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Diet of and Prey Availability for Reintroduced Juvenile Lake Sturgeon (*Acipenser fulvescens*) in Ft. Loudoun Reservoir, Tennessee

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To the Graduate Council:

I am submitting herewith a thesis written by Todd Michael Amacker entitled "Diet of and Prey Availability for Reintroduced Juvenile Lake Sturgeon (*Acipenser fulvescens*) in Ft. Loudoun Reservoir, Tennessee." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Brian Alford, Major Professor

We have read this thesis and recommend its acceptance:

Bernie Kuhajda, Benjamin Keck

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

Diet of and Prey Availability for Reintroduced Juvenile Lake Sturgeon (*Acipenser fulvescens*) in Ft. Loudoun Reservoir, Tennessee

A Thesis Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Todd Michael Amacker
May 2016

Acknowledgements

I am most grateful for my soul mate Kendra Robin. You have made me a better person ever since the day I met you, but I suppose that I still have a long way to go. Thank you for patiently listening to my incessant, passionate outbursts about natural history and conservation.

As I write I am watching my four-year-old daughter, Elodie Robin, collect small flowers in our front yard at the onset of spring. Thank you for listening to NPR during our morning commute to Knoxville in return for listening to music on the return trip. You are my heartbeat, and I thank you for enabling me to experience love in the purest form.

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I owe a great deal of this project's success to the entirety of the Southeastern Lake Sturgeon Working Group for their support and encouragement, especially the staff based at the U.S. Fish and Wildlife Service National Fish Hatchery in Warm Springs, Georgia. I must also thank the Wisconsin Department of Natural Resources for providing the broodstock used for the successful reintroduction of *Acipenser fulvescens* into the Upper Tennessee River System.

I should also thank Joyce Coombs for being one of the kindest people I have ever met. I thoroughly enjoyed our daily chats, and I feel privileged to be able to call you a friend. Last but not least I thank the remainder of my research committee; Drs. Bernie Kuhajda and Benjamin Keck. I appreciate the effort that both of you put into growing me academically, and I hope for many future conversations about the ecology, evolution, and conservation of freshwater organisms in the American Southeast and beyond.

Abstract

After fifteen years of reintroducing juvenile Lake Sturgeon (*Acipenser fulvescens*) in the Upper Tennessee River Basin, fisheries biologists are researching basic ecological traits of subsistent organisms. I set out to seasonally assess whether Lake Sturgeon forage opportunistically or selectively in Ft. Loudoun Reservoir. After anesthetizing individual juvenile Lake Sturgeon caught on trotlines in a 13-km reach of the reservoir, I used colonic flush and gastric lavage techniques to describe diets quantitatively. I also used two methods to assess available prey items in the study area by 1) taking systematic benthic grabs along several transects across the width of the reservoir and 2) opportunistically deploying rock cages filled with various types of hard substrate to assess potential prey that colonize hard surfaces. After identifying macroinvertebrates to their lowest taxonomic level, the foraging modes of Lake Sturgeon were determined by comparing the relative abundances of invertebrate taxa in the gut contents of each sturgeon specimen to the relative abundances of the same invertebrate taxa collected from the resource base. Indices that quantify resource overlap or segregation were used to determine how selective Lake Sturgeon in Ft. Loudoun Reservoir were with respect to diet.

I conclude that Lake Sturgeon in Ft. Loudoun Reservoir forage primarily in the benthos where they utilize a relatively narrow niche consisting mostly of larval chironomids, some genera of which they prey upon selectively. Comprehensive conclusions regarding Lake Sturgeon foraging patterns, niche utilization, and selective predation can only be drawn if researchers a) determine the seasonally available prey base by identifying macroinvertebrates to genus/species level b) analyze diet composition (again, identifying prey items to genus/species) from both stomach and intestinal contents and c) use a combination of indices that determine how selective, if at all, Lake Sturgeon are when utilizing the available prey base.

Preface

Thanks to its vast array of distinctive habitats, Tennessee is the most biodiverse inland state in the entire country. The diversity of aquatic organisms is especially impressive (perhaps unrivaled in the Temperate World), a nod to the 19 river basins contained within the state's borders. But Tennessee boasts other species-rich taxa that inhabit high mountain ranges, forests, grasslands, and a vast network of poorly explored caves.

Because Southern Appalachia avoided glaciation during the last Ice Age, preventing the homogenization of its geological features, the fragmentary distribution of these diverse habitats consequently secluded species for thousands of years. These islands of isolation could manifest as a high elevation mixed forest (resulting in the Red-cheeked salamander) or a sandstone outcrop (resulting in an ant-pollinated succulent, the Elf Orpine).

And then there are the large rivers like the Mississippi, the Cumberland, and the Tennessee. Each of these systems has dinosaur fish swimming in them. They come in the form of sturgeon, paddlefish, gars, and bowfin, all of which have changed relatively little over millions of years. One species, the Lake Sturgeon (*Acipenser fulvescens*), disappeared from our rivers and reservoirs by the early 1960's. Luckily, this species has one of the largest distributions of any freshwater fish on Earth, and aquatic biologists in Tennessee have fought to reintroduce the Lake Sturgeon into the Upper Tennessee Basin using brood stock from more robust populations in Wisconsin.

It seems that the Lake Sturgeon is safe from the unfortunate fate of dozens of other aquatic species in Tennessee that have gone extinct, like the Harelip Sucker (*Moxostoma lacerum*) or the Tennessee Riffleshell (*Epioblasma propinqua*). Numerous extant species of freshwater fish and mussels (many with limited range sizes) face imminent threats from habitat loss, biological invasions, and pollution.

Still comforting is the fact that, from my home in Sevierville, Tennessee, I can drive ten minutes to a branch of the Little Pigeon River, stick my head into its flowing waters, and witness a unique form of immortality. How is this achieved? In the words of the prolific biologist and naturalist Edward O. Wilson:

"It resides in the remnants of the natural world we have not yet destroyed. The rest of life is a parallel world. It could exist and continue evolving for what to the human mind is an eternity."

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Chapter 1

Introduction

Synopsis

One of America's largest freshwater fish, the Lake Sturgeon (Acipenseridae: *Acipenser fulvescens*) was once common in most inland rivers and lakes of the United States and Canadian Midwest (Peterson et al. 2007). The mechanisms for their decline are well-documented and anthropogenic in nature. They include overharvesting, habitat fragmentation, and habitat degradation (Pollock et al. 2015). Currently imperiled across much of their range, rehabilitation efforts have been employed to enhance recovery (Haxton 2011) and numerous state and federal agencies have funded research projects that assess the size of remnant stocks, quantify the availability of spawning habitat, and investigate factors affecting spawning success (Peterson and Vecsei 2007). Though many anthropogenic factors continue to impede restoration and conservation initiatives, Lake Sturgeon populations in the Northern U.S. and Southern Canada have benefited from a few distinct advantages (Bezold and Peterson 2008). Remnant stocks of Lake Sturgeon that avoided extirpation still persist, and managers have concentrated efforts on improving spawning and rearing habitat and limiting the supplemental stocking of hatchery-reared juveniles (Drauch and Rhodes 2007). The result has been a relatively healthy population of Lake Sturgeon in the northern reaches of its range. The Winnebago System in Wisconsin harbors one of the largest self-sustaining stocks of Lake Sturgeon in North America, where recreational anglers can sustainably harvest sturgeon (Bruch 1999).

