus a higher MLL directly aimed at increasing the abundance of large Muskellunge would probably be poorly received. A 40- to 48-in PSL may mitigate the fears of Smallmouth Bass anglers. While the PSL would likely increase average condition and the proportion of large Muskellunge in the population, the overall number and density of Muskellunge would likely decrease as smaller Muskellunge were exposed to harvest and the population was effectively "thinned out."

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 rates and condition of

some size classes. Additionally, the stated goal of achieving trophy size ($\geq$50 in)

Muskellunge has yet to be achieved. A PSL has the potential to help managers achieve

the trophy-oriented goal without sacrificing growth rate and condition, both of which are

often considered measures of management effectiveness and efficiency.

Protected-slot limits are still a novel approach to managing Muskellunge, and esocids

in general, and have only been implemented and studied in a handful of places, typically

in Northern Pike 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

protected-slot limits showed considerable increases in size structure with increased

proportions of fish $\geq$24 in (Pierce 2010). However, the remaining lakes demonstrated

little to no improvement in size structure. Movement between water bodies and angler

non-compliance were both cited as possible causes for the regulations' failure in the two

lakes demonstrating limited or no improvement in size structure. Ultimately, more long-

term, empirical research is needed to identify the effects and potential pitfalls of PSLs on

large sport fish such as Muskellunge.

The ability of any length-related harvest restriction (MLL or PSL) to improve fishery

quality will at least partially depend on the level of fishing mortality experienced by the

population, as demonstrated by the declining trends in PSD-T with increasing fishing

mortality in my models (Figure 1.8a). With PSLs, managers should take precautions to

prevent harvest rates that may inadvertently overexploit a fishery rather than simply

reduce the abundance of smaller size classes. In this case, it may behoove managers to

limit the harvest of newly vulnerable smaller fish until mortality under the new regulation

can be estimated. Managers can limit such harvest using possession or bag limits, or closed seasons.

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. 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). While this has not been directly documented for Muskellunge, it has been documented in Northern Pike (Griffiths et al. 2004; Blanck and Lamouroux 2007). Additionally, competing angler interests may dissuade managers from setting regulations with the highest predicted trophy production; and excessive harvest of large individuals, as can be common in 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). The recognition of system-specific constraints on trophy potential for Muskellunge and other sport fishes has led to a growing emphasis on specific regulations for individual water bodies and populations (Radomski et al. 2001), 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, I strongly urge that management objectives be constructed with system-specific constraints in mind.

This study demonstrated a substantial improvement in some measures of Muskellunge fishery quality as a result of the 42-in MLL, and provided evidence that a

higher MLL would likely further improve fishery quality and trophy production. Although a higher MLL may not be a regulatory option available to managers due to social constraints, my modeling showed that a PSL might be a more agreeable regulatory option that might promote higher trophy production than the current regulation. While a high MLL or PSL may accomplish VDGIF objectives for the Muskellunge fishery, their ability to increase trophy production relies on maintaining low mortality, and the VDGIF should carefully monitor mortality and the Muskellunge population to ensure a 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.

# Chapter 2

## Increasing Muskellunge abundance in the New River, Virginia and the implications for predation on Smallmouth Bass

### Abstract

The possibility of predation between sport fishes has incited many bitter conflicts between angler groups and fisheries managers. In North America, Europe, and Asia, esocids in particular are often at the center of these conflicts because of their reputation as predators that alter prey fish populations. The stocking of Muskellunge *Esox masquinongy* in the New River, Virginia, created such tension in the angling community, particularly related to potential predation on Smallmouth Bass *Micropterus dolomieu*. Although Smallmouth Bass had previously been shown to compose only a minor part of Muskellunge diet in this system (i.e., 4% based on % wet weight for an average Muskellunge), bass anglers feared that a substantial increase in Muskellunge abundance following the institution of a 42-in minimum length limit might increase the effect Muskellunge have on Smallmouth Bass. The purpose of this study was to determine if the regulation altered Muskellunge predation on Smallmouth Bass. I assessed changes in (i) the Muskellunge population, (ii) the importance of Smallmouth Bass in Muskellunge diet, and (iii) the overall consumption of Smallmouth Bass. To achieve these objectives, Muskellunge growth, density, population structure, and food habits were examined and combined with bioenergetics modeling. While growth of individual Muskellunge was somewhat slower, I found substantial increases in both the density of adult Muskellunge and size structure since the institution of the 42-in MLL. Despite these increases in

density and size structure, my modeling did not indicate any notable increase in the consumption of Smallmouth Bass. This seems largely due to the fact that Smallmouth Bass continue to be a small component of Muskellunge diet overall and within various size classes of Muskellunge. Muskellunge likely play a small role in shaping Smallmouth Bass population dynamics and production in the New River; however, a fuller understanding of this role would be enabled by a detailed study of Smallmouth Bass production and the myriad factors influencing it.

**Introduction**

The management of a recreational fishery composed of multiple sport fishes can pose a challenge to managers, as they must seek to maintain the ecological balance of the system and the satisfaction of different angler groups who may have competing interests. The presence or perceived presence of predatory interactions between sport fishes is a common issue that has incited many bitter conflicts between angler groups and between anglers and fisheries managers (e.g., Churchill et al. 2002). This type of conflict is especially prevalent in fisheries involving several top-level predators. Large predatory fishes have the potential to alter the size structure and dynamics of prey fish populations, eliminate species, and drastically change aquatic communities (He and Kitchell 1990). The ability of predatory fishes to wield such ecological influence often generates fear— and sometimes hatred—towards predator populations and the fisheries they support. Fisheries managers must understand how interactions between sport fishes, real or perceived, affect anglers' perceptions of species, and develop their understanding of the

occurring biological interactions to educate anglers and appropriately address concerns and conflicts.

   Esocids, and Muskellunge *Esox masquinongy* in particular, have long held a reputation amongst anglers as "voracious predators" (Goddard and Redmond 1978; Cook and Solomon 1987). Esocids have been blamed by anglers for altering many sport fish populations—Smallmouth Bass *Micropterus dolomieu*, Largemouth Bass *Micropterus salmoides*, Walleye *Sander vitreus*, Black Crappie *Pomoxis nigromaculatus*, and Yellow Perch *Perca flavescens*. But scientific evidence identifying negative predatory impacts of Muskellunge (and of other esocids) on other sport fishes is generally lacking. For instance, angler concern about the effects that introduced Muskellunge might have on other sport fishes prompted the Minnesota Department of Natural Resources (MDNR) to evaluate responses in abundance of seven sport fish populations after Muskellunge introduction. The MDNR found no consistent changes in the relative abundance of Northern Pike, Walleye, Yellow Perch, Bluegill *Lepomis macrochirus*, Black Crappie, White Sucker *Catostomus commersonii*, or Cisco *Coregonus artedi* in 41 lakes following Muskellunge introduction (Knapp et al. 2012). There was similar concern regarding the effects Muskellunge might have on Largemouth Bass in several Illinois lakes, but Muskellunge were found to exhibit little predation on Largemouth Bass *Micropterus salmoides* or other game species (Wolter et al 2012). Walleye and bass species *Micropterus spp.* were also not important parts of Muskellunge diets in Pennsylvania (Woomer et al. 2012) and Wisconsin (Frey 2003). Furthermore, many sympatric populations of Muskellunge and other sport fishes, such as Smallmouth Bass and Walleye, exist naturally and support successful fisheries with seemingly little conflict

(Kerr 2016). With the exception of salmonids (trout and salmon), there is very little research demonstrating that sport fish are substantial components of Muskellunge diet.

The cases in which Muskellunge have been shown to impact other sport fishes via direct predation (e.g., Yellow Perch, Maloney and Schupp 1977; Largemouth Bass, Gammon and Hasler 1965; Walleye, Gaeta et al. 2015) are few and are thought to have resulted from insufficient availability of preferred forage. Muskellunge generally prefer soft-rayed fishes, such as catostomids, cyprinids, and shad *Dorosoma spp.,* but predation on less-preferred species has been documented during periods of insufficient preferred forage (Kerr 2016). For example, predation on game species, such as Largemouth Bass, was higher during years of low Gizzard Shad *Dorosoma cepedianum* abundance in several Illinois lakes (Wolter et al. 2012). While fluctuations in the abundance and availability of preferred forage seem correlated with consumption of less-preferred prey, fluctuations in predator abundance are likely equally important. As the abundance of predators increases, available forage must be split between more individuals, and the potential for competition increases. As competition for preferred forage increases, predators may fill voids in their diets with less-preferred species. Although the effects of increased esocid abundance have been examined in terms of 'stunting,' mortality, and reduced condition of Muskellunge and Northern Pike (e.g., MDNR 1983; Diana 1987; Cornelius and Margenau 1999), little research has been conducted on the related implications of increased esocid abundance on diet composition. Thus, there is a limited understanding on how changes in diet composition prompted by increased competition might alter the overall impact that Muskellunge or Northern Pike have on other sport fishes.