In stark contrast, the southern United States have relied heavily on intensive stocking efforts, with most native populations being extirpated by the mid-twentieth century (Bezold and Peterson 2008). Because intensive stocking efforts in the Southeastern U.S. didn’t begin until 2000, with planning stages beginning in 1998, subsequent studies investigating the ecology and behavior of reintroduced specimens have only begun to give scientists an understanding of the region’s resurrected Lake Sturgeon population. Unlike the well-studied northern populations, there are several aspects of Lake Sturgeon ecology and management that scientists in the Southeastern U.S. have yet to address. One such research need is an assessment of diet and prey availability of Lake Sturgeon residing in the impounded portions of the Upper Tennessee River Basin, where most reintroduced Lake Sturgeon congregate (SLSWG Management Plan 2013). Due to lower latitudes and the serially impounded environment of the Upper Tennessee River Basin, it is likely that food availability will be different than that found in the northern reaches of the Lake Sturgeon’s range. The present exploratory study will be significant in the future management of southeastern Lake Sturgeon by providing baseline data on foraging habits of and prey availability for juvenile stocked Lake Sturgeon in Upper Tennessee River reservoirs. Furthermore, the results of my study will facilitate future assessments of the growth, recruitment and bioenergetics of the restored Southeastern Lake Sturgeon stock.

Background

Lake Sturgeon are fish in an ancient clade of fishes, with Acipenseriformes first appearing in the fossil record during the Upper Cretaceous (Peterson and Vecsei 2004), earning them the title ‘living fossil’. They and other species in the subclass Chondrostei retain many of the features possessed by their ancestors (Harkness and Dymond 1961) and are one of only forty eight extant non-teleost Actinopterygian species remaining (Liem et al. 2001).

With regard to morphological characteristics, *A. fulvescens* is broadest towards the anterior portion of its body and tapers posteriorly, ending with a heterocercal tail. The snout is short and blunt, with a lateral row of four sensory barbels on its ventral surface anterior to its mouth, enabling the fish to sense benthic prey. The mouth is inferior and protrusible; it also lacks teeth, and its lips are fleshy. Five rows of bony plates, or scutes, are arranged in longitudinal rows along the body; two on either side and one along the dorsum. The scutes terminate in a sharp-pointed spur that becomes smoother as the fish ages. Young individuals have a spiny appearance, which is in sharp contrast to the smooth condition in adults (Harkness and Dymond 1961). Large skin blotches indicative of young specimens disappear when individuals reach 60 centimeters, giving way to a uniform olive-brown to grey color on back and sides, with the underside a solid white (Scott and Crossman 1973). The stomach of a Lake Sturgeon is specialized for allowing the consumption of certain hard-shelled prey items (notably snails, mussels, and clams), and thus contains thick, muscular walls capable of crushing gastropods and bivalves (Harkness and Dymond 1961). Lake Sturgeon possess a physostomous swim bladder which retains a connection between the alimentary canal and the gut via a pneumatic duct. This allows for the fish to gulp atmospheric air to initiate the inflation of its swim bladder (Harkness and Dymond 1961).

Ecomorphology of Sturgeon Feeding

Ecomorphology examines the relationship between an organism's morphology and its environment, subsequently providing insights into how that organism survives and reproduces (Van der Klaauw 1948). This discipline is of special interest to Lake Sturgeon biologists, as form-function relationships are critical in understanding precisely how these fish meet their life-history requirements. Lake Sturgeon have evolved to forage in benthic environments, and their unique mouth placement has enabled the development of a specific feeding behavior (Vecsei and Peterson 2004). Respiration is accomplished by a unique arrangement of the mouth, buccal cavity, gill arches, and suboperculum (although Lake Sturgeon are primarily continuous cruisers, their morphology prevents them from ram ventilation due to their inferior mouth placement). A unique morphological adaptation allows for water to flow into the opercular chamber, through the gill arches, and back out the opening of the suboperculum, even when continuously feeding from the benthos (Vecsei and Peterson 2004).

Lake Sturgeon have been referred to most accurately as 'supra-benthic cruisers' (Vecsei and Peterson 2004), as they are not a truly benthic fish. However, they do feed primarily on benthic invertebrates and rely heavily on tactile, olfactory, chemosensory, and electrosensory receptors to locate them (Harkness and Dymond 1961). Feeding occurs as a fish sweeps the benthos (or variable adjacent surfaces) while keeping its barbels in contact with the substrate. When a prey item is detected, suction is used to capture the prey by rapidly extending their protrusible mouth and creating a negative pressure gradient in the buccal cavity by closing the suboperculum during suction and swallowing prey whole (Vecsei and Peterson 2004). Sturgeon expel non-edible materials through the subopercula or mouth (Scott and Crossman 1973). Nonetheless, substances like mud and gravel manage to pass through their digestive system. Though Lake Sturgeon inhabit a variety of substrate types, prey availability (quantity and quality) is undoubtedly an important factor in determining habitat selection (Harkness and Dymond 1961).

Food quantity and quality as well as temperature are the main factors influencing the bioenergetics of fishes (LeBreton and Beamish 2005). Thus, quantitative assessment of diet is an important aspect of fisheries management (Chipps and Garvey 2007), and managing prey resources is vital in conserving threatened or endangered fish (Finnoff and Tschirhart 2003). Accurate descriptions of fish diets and feeding patterns not only help to assess habitat selection and growth, but also outline trophic interactions in large river systems (Vander Zanden et al. 2000). Furthermore, such studies can be used to assess habitat suitability and/or establishment of non-native species (e.g. zebra mussels, *Dreissena polymorpha*).

Determining the carrying capacity for Lake Sturgeon in the Tennessee River is a priority research agenda in need of immediate attention. Response of the fish in their habitat will be a useful tool to assess reintroduction success (SLSWG Management Plan 2013). Compared to marine or estuarine habitats, which are rich in benthic invertebrate resources, deep riverine systems (where Lake Sturgeon spend the entirety of their lives) tend to be less rich (Vannote et al. 1980). There is a high energy cost of foraging in these deep large-river and reservoir environments, which can be taxing for sturgeon (Sulak and Randall 2002). Understanding the availability of prey items in the Tennessee River can help managers better understand how Lake Sturgeon are faring in their newly reclaimed environment. Growth rates for sturgeon have also been shown to decline when dams decrease productivity by altering downstream and upstream habitats (Everett et. al 2003), therefore creating a more comprehensive representation of Lake Sturgeon stressors (including food web dynamics) can aid managers in restoration efforts. Although Harkness (1923) reported that Lake Sturgeon from Ontario, Canada consumed crayfish, mollusks, insect larvae and nymphs, fish eggs, fishes (rarely), nematodes, leeches, amphipods, and decapods, a more detailed study of Lake Sturgeon diet in the Upper Tennessee River Basin is of considerable importance, because significant differences in geographic range can yield different results. I set out to a) identify the seasonally available benthic prey base for juvenile Lake Sturgeon in Fort Loudoun Reservoir by dredging sediments and deploying passive rock baskets to determine relative abundance of invertebrate taxa b) analyze juvenile Lake Sturgeon diet composition from stomach and intestinal contents to determine the composition of their diet and the relative abundance of prey items consumed and c) determine whether juvenile Lake Sturgeon in Fort Loudoun Reservoir forage selectively or opportunistically on seasonally available benthic invertebrates.

Study Area

The portion of the Upper Tennessee River Basin between Knoxville, TN and Chattanooga, TN roughly forms the primary focal point of Lake Sturgeon reintroduction in the Upper Tennessee River Basin (SLSWG Management Plan 2013). Fort Loudoun Reservoir is located on the Tennessee River in close proximity to Knoxville, and is the uppermost of nine Tennessee Valley Authority (TVA) reservoirs that form a continuous navigable channel from Knoxville downstream to Paducah, Kentucky. Within the central portion of Fort Loudoun Reservoir, a reach of riverine habitat (Figure 1) was subjectively chosen to carry out this particular study. Stretching from river mile marker (RMM) 625 upstream to 633 (13 km), this study area was determined by analyzing habitat utilization data collected from a separate Lake Sturgeon telemetry study using sonic VEMCO transmitters (Saidak 2015). These areas consistently harbor juvenile Lake Sturgeon and movement data revealed that previously tagged specimens reliably inhabited or otherwise repeatedly passed through this study area.

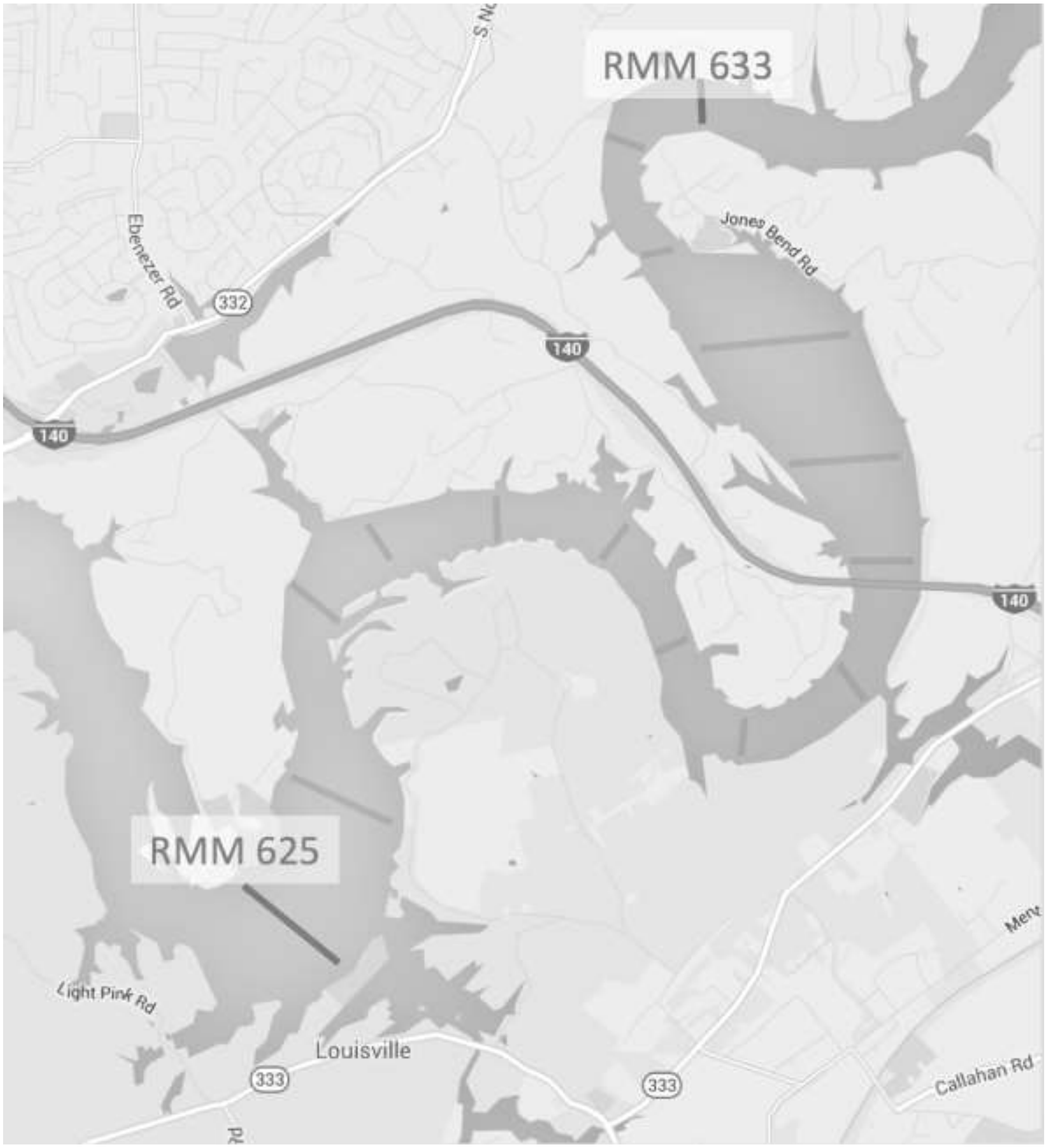

Figure 1. A stretch of riverine habitat in Fort Loudoun Reservoir, Tennessee between river mile markers 625 and 633, which is known to reliably harbor Lake Sturgeon (Acipenser fulvescnes) (Saidak 2015); cross hatches symbolize the entirety of the study area

Chapter 2

Materials and Methods

To assess benthic prey availability for Lake Sturgeon in the Fort Loudoun Reservoir study area, 305-mm^2 Peterson dredge samples were taken from locations on the reservoir bottom. These locations were determined using a systematic sampling method whereby benthic dredges were taken at 3-5 points (depending on the width of the river) spaced equidistantly along each transect from bank to bank. A series of transects perpendicular to the river flow were distributed evenly between river miles 625 and 633, roughly 1 kilometer apart (see Figure 1).

The Peterson dredge, attached to 30 meters of steel cord, was deployed by a winch connected to a custom-made boom crane constructed of stainless steel. After pulling a pin that securely anchored the dredge in place, the weight of the dredge allowed it to free spool into the water column where it continued to plunge until reaching the benthos (which occurred at a wide variety of depths). The battery-powered winch then retrieved the dredge along with its content.