An opportunity to improve understanding on how potential changes in diet composition might alter the impact that Muskellunge predation has on other sport fish is presented in the New River, Virginia. The Virginia Department of Game and Inland Fisheries (VDGIF) first introduced Muskellunge into the New River in 1968 and annually stocked the predator in the summer months as 4-6-in fingerlings from 1982 to 2003. During this period the Muskellunge fishery began to develop and was managed under a 30-in minimum length limit (MLL) and a bag limit of two fish per day (Brenden et al. 2007). As the Muskellunge fishery developed, anglers supporting the New River's most-popular sport fishery—Smallmouth Bass—complained that large Muskellunge were preying on Smallmouth Bass and impacting the quality of the bass fishery. The VDGIF addressed these concerns by conducting a 3-year diet study and found that Smallmouth Bass represent only 4% (based on average % wet weight per individual) of prey consumed by Muskellunge (Brenden et al. 2004). Bioenergetics modeling based on that study concluded that annual consumption of Smallmouth Bass was only about 0.9 kg·ha$^{-1}$·yr$^{-1}$ (Brenden et al. 2004). Annual production of Smallmouth Bass, which represents the biomass that can be removed from a population without affecting the long-term standing stock (Ney 1990), had been estimated in other parts of the New River at 32.1 kg·ha$^{-1}$·yr$^{-1}$ (Roell and Orth 1993). Thus, it was concluded that Muskellunge predation would not exert a significant effect on the Smallmouth Bass population (Brenden et al. 2004). Because annual electroshocking data indicated that the Muskellunge population was growing, in 2004 the VDGIF elected to initiate a biennial stocking schedule that would allow assessment of natural reproduction. The VDGIF also switched to fall stockings of 9-12-in advanced fingerlings instead of summer stockings of younger 4-6-in fingerlings,

in an attempt to boost the survival of stocked young of the year. In 2012, the agency

discontinued stocking. Based on the prevalence of young-of-the-year Muskellunge

following years without stocking, natural reproduction was deemed enough to sustain the

Muskellunge population (J. Williams, VDGIF, personal communication). In 2006 the

VDGIF increased the MLL for Muskellunge from 30 to 42 in and decreased the bag limit

from two to one fish per day to promote the production of trophy- ($\geq$50 in) and citation-

sized ($\geq$40 in; a statewide trophy standard set by the VDGIF as part of the agency's

angler recognition program) Muskellunge. In the years following the regulation change,

Smallmouth Bass anglers again voiced complaints that the growing numbers of large

Muskellunge were lowering their catch rates and reducing the quality of the Smallmouth

Bass fishery. These declines were corroborated by some site-specific biomass estimates

of Smallmouth Bass that demonstrated substantial declines from 2005 to 2010. For

example, Smallmouth Bass biomass at the Whitethorne site (see Figure 1 in thesis

introduction, page 5) exhibited a 40% decrease from 27.2 kg·ha$^{-1}$ (95% CI: 25.9 – 28.7)

in 2005 to 16.3 kg·ha$^{-1}$ (95% CI: 14.4 – 18.9) in 2010. Furthermore, there was a steady

decrease in the number of Smallmouth Bass citations submitted after 2010 (see Figure 2

in thesis introduction, page 5; anglers can submit a citation for any Smallmouth Bass

caught that is $\geq$20 in or $\geq$5 lbs as part of the Virginia Angler Recognition Program

[VARP]; VDGIF 2017). Although the previous diet study had found the Smallmouth

Bass were not an integral part of Muskellunge diet, managers realized that a substantial

increase in Muskellunge abundance warranted a new study. An increase in Muskellunge

abundance might cause intraspecific competition and force Muskellunge to prey on less-

preferred items, such as Smallmouth Bass.

Given the potential of a larger Muskellunge population to alter the New River's Smallmouth Bass fishery, the purpose of this study was to determine if the regulation change altered Muskellunge predation on Smallmouth Bass. Our objectives were to assess changes in: (i) Muskellunge population structure, density, and body growth; (ii) the importance of Smallmouth Bass to Muskellunge diets; and (iii) consumption of Smallmouth Bass by the Muskellunge population. To accomplish these objectives, Muskellunge growth, density, population structure, and food habits were examined and combined with bioenergetics modeling.

**Methods**

*Study Site*

The New River begins in North Carolina, and flows northwards through Virginia and into West Virginia. There the New River joins the Gauley River to form the Kanawha River, which flows into the Ohio River. I conducted this project on the Virginia portion of the New River, with primary focus on the Muskellunge population in the lower section of the New River from Claytor Dam to the West Virginia-Virginia state line (~62 river miles, Figure 2.1). This section of the New River supports a variety of forage fish populations including White Sucker *Catostomus commersonii,* Northern Hogsucker *Hypentelium nigricans*, Gizzard Shad, Rock Bass *Ambloplites rupestris*, Redbreast Sunfish *Lepomis auritus*, and an assortment of shiner species *Notropis spp.* and *Luxilus spp* (Jenkins and Burkhead 1994).
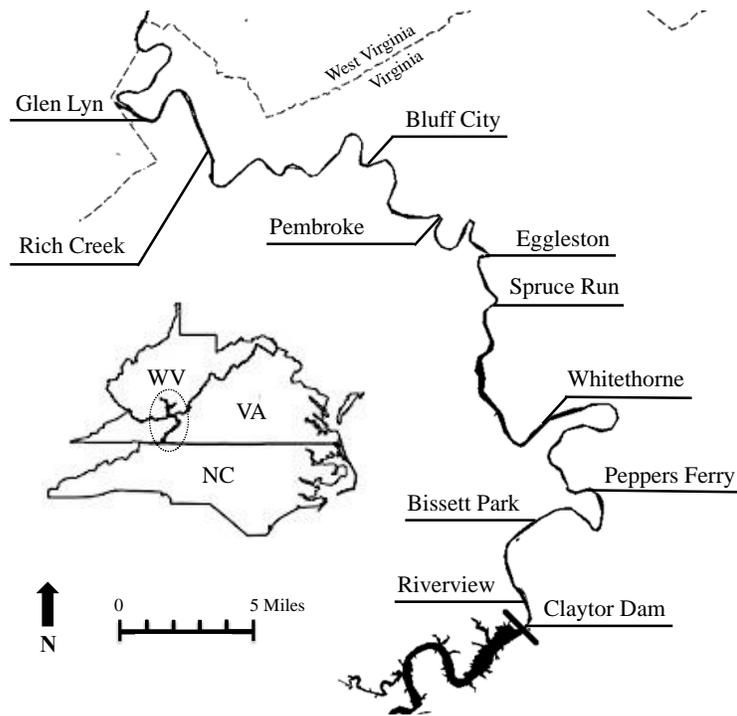
**Figure 2.1.** Map of the study area and study sites in the New River, Virginia.

*Muskellunge Sampling and Aging*

I assessed Muskellunge diet at 11 sites (Figure 2.1), which were selected based on boat access, boat maneuverability, and whether the site was sampled in the previous Muskellunge diet study in 2000-2003 (to allow direct comparison to the results of Brenden et al. 2004). Muskellunge were sampled with boat electrofishing twice weekly during daylight hours from early winter (December) through early summer (July) in 2013-2015.  These months coincided with the sampling period of the previous Muskellunge diet study (Brenden et al. 2004). The electrofishing system was composed of two drop-wire boom-mounted anodes and a Type VI-A electrofisher (Smith Root, Vancouver, Washington, USA). I used pulsed-DC output at approximately 4 A and 60 Hz, and sampled along the 3-ft depth contour of the river where Muskellunge could be effectively dipped. All captured Muskellunge were measured (total length; TL) to the nearest mm and weighed to the nearest 5g. I clipped the leading pelvic-fin ray from each Muskellunge, and ages of Muskellunge were estimated from sectioned, pelvic-fin rays following Brenden et al. (2007) and Koch and Quist (2007). I also obtained length estimates and pelvic fin rays from a local angler to increase my sample size of large individuals. Briefly, section preparation included cleaning the fin ray, mounting the ray in an epoxy mold, and cutting a thin section (0.5 – 0.75mm) using an Isomet low-speed saw (Koch and Quist 2007). Each section was then mounted on a glass microscope slide and polished using wetted sandpapers and finished with alumina slurry on a Buehler polishing cloth. The polished sections were photographed using a digital camera attached to a stereo-zoom microscope (Olympus SZ60 America Inc., Melville, New York, USA). Three readers independently aged each fish from the photograph (and verified ages on the

section under the microscope as needed). 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 sample was excluded from age-and-growth analyses (Quist et al. 2012).