The sediment from each dredge sample was emptied into a large plastic tub and homogenized by hand. Three randomly chosen 1-L subsamples were selected and deposited into a sieve bucket equipped with 500-µm wire mesh. The sieve bucket was then lowered into the river water where it was twisted and oscillated simultaneously, leaving only benthic invertebrates and coarse particulate organic matter. Specimens were then placed in jars filled with 70% isopropanol where they were preserved until identification took place at the University of Tennessee Fisheries Research Lab in

Knoxville (UT-Knoxville). If samples contained an unusual amount of organic matter that makes picking invertebrates difficult or time consuming in the field, these samples were placed in their entirety in 70% isopropanol and picked and sorted in the laboratory.

Samples were identified using the most current dichotomous keys and stored at UT-Knoxville. A percentage of invertebrate identifications were then passed through a quality control process administered by the primary investigator, Dr. Brian Alford, to ensure taxonomic identifications were in agreement. At least 30 dredge samples were taken seasonally within the study area to account for phenological changes in prey availability as invertebrate metamorphose from aquatic immature forms to terrestrial adults. Two seasons were sampled and occurred during a) warm weather months (May-September) and b) cool weather months (October-April).

While the diet of Lake Sturgeon may be primarily composed of benthic invertebrates from fine sediments (e.g., silt, clay, sand), the prey base available on or near hard substrate (i.e., epibenthic or lithophilic invertebrates) was also taken into account. To characterize this assemblage, rock basket samplers filled with hard substrate (riprap, limestone, and clay tiles) were deployed opportunistically in areas containing hard substrate. Available hard substrate surfaces can include bridge pilings, rocky cliffs, gravel, cobble, and boulders contained within the study area, generally occurring in 1-3 meters of water. The cages were located via GPS tracking, which was further aided by fastening orange buoys to the end of each rope. Cages remained in place for a one month period, allowing invertebrates to passively colonize the substrate within the cages via drift or active movement from surrounding surfaces. At this point they were retrieved and processed in the field. Each cage was slowly retrieved from the research vessel by carefully pulling up the rope to which each cage is fastened. Invertebrates were picked with forceps not only from the substrate contained within the cage, but also from the cage itself, which was placed on a large, plastic laboratory tray. Each piece of hard substrate was then placed in a separate laboratory tray as they were combed over for invertebrate specimens. These specimens were also preserved in 70% isopropanol, identified using the most current dichotomous keys, and passed through a quality control process administered by Dr. Brian Alford.

The prey availability study was accompanied by a diet study that evaluated the stomach and intestinal content of all Lake Sturgeon captured, regardless of age or size, in Fort Loudoun Reservoir. Trotlines were deployed opportunistically during cool (November-December) weather months to take advantage of safe sturgeon-handling techniques employed by SLSWG biologists. However, the first ever attempt to sample Lake Sturgeon diet in the Southeast during summer months was also made. In order to limit undue stress to Lake Sturgeon specimens sampled in the summer, only the colonic flush technique was administered in order to expedite the processing time. Before performing gastric lavage and colonic flush techniques, specimens were sedated using 100mg of MS-222 (Tricaine Methanesulfonate) per liter of river water for 2-4 minutes, which was mixed in a large metal holding tub. While an individual fish was being processed, additional specimens remained in the holding tub (up to 3 at a time) until a new individual could be processed. After being processed, each fish was resuscitated by hand until they swim away under their own power.

The methods used for gastric lavage and colonic flush techniques are briefly described below:

1) Gastric lavage is a non-lethal method for examining the content of fish stomachs. A pump sprayer is attached to a soft plastic tube that is inserted into the pharynx of a sedated fish. Water is gently but consistently pulsed into the stomach until the fish begins to convulse, at which point the contents of its stomach are expelled into the dissecting tray.

2) Colonic flushing is a non-lethal method for examining fecal matter contained in the intestinal tract, whereby a bottle is filled with river water and the end gently inserted 30–50 mm through the anus and into the colon. The bottle is gently squeezed in short pulses, and feces expelled into a dissecting pan (The colon is flushed until the expelled water is clear, generally a 15-30 second process.)

After a successful gastric lavage or colonic flush (occasionally stomachs and/or colons were empty), the contents contained in the dissection tray are strained in a 500-µm mesh sieve, picked, and preserved in 70% ethanol for later identification in the lab.

Analyses

The foraging modes of Lake Sturgeon were determined by comparing the relative abundances (i.e., percent composition) of invertebrate taxa in the gut contents of each sturgeon specimen to the relative abundances of the same invertebrate taxa collected from the resource base. The resource bases sampled included a) benthic sediment and b) hard substrate. Invertebrates were identified to their lowest possible taxonomic level using the latest dichotomous keys. Levins’ niche breadth index (NB) was used to determine if Lake

Sturgeon in Fort Loudoun Reservoir fed on a relatively large or small array of prey taxa (Levins 1969). The equation is:

$$\mathrm{NB} = 1 / (s^{*} \sum r_i 2),$$

where 's' is taxa richness and 'r_i' is the relative abundance of taxon 'i' found in the diet of the Lake Sturgeon community sample. Values of NB discern between specialists (NB = 1/s) and generalists (NB = 1.0). Both niche breadth and proportional similarity should be used together to obtain a broader, more precise dietary assessment, as using NB alone does not take available prey into consideration. Therefore, proportional similarity (PS) was used to determine the foraging mode of the Lake Sturgeon community sample. The equation is as follows:

$$\mathrm{PS} = 1 - 0.5 \sum |r_i - q_i|,$$

where 'r_i' is the relative abundance of prey taxon 'i' found in the Lake Sturgeons' diet, and 'q_i' is the relative abundance of the same prey taxon found in the prey base; separate calculations were performed for the benthic grabs and the rock cages.

To identify specific prey taxa that were selected or not selected, Manly's index was used (Manly et al.1993). Krebs (1989) describes Manly's index as the best index for describing resource preferences by populations. The equation for Manly's index is as follows:

$$\alpha_i = r_i/q_i \, [1/\sum(r_i/q_i)]$$

The equation yielded the number of prey taxa available in the resource base (symbolized by 'm'). A value less than 1/m indicates a prey taxon that was consumed disproportionately less than its relative abundance in the resource base. Values approaching 1/m indicate that a prey taxon was consumed in direct proportion to its availability, and values greater than 1/m indicate a prey taxon that was consumed disproportionately more than its relative abundance in the resource base, with values near 1 indicating stronger selection of a prey taxon.

In addition, a jacknife resampling technique was used to estimate variance and bias in the PS and NB estimates. It works by systematically omitting a single observation from the dataset, calculating the estimate, and then finding the average of these calculations.

While my first two research objectives are descriptive in nature, the aforementioned analyses were used in concert to satisfy the third objective; by defining the niche breadth, preferred foraging habitat, and seasonally selected prey items, Lake Sturgeon foraging modes in Fort Loudoun Reservoir can be objectively determined.