*Assessing Change in the Muskellunge Population*

In order to assess changes in the New River Muskellunge population, I estimated population structure, individual growth rate, and abundance in 2013-2015, and compared my estimates (hence referred to as the 'current' population) to those estimated when the Muskellunge fishery was regulated under a 30-in MLL (hence referred to as the 'previous' population) (Brenden et al. 2007). I calculated current proportional size-distribution indices for stock, quality, preferred, memorable, and trophy Muskellunge (Gabelhouse 1984; Neumann et al. 2012; Table 2.1) and compared my estimates to those for the previous population using the confidence-interval approach described by Gustafson (1988). To complement the comparison of size-distribution indices, I also compared the current length-frequency distribution of Muskellunge to the previous length-frequency distribution using the Kolmogorov-Smirnov test.

I described the current growth rate of individual Muskellunge using the von Bertalanffy growth equation,

$$L_t = L_\infty [1 - e^{-k(t-t_0)}] , \qquad \text{Eq. 1}$$

where $L_t$ is the total length (mm) at time $t$, $L_\infty$ is the mean asymptotic length, $k$ is the growth coefficient, and $t_0$ is a time coefficient at which length would be 0 mm (Isley and Grabowski 2007). Length data used to fit the growth curve were those collected in the field, and ages of Muskellunge were those estimated from sectioned pelvic-fin rays. I

| Harvest Regulations (Dates instituted) | Size Category | Length (in) | Labels (i.e., referred to in the manuscript as) |
|---|---|---|---|
| | Substock | < 20 | Small |
| 30-in MLL (c. 1975 – 2006) | Stock | 20 - <30 | Medium |
| | Quality | 30 - <38 | |
| | Preferred | 38 - <42 | |
| | Memorable | 42 - <50 | Large |
| 42-in MLL (2006 – 2016) | Trophy | ≥50 | |
| | Citation | ≥40 | |

**Table 2.1.** Minimum length limit (MLL) harvest regulations for New River Muskellunge and proportional size distribution size categories for Muskellunge (Gabelhouse 1984; Neumann et al. 2012). Citation-size Muskellunge are defined by the VDGIF and are a local trophy standard. Anglers who catch Muskellunge of this length are recognized through the Virginia Angler Recognition Program (VARP); https://www.dgif.virginia.gov/fishing/trophy-fish/citations. Throughout this study, Muskellunge are referred to as small, medium, and large Muskellunge and denote the size classes of Muskellunge defined in this table.

calculated $L_\infty$ based on the maximum length observed in my sample (Froese and Binohlan 2000), and estimated $k$ and $t_0$ based on my age-and-length data. I fit growth curves separately for each sex, but I chose to use the model for female growth to inform subsequent bioenergetics modeling. While bioenergetics simulations could have been performed for each sex and then combined, the ratio of male to female Muskellunge changed with size, and I lacked enough information to determine this ratio for the progressively larger size classes. I also had no reason to believe that diet composition differed between male and female Muskellunge within a given size class. Furthermore, I selected female growth over male growth to inform bioenergetics simulations because female New River Muskellunge are known to grow larger than male New River Muskellunge (Brenden 2005), and thus provide a better foundation on which to predict consumption by Muskellunge at large sizes.

I used depletion data collected by the VDGIF and the Leslie model to estimate Muskellunge abundance and then density of adult Muskellunge ($\geq$30 in) at three sites (i.e., Whitethorne, Eggleston, and Rich Creek) in the New River in 2005 and 2014. An average of density was calculated and compared across years to assess changes since the institution of the 42-in MLL. For each depletion, 15 electroshocking boats lined the width of the river and, holding that line, shocked a pre-defined area. As fish were shocked, they were removed from the river and put into live wells. This process was done three times (i.e., a three-run depletion). Over the three runs, the removal of fish reduced the local population size, which was indicated by a decline in catch per unit effort with cumulative catch. By fitting a line to these data, I calculated the point at which CPUE equaled 0 and that point of cumulative catch represented the number of Muskellunge in the population. I

calculated a 95% confidence interval around the population estimate using the t distribution with standard error (Seber 2002). Abundance estimates were converted to density estimates via dividing by the area sampled, and an average of Muskellunge density across the three sites was used in subsequent bioenergetics modeling.

*Assessing Change in Muskellunge Food Habits*

To assess changes in the importance of Smallmouth Bass in Muskellunge diets, I compared the current average diet composition of various sizes of Muskellunge to that estimated by Brenden et al. (2004) from the previous population. Diet information was obtained using pulsed gastric lavage (PGL) on Muskellunge collected via electrofishing (Crossman and Hamilton 1978; Kamler and Pope 2001; Brenden et al. 2004). Recovered food items were stored in labeled Whirl-Paks (Whirl-Pak, Nasco, USA) and frozen for analysis in the lab. Food samples were thawed, blotted dry, counted, and identified to the lowest possible level of taxonomic resolution (Jenkins and Burkhead 1994). Each diet item was weighed (wet weight) to the nearest 0.01 g, and measured to the nearest mm (TL for fish). Due to small sample size at some sites, diet information was pooled across sites for analysis. Diets of individual Muskellunge were characterized by percentage composition by wet weight for each prey item. Prey items that only occurred once in the diet (e.g., Wood Duck *Aix sponsa*) were pooled into a single prey category (i.e., other) for analysis. Unidentifiable prey items accounted for <1% of total weight of prey consumed and were removed from further analyses. The remaining prey categories were re-scaled accordingly.

To inform subsequent bioenergetics simulations, I also examined diet composition for ontogenetic and seasonal fluctuations. I compared diet composition between size classes

of Muskellunge and between seasons using a multi-response permutation procedure (MRPP; Mielke and Berry 2001). An MRPP is a distribution-free, nonparametric method that tests for group differences by comparing observed intra-group average distances to distances calculated after permutation of the observed data (Cade and Richards 2001). When an overall difference in diet composition was found between size categories, pairwise MRPP comparisons were made post-hoc to determine which size categories were significantly different. Then, I tested for seasonal differences within the significantly different size categories. All MRPP comparisons were conducted in RStudio (Version 0.99.473), and p-values for the tests were calculated using a Pearson Type III approximation to the permutation distribution (Cade and Richards 2001). The overall tests for diet differences between size classes and seasons were evaluated for significance with an $\alpha = 0.05$. The $\alpha$ for the pairwise comparisons was determined using the step-up false discovery rate method (García 2004), and $\alpha = 0.003$ for comparisons by length and $\alpha = 0.009$ for comparisons by season.

*Assessing Change in Predation on Smallmouth Bass*

To assess change in consumption of Smallmouth Bass by the Muskellunge population, I used bioenergetics modeling to estimate the biomass of Smallmouth Bass ($kg \cdot ha^{-1}$) consumed annually by Muskellunge. This estimate was then compared to that made for the previous Muskellunge population (Brenden et al. 2004). In addition to size- and season-specific information on diet composition, the bioenergetics simulations also required data on water temperature, prey energy densities, predator energy density, and physiological parameters for the target species (Hanson 1997; Figure 2.2). Temperature for each day of year was calculated by averaging temperature data from 2009 to 2012
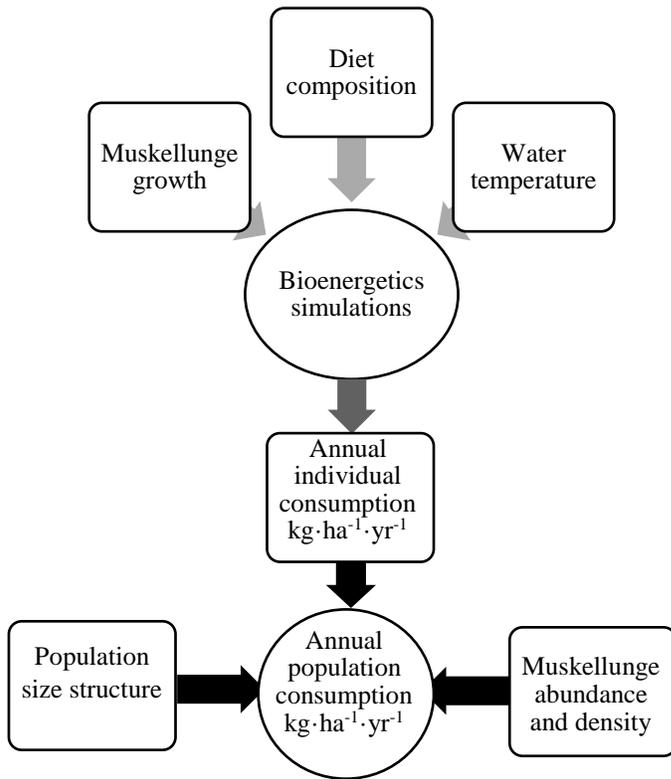
**Figure 2.2.** Flow chart of inputs and outputs for my bioenergetics simulations.

from the USGS gage on the New River in Radford, Virginia (Figure 2.3). Temperatures

ranged 3.3-25.6 °C. Energy densities for Muskellunge and for prey items were obtained

from the literature (Kitchell et al. 1974; Adams et al. 1982; Rice et al. 1983; Bevelhimer

et al. 1985; Shuter and Post 1990; Roell and Orth 1993) and the previous study on the

diet of New River Muskellunge (Brenden et al. 2004; Table 2.2).  Parameter estimates for

respiration, consumption, egestion, and excretion were borrowed from Bevelhimer at al.

(1985).

   I used an R-based version of Fish Bioenergetics 3.0. (Hanson 1997). The

bioenergetics model is based on the equation,

$$C = (R+A+S)+(F+U)+(\Delta B+G);\ \text{Eq. 2}$$

where C = consumption, R = respiration, A = active metabolism, S = specific dynamic

action, F = egestion, U = excretion, ΔB = somatic growth, and G = gonad production

(Hanson 1997). I first estimated average consumption for an individual Muskellunge

within a given size category by converting the start and end lengths of the size category

to average weights and then simulating consumption over the amount of time the fish

spent in that size category (Table 2.3; as indicated by the von Bertalanffy growth curve.

This estimate was then converted to annual consumption given the number of days that

an individual spent in that size category. For example, a memorable Muskellunge has

start and end lengths of 42 and 50 inches, which I converted to average weights of 7761

and 12286 g respectively using the length-weight regression

$$Log(W) = 2.680836 \cdot \log(L) - 4.235842, \qquad \text{Eq. 3}$$
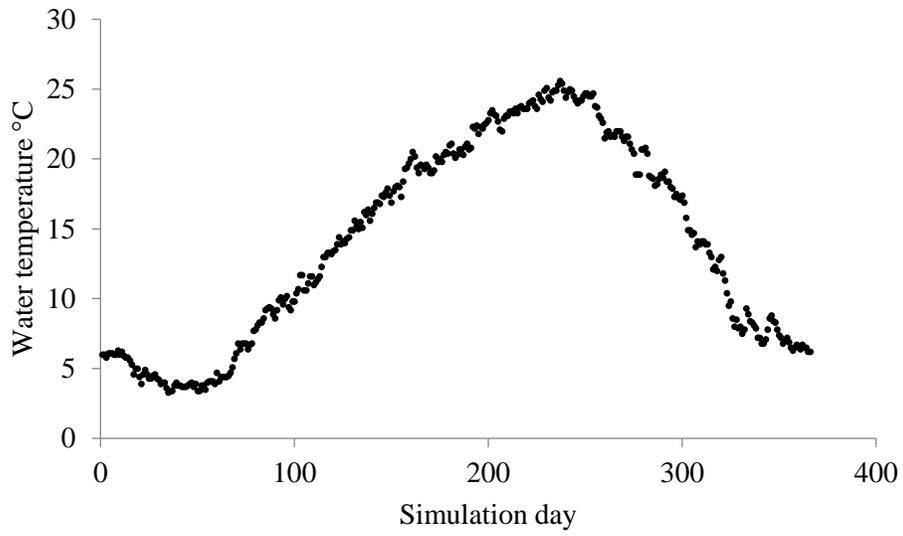
**Figure 2.3.** Water temperatures used in bioenergetics simulations by simulation day. Temperatures were averages calculated from daily water temperatures taken by the USGS gage at Radford, Virginia from 2009 – 2012.

| Prey group or species | Energy density (kJ·g$^{-1}$) | Source |
|---|---|---|
| Muskellunge *Esox masquinongy* | 3.600 | Bevelhimer et al. 1985 |
| Smallmouth Bass *Micropterus dolomieu* | 4.186 | Shuter and Post 1990 |
| Gizzard Shad *Dorosoma cepedianum* | 5.85 | Adams et al. 1982 |
| Minnows *cyprinid spp.* | 4.853 | Brenden et al. 2004 |
| Rock Bass *Ambloplites rupestris* | 4.167 | Brenden et al. 2004 |
| Redbreast Sunfish *Lepomis auritus* | 4.186 | Kitchell et al. 1974 |
| White Sucker *Catostomus commersonii* and Northern Hogsucker *Hypentelium nigricans* | 5.313 | Brenden et al. 2004 |
| Largemouth Bass *Micropterus salmoides* | 4.186 | Rice et al. 1983 |
| Catfish *ictalurid spp.* | 4.184 | Roell and Orth 1993 |
| Other[a] | 6.750 | |
| Wood Duck *Aix sponsa* Pied-Billed Grebe Podilymbus podiceps | 10.920 | Drobney 1980 |
| Striped Bass *Morone saxatilis* | 6.488 | Hartman and Brandt 1995 |
| Rainbow Trout *Oncorhynchus mykiss* | 5.764 | Rand et al. 1993 |
| Yellow Perch *Perca flavescens* | 4.500 | Rottiers and Tucker 1982 |

**Table 2.2.** Prey items and their energy densities used in bioenergetics simulations.
[a] The 'Other' category consisted of food items that only appeared once in Muskellunge diet, and the energy density used was a weighted average of all items within the 'Other' category.

| Size Class | Size | Start Weight | End Weight | Days Spent in Size Class |
|---|---|---|---|---|
| Substock | 0 -20 | 0 | 1.065 | 719 |
| Stock | 20 - 30 | 1.065 | 3.102 | 551 |
| Quality | 30 - 38 | 3.102 | 5.966 | 686 |
| Preferred | 38 - 42 | 5.966 | 7.761 | 475 |
| Memorable | 42 - 50 | 7.761 | 12.286 | 1920 |
| Trophy | 50+ | 12.286 | 12.785 | 394 |

**Table 2.3.** The start and end lengths and weights of Muskellunge by size category (Neumann et al. 2012) and time spent in size category based on female von Bertalanffy growth curves used to simulate consumption.

constructed from my length and weight data. I used a correction factor of 1.01 when calculating weights because values back-transformed from the log scale can be biased (Ogle 2016). Using the von Bertalanffy growth equation, I estimated the age at start and end lengths as 6.7 yr and 11.9 yr respectively for a total of 1,920 days. I then ran a bioenergetics simulation for 1,920 days with 7761 and 12286 g as the start and final end weights. The resulting estimate of consumption was then converted to annual consumption given that the individual spent 1,920 days as a memorable-sized fish. Then, using my data on the Muskellunge population's size structure and density, I extrapolated individual annual consumption to population annual consumption ($kg \cdot ha^{-1}$).

Given the seasonal differences in diet composition that became apparent in preceding analyses, the bioenergetics simulations for quality-, preferred-, and memorable-size Muskellunge were divided into four periods: winter (January and February), spawning season (March), spring (April and May), and summer (June and July). Due to small sample sizes, diet composition from August through December was linearly interpolated based on summer and winter diet compositions.

**Results**

I captured a total of 528 Muskellunge from 2013 to 2015 ranging 10-49 in TL. I received information on 48 additional Muskellunge from the cooperating local angler, and those individuals ranged 40-52 in. Of Muskellunge for which sex was identified, the sex ratio was roughly equal (female 51%; male 49%). Of the 528 Muskellunge sampled, 500 underwent gastric lavage and approximately 43% of those individuals had items in

their stomachs ($n = 215$). The majority of samples were collected during the spawning, spring, and winter seasons, respectively (Table 2.4).

*Changes in the Muskellunge Population*

Both the size structure and density of adult Muskellunge in the New River have increased following the institution of a 42-in MLL, and the growth rate ($k$) of Muskellunge has slowed. With the exception of PSD-T, the population's size-distribution indices increased substantially since the institution of the 42-in MLL (Table 2.5). This shift toward greater size structure was mirrored in the length-frequency distribution, which showed greater proportions of large individuals than the previous population (Kolmogorov-Smirnov test; $p < 0.0001$; Figure 2.4). The average density of adult Muskellunge increased fourfold (Table 2.6). Current density of adult Muskellunge was estimated at 1.69 individuals·ha$^{-1}$ (95% confidence interval [CI]: 0.47 – 19.02 individuals·ha$^{-1}$) compared to the population's previous density of 0.31 adult Muskellunge·ha$^{-1}$. While $L_\infty$ increased approximately 6 in for female Muskellunge compared to that estimated from the previous population, current growth rate ($k$) of female Muskellunge was somewhat slower (Table 2.7).