Chapter 3

Results and Discussion

Results

All 32 Lake Sturgeon specimens sampled were caught on trotlines in the specified study area in Fort Loudoun Reservoir (30 in the fall, 2 in the summer). The fishes ranged from total lengths of 22 cm to 82.5 cm and weights of 0.06 kg to 4.3 kg. The average length for all fishes was 69 cm and the average weight was 1.68 kg (see Table 1 for size classes). I identified a total of 6,581 invertebrates from Lake Sturgeon diets between cool (6,416) and warm months (165). The invertebrate taxa found in cool month diets (see Table 2 for frequency of occurrence) were comprised of 9 families and 14 genera, while warm season diets consisted of 3 families and 7 genera. From the resource base I identified a total of 1,667 invertebrates between cool (775) (see Figure 2) and warm months (892) (see Figure 3). The invertebrate taxa found in the cool month prey base consisted of 19 families and 40 genera, while the warm season prey base consisted of 15 families and 18 genera. To insure that a sufficient number of Lake Sturgeon individuals were sampled in order to adequately assess diet composition, a species-sample curve was employed (Brower et al. 1997) (see Figure 4). The cumulative number of invertebrate taxa consumed increased gradually until it plateaued. Chironomid (Diptera) larvae dominated Lake Sturgeon diets during both the cool and warm months (see Figure 5), representing relative abundances of 96% during cool months and 93% during warm months. Other invertebrate taxa that contributed to Lake Sturgeon diets in the cooler months, albeit to a much lesser degree, include burrowing mayfly nymphs (*Hexagenia*

Table 1. Size classes of Lake Sturgeon (Acipenser fulvescens) from Fort Loudoun Reservoir and associated niche breadth (NB) and proportional similarity (PS)

Size class	***NB***	***PS (Benthos/Cages)***
< 66 cm TL (n=3)	0.28	0.50/0.07
66-75 cm TL (n=20)	0.16	0.53/0.09
> 75 cm TL (n=5)	0.19	0.52/0.08
Avg. fish = 69 cm, 1.68 kg		

Table 2. Frequency of occurrence (%FO) for each taxon consumed by Lake Sturgeon (Acipenser fulvescens) during cool months (October-April); data were insufficient for warmer months (May-September)

Taxon consumed	***%FO***
Chironomidae	100%
Hexagenia	67%
Ceratopogonidae	63%
Chaoboridae	53%
Oligochaeta	23%
Pupa	17%
Musculium	17%
Corbicula	7%
Nematoda	3%

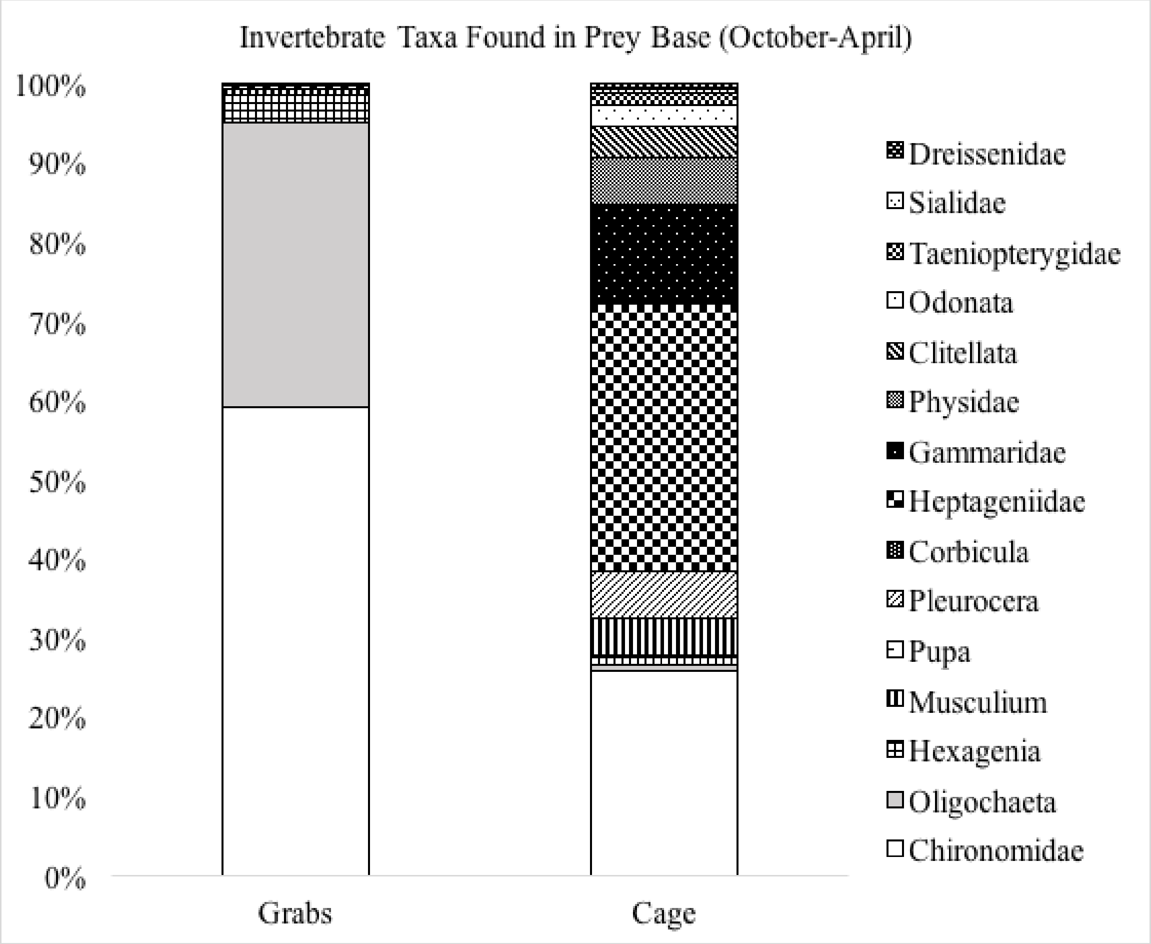

Figure 2. Invertebrate taxa available to Lake Sturgeon (Acipenser fulvescens) in both the benthos and on hard substrate in Fort Loudoun Reservoir during cooler months (October-April)

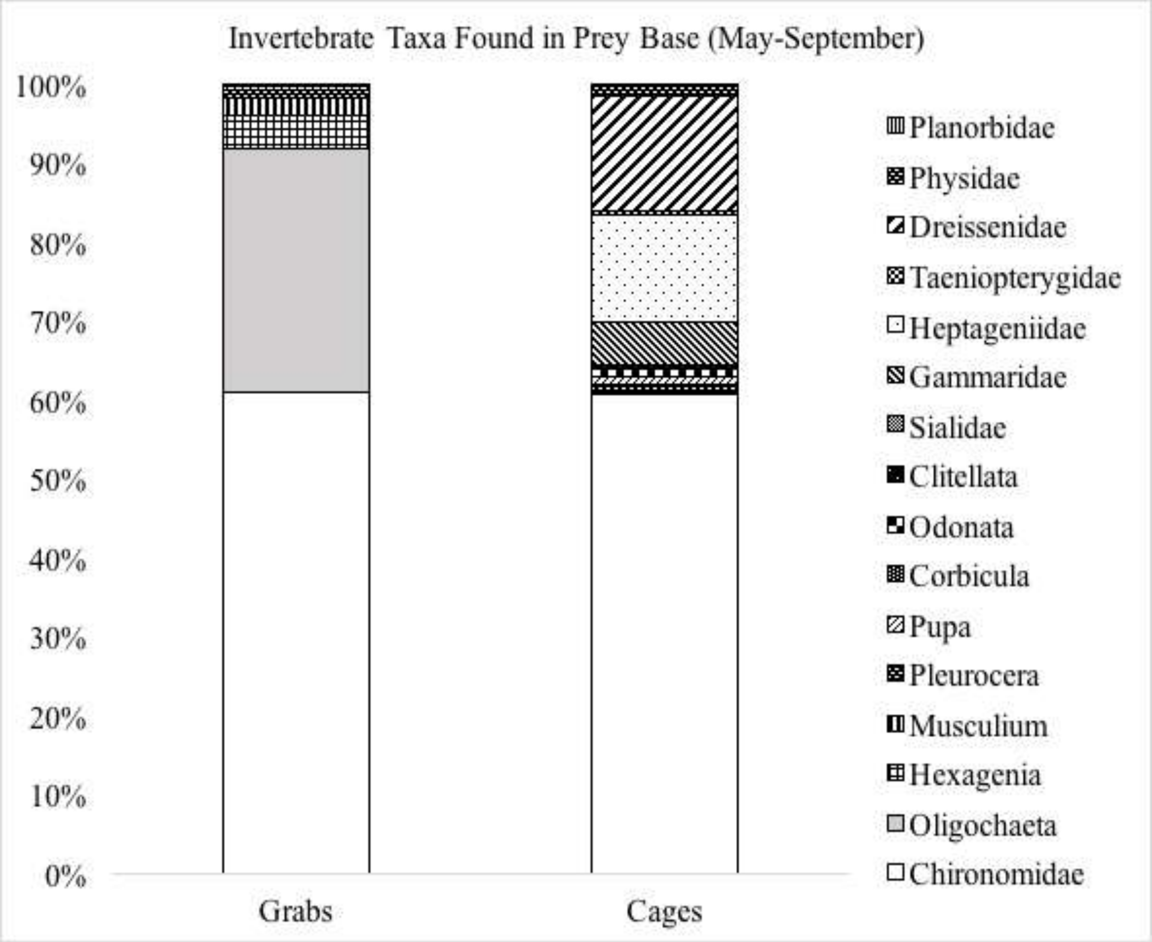

Figure 3. Invertebrate taxa available to Lake Sturgeon (Acipenser fulvescens) in both the benthos and on hard substrate in Fort Loudoun Reservoir during warmer months (May-September)

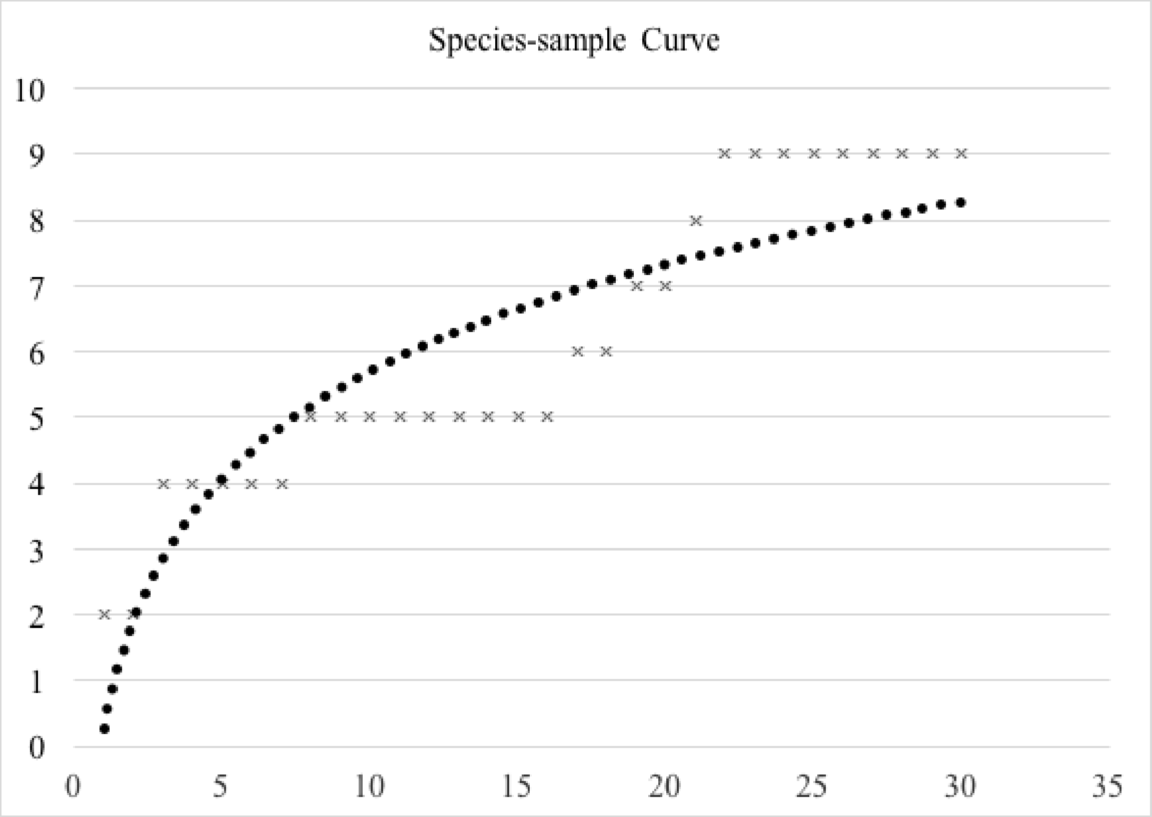

Figure 4. A species-sample curve revealing that an adequate number of Lake Sturgeon (Acipenser fulvescens) individuals (x axis) were sampled in order to properly assess the cumulative number of invertebrate taxa consumed (y axis) (a trend line shows that the cumulative number of invertebrate taxa consumed, signified by grey x's, plateaus); only cool season fish (October-April) were assessed, as warm season data (May-September) were insufficient