*Changes in Muskellunge Food Habits*

Smallmouth Bass still represented a minor component of current Muskellunge diet overall, within various size classes, and across seasons. I found a significant difference in diet composition between size categories of Muskellunge ($p<0.001$), and post-hoc pairwise MRPP comparisons revealed three distinct groups: substock Muskellunge (hence referred to as small Muskellunge); stock-size Muskellunge (hence referred to as

| Season | $n$ |
|---|---|
| Winter (January-February) | 54 |
| Spawning (March) | 70 |
| Spring (April-May) | 58 |
| Summer (June-July) | 25 |
| Fall (September-October) | 8 |
| Total | 215 |

**Table 2.4**. The seasonal distribution of Muskellunge diet samples from the New River, Virginia. Months were separated into seasons based on statistically significant differences in diet composition.

| Harvest regulation (dates instituted) | Dates sampled | PSD | PSD-P | PSD-M | PSD-T |
|---|---|---|---|---|---|
| 30-in MLL (1980 – 2006) | 2000 – 2003 | 64 | 25 | 5 | 1 |
| 42-in MLL (2006 – 2016) | 2013 – 2015 | 84 (81 – 88) | 43 (38 – 48) | 16 (13 – 20) | 0 |

**Table 2.5.** Proportional size distribution (Neumann et al. 2012) values (and 90% confidence intervals) for the New River, Virginia Muskellunge population sampled under two different harvest regulations (MLL = minimum length limit). Data are from Brenden et al. (2007; 30-in MLL) and this study (42-in MLL).

| Year | Average density of adult Muskellunge |
|---|---|
| 2005 | 0.31 (0.25 – 0.50) |
| 2014 | 1.69 (0.47 – 19.02) |

**Table 2.6.** Average density of adult Muskellunge (Muskellunge·ha$^{-1}$) (and 95% confidence intervals) in the New River, Virginia (i.e., Eggleston, Rich Creek, and Whitethorne), as calculated from depletion catch-and-effort data.

| | Von Bertalanffy Parameter | 30-in MLL (2000 – 2003) | 42-in MLL (2013 – 2016) |
|---|---|---|---|
| | $L_\infty$ | 47 | 53 |
| Females | $k$ | 0.3999 | 0.233 |
| | $t_0$ | -0.0895 | -0.065 |
| | $L_\infty$ | 42 | 44.5 |
| Males | $k$ | 0.4868 | 0.283 |
| | $t_0$ | -0.468 | -0.496 |

**Table 2.7.** Estimates for the three von Bertalanffy parameters ($L_\infty$, $k$, $t_0$) for female and male New River Muskellunge under a 30-in MLL (Brenden et al. 2007) and under a 42-in MLL (and dates sampled).

Dates sampled: 2000 - 2003
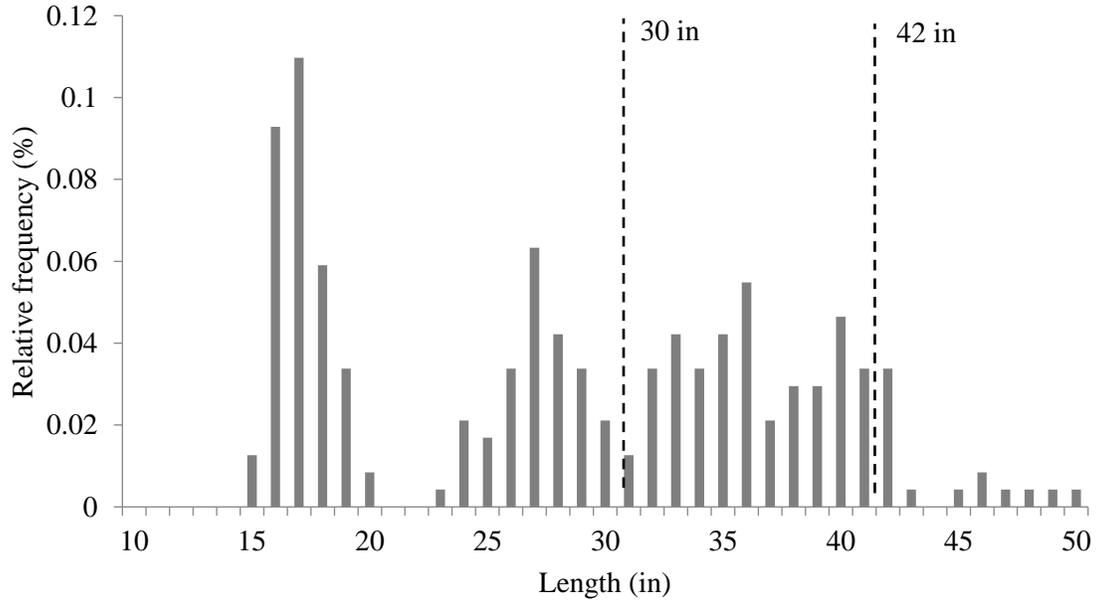


Dates sampled: 2013 - 2015
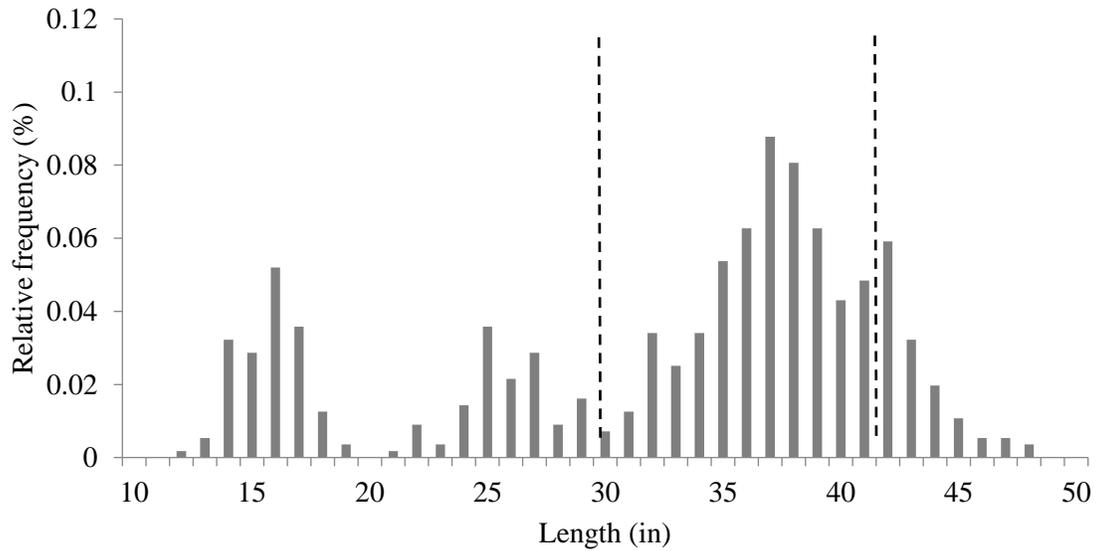


**Figure 2.4**. Length-frequency distributions for the New River Muskellunge population under the 30-in MLL (top) and the 42-in MLL (bottom). Dashed lines mark the 30- and 42-in MLLs. Data are from Brenden et al. (2004; top) and this study (bottom).

medium-size Muskellunge); and quality, preferred, and memorable Muskellunge (hence referred to as large Muskellunge) (Table 2.1). While the prominence of Smallmouth Bass in the diet of small Muskellunge increased, Smallmouth Bass were completely absent in the current diet of medium-size Muskellunge. Overall, diet composition of small and medium-size Muskellunge was similar to that under the 30-in MLL with the majority of diet ($\geq$75%) made of cyprinids, Rock Bass, and Redbreast Sunfish.

In the current diet of large Muskellunge, the importance of Smallmouth Bass was actually lower (3%) than in the diet under the 30-in MLL (11%; Brenden et al. 2007). Overall, diet composition of large Muskellunge was similar to that under the 30-in MLL in that catostomids, Rock Bass, cyprinids, and Redbreast Sunfish still composed over 70% of their diet. However, the remaining 30% of the current diet incorporated a larger diversity of prey items. I found a higher prevalence of ictalurids, Gizzard Shad, and 'other' items (i.e., items that only appeared once in Muskellunge stomachs), such as a Striped Bass *Morone saxatilis*, several birds, a Rainbow Trout *Oncorhynchus mykiss*, and a Yellow Perch.

I found no significant difference in Muskellunge diets between seasons for small and medium-size Muskellunge. However, large Muskellunge did exhibit significant seasonal differences in diet composition. While catostomids, Rock Bass, and Redbreast Sunfish were constants in the diet of large Muskellunge across seasons, cyprinids composed 27% of Muskellunge diet in the winter (January – February), Gizzard Shad composed 23% of Muskellunge diet in the spawning season (i.e., March), and "other" items composed 14% of Muskellunge diet in the summer (June – July) (Table 2.8). These size and seasonal differences in diet were incorporated into subsequent bioenergetics simulations.

| Size Category | | Gizzard Shad | Other | Ictalurids | Unknown | Largemouth Bass | Smallmouth Bass | Rock Bass | Redbreast Sunfish | Cyprinids | Catostomids |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Prey Type (% wet weight for an average Muskellunge) | | | | | | | | | |
| Small | 30-in MLL | -- | -- | -- | 17 | -- | -- | 21 | 7 | 55 | -- |
| | 42-in MLL | 12.5 | -- | 4 | -- | -- | 6.5 | 5 | 8 | 59 | 4 |
| Medium | 30-in MLL | -- | -- | -- | 15 | -- | 2 | 9 | 45.5 | 28 | -- |
| | 42-in MLL | 4.5 | -- | 2 | -- | -- | -- | 24.5 | 31 | 37.5 | -- |
| Large | 30-in MLL | 12.5 | -- | -- | 9 | -- | 9.5 | 4.5 | 13.5 | 12.5 | 38 |
| | 42-in MLL Overall | 7 | 8 | 7.5 | -- | 2 | 3 | 13 | 25 | 16.5 | 18 |
| | Winter | -- | 8 | 11 | -- | 3 | -- | 6.5 | 31 | 26.5 | 14.5 |
| | Spawning | 23.5 | 9 | 7 | -- | 2 | -- | 10.5 | 9.5 | 21.5 | 16.5 |
| | Spring | -- | -- | 7.5 | -- | 2.5 | 6.5 | 25.5 | 19 | 7.5 | 31 |
| | Summer | 5 | 14.5 | 5 | -- | -- | 6 | 9.5 | 41 | 10 | 9.5 |

**Table 2.8.** Diet composition (% wet weight for an average Muskellunge) of New River Muskellunge by size class (Neumann et al. 2012) under the 30-in and 42-in MLLs, and diet composition by season for quality, preferred, and memorable-size Muskellunge under the 42-in MLL. Months were separated into the following seasons: Winter, January – February; Spawning, March; Spring, April – May; Summer, June – July. Due to small sample sizes, the diet composition of other months was not estimated. The 'Unknown' category refers to partially digested and unidentifiable fish, and the 'Other' category delineates prey items only found once in the stomachs of Muskellunge (e.g., Wood Duck *Aix sponsa*, Pied-billed Grebe *Podilymbus podiceps*). Data describing Muskellunge diet under the 30-in MLL are from Brenden et al. (2004), and data describing Muskellunge diet under the 42-in MLL are from this study.

*Predation on Smallmouth Bass*

Current estimated annual consumption of Smallmouth Bass by Muskellunge (Table 2.9) had not notably increased compared to the previous estimate. At 1.68 adult Muskellunge·ha$^{-1}$ and the population's current size structure, I calculated that Muskellunge consumed a total of 0.93 kg of Smallmouth Bass·ha$^{-1}$·yr$^{-1}$ (95% CI: 0 – 2.9 kg·ha$^{-1}$·yr$^{-1}$) compared to 0.9 kg of Smallmouth Bass·ha$^{-1}$·yr$^{-1}$ estimated previously. My bioenergetics model simulations predicted current total annual consumption of all prey to be over twice as high as the previous estimation of total annual consumption. I predicted total consumption at 23.4 kg·ha$^{-1}$·yr$^{-1}$ (95% CI: 0.8 – 72.9 kg·ha$^{-1}$·yr$^{-1}$) compared to 9 kg·ha$^{-1}$·yr$^{-1}$ (Brenden et al. 2004). Redbreast Sunfish, cyprinids, Rock Bass, and catostomids accounted for about 75% of biomass consumed by Muskellunge·ha$^{-1}$·yr$^{-1}$ (Table 2.9), which is similar to the estimated proportion of consumed biomass composed by those species previously (~83%) (Brenden et al. 2004). Of the prey species, my simulations predicted that annual consumption was highest for Redbreast Sunfish at 14.8 kg·ha$^{-1}$ (95% CI: 0.2 – 23.2 kg·ha$^{-1}$·yr$^{-1}$).

**Discussion**

My results indicate that the institution of a 42-in MLL on the New River Muskellunge fishery did not notably alter Muskellunge predation on Smallmouth Bass. Although the density of adult Muskellunge doubled and population size structure increased substantially following the regulation change, my modeling indicated that Muskellunge consumption of Smallmouth Bass remained low. This relatively stable level of consumption was largely the result of Smallmouth Bass becoming a smaller component

| Size Category | Other | Ictalurids | Cyprinids | Gizzard Shad | Largemouth Bass | Smallmouth Bass | Redbreast Sunfish | Rock Bass | Catostomids | Sum |
|---|---|---|---|---|---|---|---|---|---|---|
| Substock | 0.00 | 0.04 | 0.57 | 0.12 | 0.00 | 0.06 | 0.08 | 0.05 | 0/04 | 0.97 |
| Stock | 0.00 | 0.04 | 0.72 | 0.09 | 0.00 | 0.00 | 0.60 | 0.47 | 0/00 | 1.93 |
| Quality | 0.81 | 0.52 | 1.07 | 0.29 | 0.09 | 0.35 | 2.64 | 0.87 | 1.10 | 7.74 |
| Preferred | 0.81 | 0.48 | 1.04 | 0.26 | 0.08 | 0.32 | 2.57 | 0.75 | 1.97 | 8.28 |
| Memorable | 0.47 | 0.30 | 0.62 | 0.16 | 0.05 | 0.20 | 1.53 | 0.49 | 0.61 | 4.44 |
| Trophy | 2.10 | 1.39 | 4.02 | 0.92 | 0.21 | 0.93 | 7.42 | 2.64 | 3.72 | 23.36 |

**Table 2.9.** Estimated annual consumption (kg·ha$^{-1}$·yr$^{-1}$) per prey item for the various size classes of New River Muskellunge. The 'Other' category refers to items only observed once in the diet of Muskellunge, such as a Wood Duck *Aix sponsa* and Pied-Billed Grebe *Podilymbus podiceps*.

of the diets of large Muskellunge, compensating for the increase in density of Muskellunge. Small differences in the proportion of Muskellunge diet composed by Smallmouth Bass within various size classes of Muskellunge may be related to temporal changes in the availability of appropriately sized Smallmouth Bass.

*Muskellunge Population Change*

The 42-in MLL increased the density of adult Muskellunge and population size structure of Muskellunge in the New River, which likely increased the potential for intra- and interspecific competition for forage. I found the growth rate (*k*) of Muskellunge to be slightly slower following the institution of the 42-in MLL, which has been a frequently observed phenomenon following the implementation of an MLL (Brousseau and Armstrong 1987; Noble and Jones 1993; Stone and Lott 2002). Another study on New River Muskellunge found similar reductions in condition (Chapter 1), particularly for large Muskellunge. High densities of adult Muskellunge elsewhere have been linked to reductions in growth rate and condition (e.g., Hanson 1986), including systems with densities similar to that of the New River. For instance, the Muskellunge population in Bone Lake, Wisconsin, exhibited decreased condition following the implementation of a 40-in MLL at a density of 0.99 adult Muskellunge·ha$^{-1}$ (Cornelius and Margenau 1999).

In addition to higher intraspecific competition for forage, a larger Muskellunge population must also compete with other New River predators such as Largemouth Bass, Smallmouth Bass, Walleye, and Flathead *Pylodictis olivaris* and Channel catfishes *Ictalurus punctatus*. Increased competition for forage often leads to a shift in diet composition and breadth as individuals are forced to incorporate less-preferred items into their diets (Svanbäck and Bolnick 2007). The incorporation of less-preferred items into a species' diet can cause reduced growth rate and

condition. The predator may have to spend more time hunting, capturing, or consuming the prey, the prey may be of less caloric value, and/or capturing the prey may increase risk of harm to the predator. At an estimated density of 1.68 adult Muskellunge·ha$^{-1}$, the observed declines in individual growth rate and condition provide evidence of the effects of increased competition as result of increased Muskellunge density.

*Muskellunge Food Habits*

My study showed that the diets of the current and previous Muskellunge populations were largely similar in that catostomids, cyprinids, Redbreast Sunfish, and Rock Bass still composed the majority of Muskellunge diet overall and within size classes (i.e., 70%). The importance of these items in Muskellunge diets is consistent with other diet studies on Muskellunge (e.g., Bozek et al. 1999; Kerr 2016). However, while the overall diet compositions of the previous and current populations were relatively similar, there were three notable differences. First, the remaining 30% of the current diet for large Muskellunge was more diverse compared to the diet of the previous New River population, with a higher prevalence of ictalurids, Gizzard Shad, and 'other' items. Second, catostomids, while still important in the diet of large Muskellunge, composed a smaller portion of large Muskellunge diet than previously (18% currently compared to ~60%). Third, Smallmouth Bass were newly present in the current diet of small Muskellunge. These three differences could be evidence of increased competition and, in turn, could explain the observed reductions in growth rate and condition.

Alternatively, small changes in the proportion of Muskellunge diet composed by various prey items could be explained by variations in the availability of appropriately sized prey. For instance, the higher prevalence of ictalurids may be associated with fluctuations in ictalurid abundance. Ictalurid abundance at Whitethorne has doubled since 2005 based on CPUE data

from Leslie depletion estimates (Figure 2.5). The prevalence of Gizzard Shad in the diet of large Muskellunge before and after the 42-in MLL was similar, but the presence of Gizzard Shad in the diet of small and medium-sized Muskellunge was novel. Gizzard Shad are nonnative to the New River and were illegally stocked in Claytor Lake in the 1980s (Bonds 2000). The Gizzard Shad population has prospered since the introduction, and at times has composed up to a third of the lake's fish biomass (Bonds 2000). As the abundance of Gizzard Shad in Claytor Lake increased, Gizzard Shad began to appear more regularly in the New River. Since the previous study, the abundance of Gizzard Shad in Claytor Lake and subsequently downstream of Claytor Lake has increased, meaning that Gizzard Shad of appropriate size for small Muskellunge are likely more readily available.