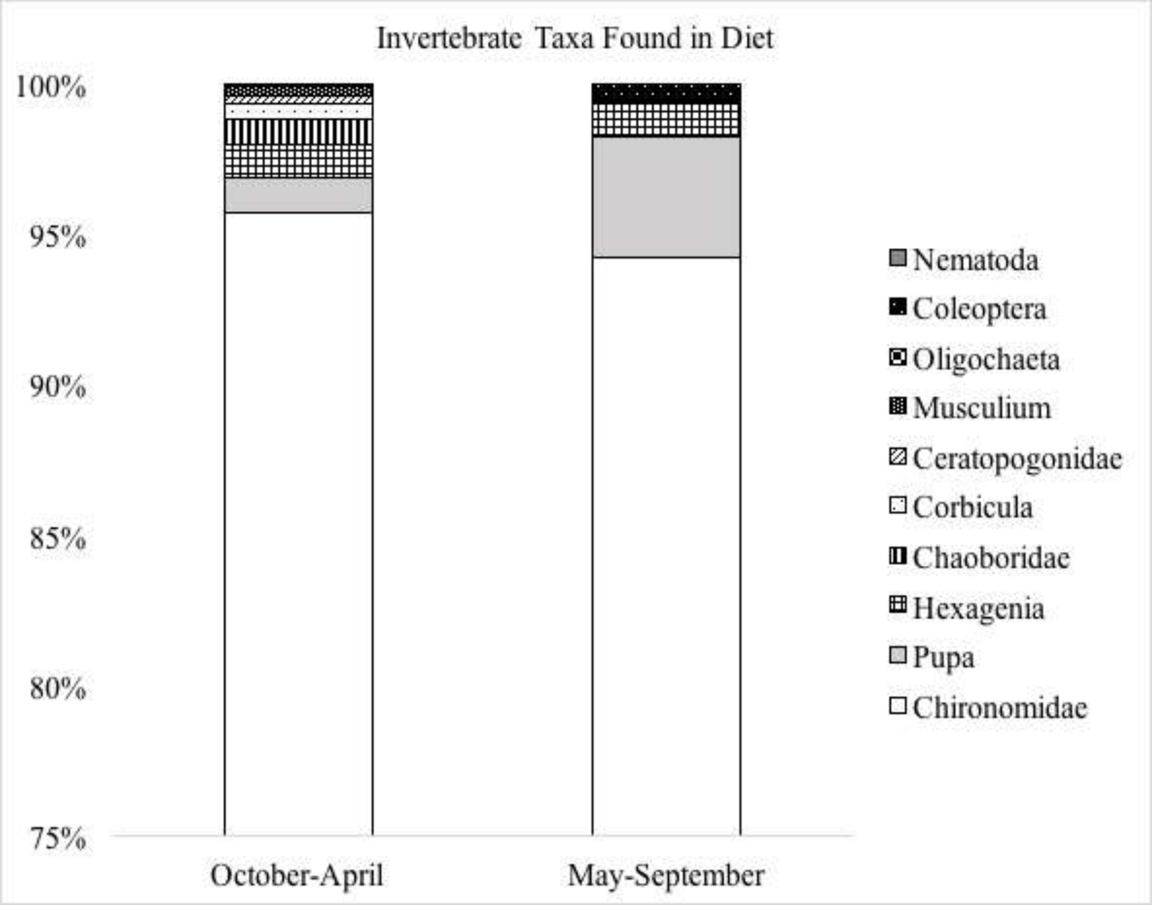

Figure 5. Invertebrate taxa recovered from the stomachs and colons of Lake Sturgeon (Acipenser fulvescens) from Fort Loudoun Reservoir during cool (October-April) and warm (May-September) months (displayed as relative abundance)

sp., 1%) and Diptera pupa (1%). The 2 fish sampled during the summer fed almost exclusively on chironomid larvae (93%), though Diptera pupa also contributed to the relative abundance (4%) along with burrowing mayfly nymphs (*Hexagenia* sp., 1%).

A total of 83 benthic dredge samples were taken between cool (37 samples) and warm (46 samples) months. During cool months the benthic prey base was comprised primarily of chironomid larvae (49%), oligochaetes (44%), and burrowing mayfly nymphs (*Hexagenia* sp., 4%). During warm months the benthic prey base was comprised mostly of chironomid larvae (60%), followed by oligochaetes (31%), burrowing mayfly nymphs (*Hexagenia* sp., 4%), fingernail clams (*Musculium* sp., 2%), and hornsnails (*Pleurocera* sp., 1%).

Rock cages were deployed a total of 28 times between cool (17 deployments) and warm (11 deployments) months. All but one of the cages (treated as an experimental outlier, see Appendix) were deployed for a month before being retrieved and processed (see Methods). Flathead mayfly nymphs (*Stenacron* sp., 34%) had the greatest relative abundance in the cool season samples, followed by chironomid larvae (25%), amphipods (*Gammarus* sp., 12%), and fingernail clams (*Musculium* sp., 4). Warm season rock cage samples were dominated by chironomid larvae (60%) followed by zebra mussels (*Dreissena* sp., 14%), flathead mayfly nymphs (*Stenacron* sp., 13%), and amphipods (*Gammarus* sp., 5%). Generally, chironomid larvae dominated individual Lake Sturgeon diets across seasons; the most chironomid larvae found in a single Lake Sturgeon was 1,065 (November 2015).

Foraging Mode

Levin's niche breadth (NB) was used to determine how wide or narrow the Lake Sturgeon population sample's foraging patterns were during both cool and warm months (see Figure 6). During cool months the NB for Lake Sturgeon was 0.14, suggesting a particularly narrow foraging niche. The proportional similarity (PS) during cooler months was relatively high for prey taxa found in the benthos (0.52) and exceptionally low for prey taxa found in rock cages (0.08) when compared to cool month diet data. Warmer months saw a higher NB, suggesting Lake Sturgeon might employ a broader niche during the summer (0.41). A PS value of 0.57 also suggests a preference for prey taxa found in the benthos compared to prey taxa found on hard substrate (PS=0.02). A jackknife resampling technique yielded an error estimate of 1% for cool months and 4% for warm months.