The abundance and biomass of catostomids, in particular Northern Hogsuckers, show conflicting trends in which abundance has increased since 2005 while biomass has decreased (J. Copeland, VDGIF, unpublished data). Thus, the catostomid population of the New River is likely composed of smaller individuals less suitable for consumption by large Muskellunge.

Similarly, variability in the composition of Muskellunge diet composed of Smallmouth Bass between this study and the previous could be a reflection of the current abundance of appropriately sized Smallmouth Bass, meaning that as the abundance of appropriately sized Smallmouth Bass changes, the portion of Muskellunge diet comprised of Smallmouth Bass also changes. Routine fall electrofishing surveys conducted by the VDGIF show that the years during and preceding the previous study (i.e., 1996-2003) had below-average CPUE (and thus relative abundance) of young-of-the-year (YOY) Smallmouth Bass (Figure 2.6). Conversely, YOY Smallmouth Bass were more abundant during the 2014 routine fall electrofishing surveys (Figure 2.6). Thus, Smallmouth Bass of appropriate size for consumption by substock Muskellunge were
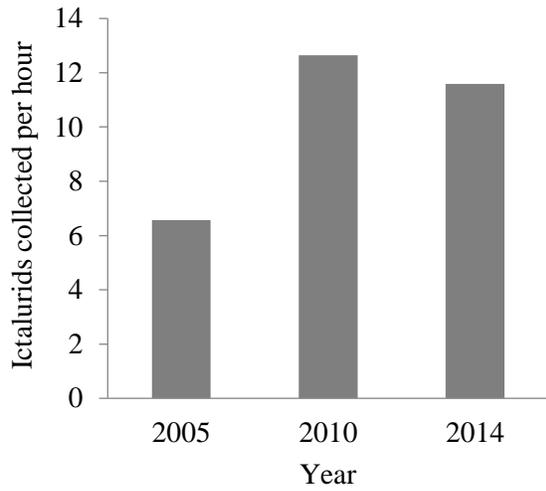
**Figure 2.5.** CPUE of Ictalurids (primarily Margined Madtoms *Noturus insignis*) at Whitethorne in the New River, Virginia, 2005-2014 from depletion surveys conducted by the VDGIF.
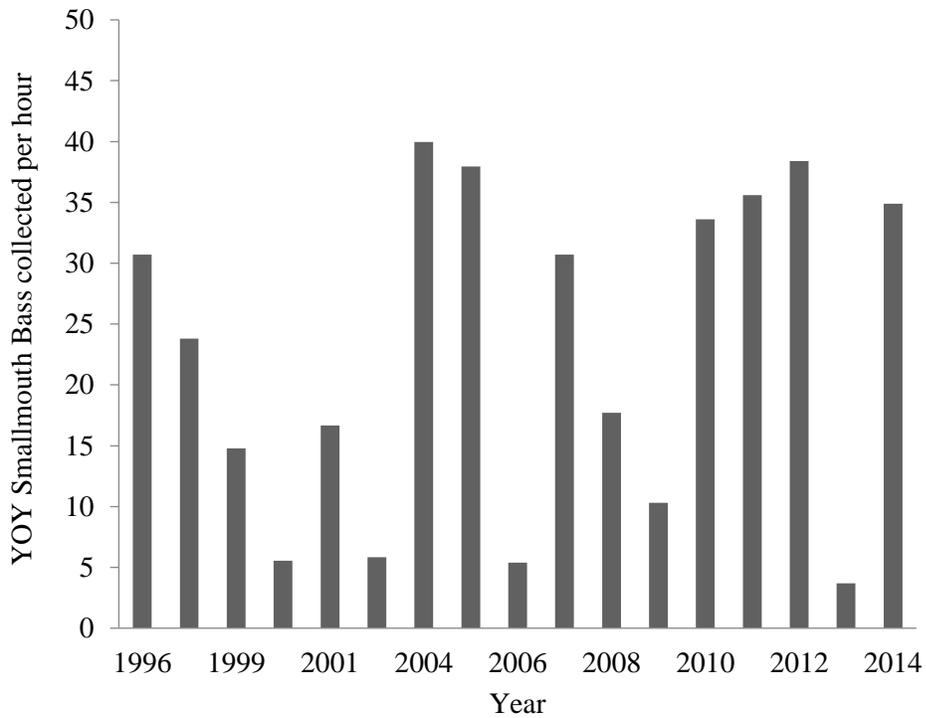


**Figure 2.6.** CPUE of YOY Smallmouth Bass in the New River, Virginia. CPUE is from routine fall electrofishing surveys conducted by the VDGIF targeting Smallmouth Bass.

more available during this study than during the previous study. In a reverse but similar trend, CPUE of 7-14-in Smallmouth Bass was above average during the previous study and below average during the current study (likely the result of missing year-classes from 1999-2003) (Figure 2.7). Thus, Smallmouth Bass of appropriate size for consumption by large Muskellunge (>30 in) were more available during the previous study than the current study.

Determining whether the cause of these changes in the diet of Muskellunge is the product of increased competition or fluctuations in the availability of appropriately sized forage is almost impossible without holding populations of prey fishes constant. Each could lead to the reductions in growth rate that I observed, and the composition of the current Muskellunge diet is likely a function of both. It is equally important to determine how much of a role Muskellunge predation has played in some of the fluctuations we observed. In the case of catostomids, it is entirely possible that the catostomid population's shift to smaller individuals is a consequence of Muskellunge predation.

*Muskellunge Predation on Smallmouth Bass*

Despite increases in adult Muskellunge density and population size structure, my bioenergetics modeling estimates of Muskellunge consumption of Smallmouth Bass did not appreciably change. Even at sites predicted to have the highest densities of adult Muskellunge, and thus the most extreme interaction between Muskellunge and Smallmouth Bass, total consumption of Smallmouth Bass was still low ($1.9$ kg$\cdot$ha$^{-1}\cdot$yr$^{-1}$ at Whitethorne).

Interpreting the impact that Muskellunge predation has on the Smallmouth Bass population requires an understanding of Smallmouth Bass annual production. Smallmouth Bass annual production has been previously estimated at $32.1$ kg$\cdot$ha$^{-1}\cdot$yr$^{-1}$ in parts of the New River (Roell and Orth 1993). If current annual production is similar, then Muskellunge predation on
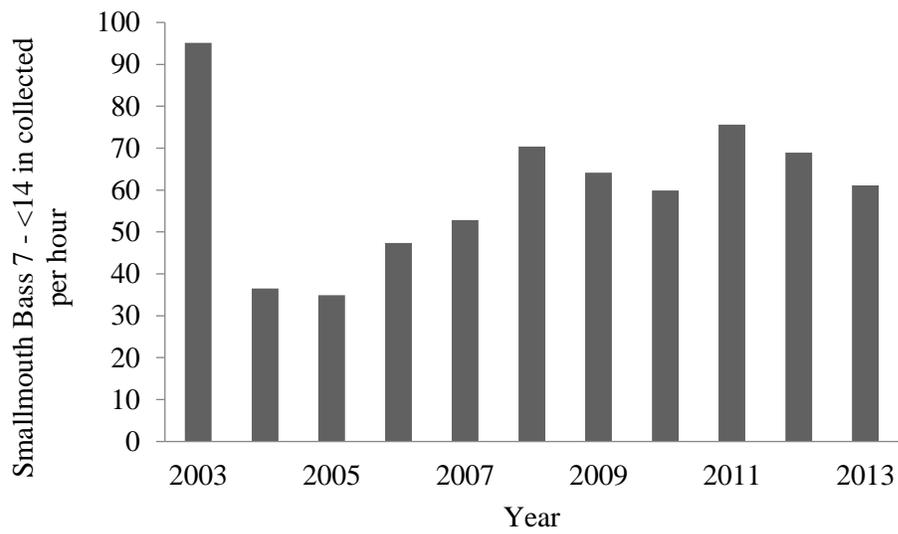
**Figure 2.7.** CPUE of Smallmouth Bass 7 - <14 in in the New River, Virginia. CPUE is from routine electrofishing surveys conducted by the VDGIF targeting Smallmouth Bass.

Smallmouth Bass should only remove about 3% of annual production, making it unlikely that Muskellunge cause a substantial impact. While biomass of adult Smallmouth Bass (i.e., Smallmouth Bass >7 in) has demonstrated an increasing trend over the last 4 years based on depletion data (J. Copeland, VDGIF, unpublished data), long-term trends ($\geq 10$ yrs) in Smallmouth Bass biomass have been more variable and make it difficult to imply with any certainty the current level of annual production of Smallmouth Bass. Thus, future research might be best focused on evaluating annual production of Smallmouth Bass and interpreting Muskellunge predation on Smallmouth Bass within that context.

*Management Implications*

Muskellunge likely play a small role in shaping Smallmouth Bass population dynamics and production in the New River. Furthermore, these findings lend credence to the idea that the New River might be capable of supporting two quality recreational fisheries. Unfortunately, these findings may not be enough to remedy the rift between angler groups and alleviate the fears of bass anglers.

My findings do not provide a complete explanation of the causes of fluctuation in bass abundance that prompted this study or fully address the impact Muskellunge might have on other New River fishes. Fluctuations in bass abundance and Muskellunge influence on other New River fishes can each influence the overall effect that Muskellunge predation has on Smallmouth Bass. Several other changes on the lower New River, including a change in the operation of Claytor Dam and changes to regulations on the Smallmouth Bass fishery, have likely played a role in shaping the Smallmouth Bass population and angler catch rates. Appalachian Power Company (AEP), the company responsible for the operation of Claytor Dam, switched in 1991 from a daily peak-power-production regime throughout the year, to a "levelized" flow regime

between 15 April and 15 October (Federal Energy Regulatory Commission [FERC] 2011). Those months span the majority of the Smallmouth Bass spawning season on the New River (Graham and Orth 1986). While the "levelized" flow regime required AEP to maintain an average minimum daily flow (i.e., 750 cfs), daily fluctuations in flow still likely influenced Smallmouth Bass recruitment (Lukas and Orth 1995; Copeland 2006). Additionally, low flows that drastically affect the abundance, production, and species composition of invertebrates have been associated with reduced growth rate of young Smallmouth Bass (Paragamian and Wiley 1987). Moreover, an 11 to 14-in PSL was instituted on Smallmouth Bass in 1987 and was increased to a 14 to 20-in PSL in 2003. PSLs instituted on bass populations in other systems have resulted in improvements in growth and size structure, but overall reductions in density (Eder 1984)—which may partially explain declines in angler catch rates and some of the fluctuations in bass abundance. Ultimately, each of these factors have likely influenced the abundance and size structure of the current New River Smallmouth Bass population.

The influence that Muskellunge have on other New River fishes was not explicitly examined in this study. While the importance of some prey species in the diets of Muskellunge did shift, I did not fully determine whether these shifts were caused by fluctuations in overall abundance of forage or by division of forage between more individuals. I also did not examine whether fluctuations in forage (with the exception of Smallmouth Bass) were the result of previous Muskellunge predation on forage populations or another source acting on the populations. Furthermore, while an increase in Muskellunge abundance may have clear implications for intraspecific competition for forage, managers know little about the implications for other fishes (i.e., what dietary overlap exists between other predators in the New River). The extent of influence that Muskellunge predation has on forage populations, particularly on those preferred

by other New River predators, could alter how Muskellunge presence and predation impact Smallmouth Bass and the New River community as a whole.

In conclusion, although Muskellunge likely play a small role in shaping the Smallmouth Bass population, a fuller understanding of this role would be enabled by a detailed study of Smallmouth Bass production and the myriad factors influencing it. As the VDGIF co-manages the New River fishery for both Muskellunge and Smallmouth Bass, it will be critical to consider how fluctuations in the availability of preferred forage and how fluctuations in the annual production of Smallmouth Bass alter the overall effect that Muskellunge predation has on the New River Smallmouth Bass population and fishery.

**Overall Thesis Conclusions and Management Recommendations**

While my results show that the current 42-in MLL was effective at improving some measures of fishery quality (i.e., size structure and abundance), my bioenergetics modeling simulations did not predict subsequent increases in Muskellunge consumption of Smallmouth Bass. This seems largely due to the fact that Smallmouth Bass continue to be a minor component of Muskellunge diet overall and within the various size classes of Muskellunge. Thus, Muskellunge likely play a small role in shaping Smallmouth Bass population dynamics and production currently in the New River.

However, these findings may not be enough to remedy the rift between angler groups and alleviate the fears of bass anglers. Reconciling VDGIF's trophy-oriented management objectives for the Muskellunge fishery with their potential to prey on and affect Smallmouth Bass has strained the agency's relationship with Smallmouth Bass anglers for more than a decade. This sometimes-bitter conflict between angler groups and between anglers and fishery managers has made evident the need for a management strategy that includes social perspective.

Based on this need, my findings on Muskellunge food habits, and my predictions of the Muskellunge population under alternative regulatory scenarios, I would recommend a 40-48-in protected-slot limit (PSL) for future management of the Muskellunge fishery. This regulation seems to best reconcile the management objectives for the Muskellunge fishery with the concerns of Smallmouth Bass anglers. Under a 40-48-in PSL, the size structure of the Muskellunge population would be somewhat similar to the population's current size structure, but the regulation would offer three additional benefits.

First, I predicted slightly higher trophy production under a 40-48-in PSL compared to the current 42-in MLL at low fishing mortalities. So while the overall size structure would be similar, a few more trophy individuals would likely be added to the standing stock of Muskellunge. An increase in trophy production could be more substantial if fishing mortality of Muskellunge under the PSL is significantly lowered. For instance, current fishing mortality of large Muskellunge is estimated at 0.73. If fishing mortality was lowered to 0.10, I predict the Muskellunge population would exhibit an increase in PSD-T of 0 to 3. Second, a 40- to 48-in PSL may mitigate the fears of Smallmouth Bass anglers by opening smaller Muskellunge to harvest and allowing the population to be "thinned out." While a slightly higher proportion of Muskellunge will reach trophy size, the overall abundance of Muskellunge, given harvest below the PSL, will decrease. This is especially true for Muskellunge < 40 in, which are responsible for a substantial proportion of Smallmouth Bass consumed by Muskellunge. Furthermore, this decrease in the overall abundance of Muskellunge may also lead to reduced bycatch of Muskellunge by bass anglers targeting other sport fish. Third, a PSL has the potential to help managers achieve the trophy-oriented goal without sacrificing growth rate and condition, both of which are often considered measures of management effectiveness and efficiency. The harvest of small, sub-slot Muskellunge would thin the density of small individuals and increase the growth rate of the remaining fish. Then, as those fish grow faster, they are protected from harvest while they are within the slot, allowing a higher proportion of individuals to reach trophy size. Given the state of the fishery and the fishing mortality reported for Muskellunge in the New River under a 30-in MLL (Brenden et al. 2007), it seems that at least some harvest below the lower limit of the PSL would likely occur.

Another reason I recommend a 40-48-in PSL regards the regulation's effect on Muskellunge predation on Smallmouth Bass. While I did not directly link the size structure and abundance of Muskellunge under the PSL to potential changes in consumption, given the overall similarity of size structure between the 42-in MLL and the 40-48-in PSL, I am inclined to predict that changes in Muskellunge predation on Smallmouth Bass would be minimal. However, if there was little or no harvest of young Muskellunge and the overall abundance of Muskellunge drastically increased, the change in Muskellunge predation on Smallmouth Bass under a PSL might be more substantial. My findings on the food habits of Muskellunge under increased competition suggest that regardless of increases in adult density and competition, Smallmouth Bass will likely remain a small component of Muskellunge diet.

The effectiveness of any PSL at improving fishery quality will at least partially depend on the level of fishing mortality experienced by the population, as demonstrated by the declining trends in PSD-T with increasing fishing mortality in my models (Figure 1.5a). Managers should take precautions to prevent harvest rates that may inadvertently overexploit a fishery rather than simply reduce the abundance of smaller size classes. Too much harvest below the protected slot would reduce the abundance of smaller fish so much that few individuals would be available to move into larger size classes. I recommend that managers limit the harvest of newly vulnerable smaller fish until mortality under the new regulation can be estimated. Managers could limit mortality by implementing possession or bag limits, or closed seasons. I also recommend that managers estimate and monitor abundance, and subsequently mortality, of Muskellunge. One possible novel method of estimating abundance would be to use a transect method at night, whereby biologists can visualize Muskellunge with light and count individuals along a predefined transect of river. By comparing those counts overtime, managers could gauge trends

in Muskellunge abundance. A night transect method would also minimize interaction with other anglers.

Whichever regulations the VDGIF selects for the Muskellunge fishery in the future, this study lays the groundwork for predicting how the Muskellunge population might respond to a new regulation and, in turn, how their predation on Smallmouth Bass might change. This study also emphasizes the ability of the New River to support two, quality recreational fisheries. Future research that would assist in effectively co-managing Muskellunge and Smallmouth Bass in the New River include an assessment of Muskellunge exploitation, a program to monitor Muskellunge mortality, and a detailed study of Smallmouth Bass production and the factors influencing it. The latter is arguably most important as it provides means of interpreting the role of Muskellunge predation in shaping the Smallmouth Bass population.

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