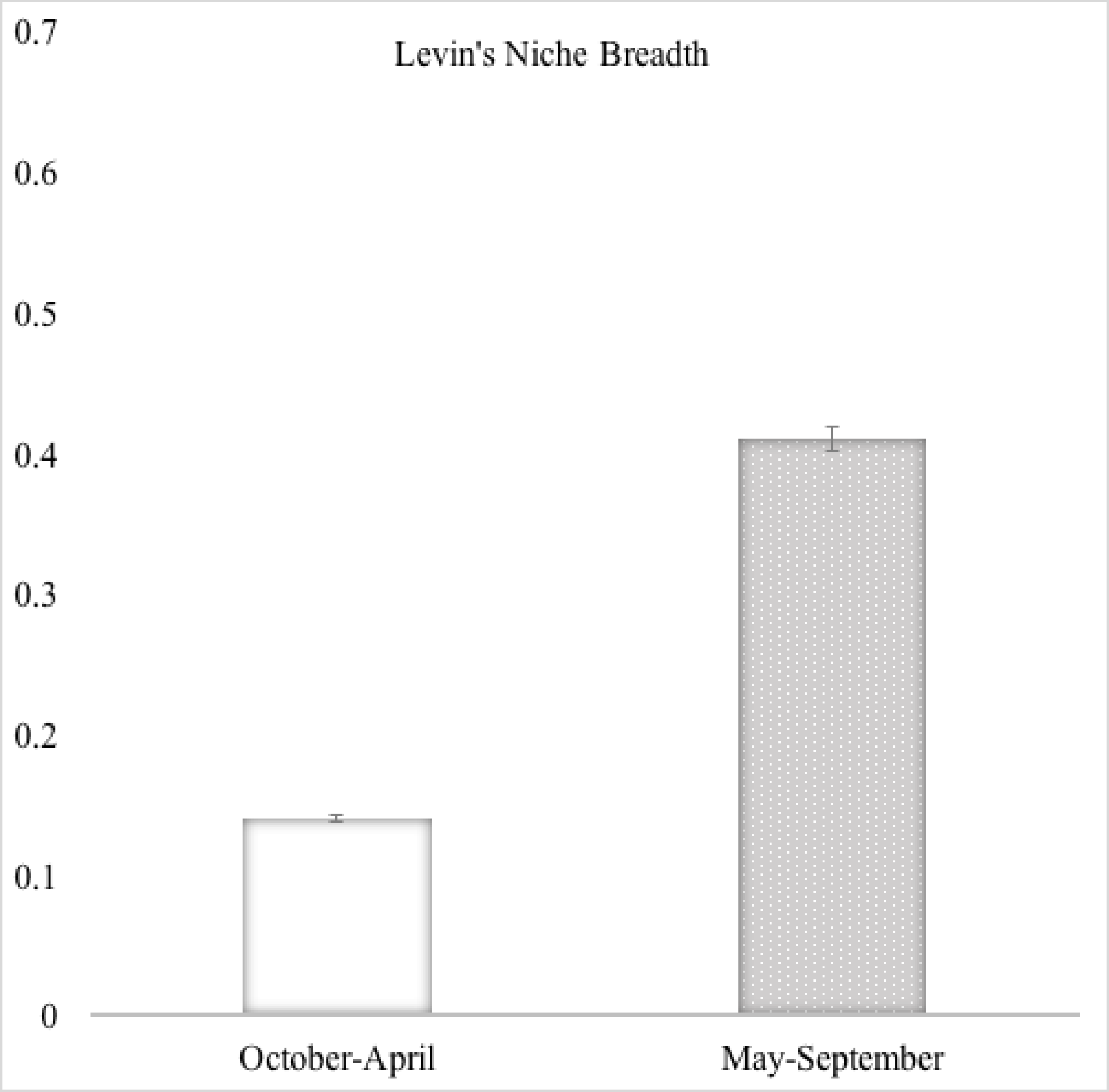

Figure 6. Levin's niche breadth (NB) indicates whether Lake Sturgeon (Acipenser fulvescens) in Fort Loudoun Reservoir utilize a relatively narrow (close to 0) or wide (approaching 1) niche

The explanation for 1) a generally low NB across seasons 2) a relatively high PS value for dredge sample to diet comparison and 3) an extremely low PS value for rock cage sample to diet comparison can be attributed a concerted effort made to identify chironomid larvae to genus/species level. Instead of all chironomids (family Chironomidae) being given equal taxonomic treatment, splitting the chironomids into different genera revealed or identified a distinct dissimilarity between chironomid genera found (and preyed upon) in the benthos and chironomid genera found (but altogether absent from Lake Sturgeon diets) on hard substrates.

I can conclude that during cooler months Lake Sturgeon in Fort Loudoun Reservoir tended to feed more like classic specialists, as they fed disproportionately more on chironomid larvae (0.96), even when that prey taxon was only available at a relative abundance of 0.50 (benthos) and 0.25 (hard substrate) respectively. The only class that was available in high relative abundance in the benthos (0.44) but preyed upon disproportionately less (0.0005) was oligochaeta.

During warmer months, though diet data is less sufficient, Lake Sturgeon also fed like specialists, disproportionately feeding on chironomid larvae (0.93) even when their relative abundances in the benthos (0.61) and rock cages (0.61) were substantially less. Oligochaetes were again available at a relatively high abundance (0.31), but no oligochaetes were found in sturgeon diets.

Manly’s index (see Table 3) identified prey taxa that were selected or not selected. During the cool season ($1/m = 0.026$), Lake Sturgeon selected five genera of larval chironomids along with Diptera pupa (likely also in the family Chironomidae) and

Table 3. Manly's α (αi) describing selective predation by darters on invertebrate prey; a chironomid taxon is indicated by an asterisk. The percent relative abundances from Lake Sturgeon (Acipenser fulvescens) diets (ri) and the resource base (qi) in Fort Loudoun Reservoir are shown. Manly's α values greater than 1/m denote selective predation by Lake Sturgeon on a prey taxon.

Invertebrate prey	α_i	r_i	q_i
Cool months (1/m = 1/39 = 0.026)			
Chironomus sp.*	0.10	0.72	0.35
Coelotanypus sp.*	0.25	0.18	0.03
Ablabesmyia sp.*	0.06	0.03	0.02
Procladius sp.*	0.10	0.01	0.01
Cryptochironomus sp.*	0.11	0.02	0.01
Pupa (Diptera)	0.15	0.01	<.01
Corbicula sp.	0.21	0.01	<.01
Warm months (1/m = 1/27 = 0.037)			
Coelotanypus sp.*	0.06	0.11	0.02
Ablabesmyia sp.*	0.59	0.19	<.01
Cryptochironomus sp.*	0.28	0.15	0.01
Pupa (Diptera)	0.05	0.04	0.01

Corbicula sp., the only completely non-chironomid prey item. During warmer months (1/m = 0.037), Lake Sturgeon selected 3 genera of larval chironomids and Diptera pupa.

Discussion

It is imperative that, when describing the foraging mode of Lake Sturgeon in the Upper Tennessee River Basin, one considers the taxonomic scale at which their prey items are identified. Identifying prey items to family, easy though it may be, would mislead the investigator into concluding that Lake Sturgeon are generalists, as numerous previous studies have suggested. This conclusion is reached because relative abundances of prey items found in stomach samples generally resemble the relative abundances of prey items available in the resource base. Instead, my results suggest that Lake Sturgeon in Fort Loudoun Reservoir forage selectively on certain seasonally available chironomid genera, whereas other prey items were avoided. The ecological conventions of certain larval chironomids might make them more prone to predation. Tube-dwellers like *Chironomus* spp. that spent more time outside of their tube feeding may have been more susceptible to predation (Hershey 1987). High population densities of *Chironomus* spp. only transpire in sediments that are deep enough to allow construction of extensive vertical tubes (Pinder 1995), which Fort Loudoun Reservoir maintains in abundance. These tubes regularly protrude 2-3 cm above the level of the sediment, making them an easy target for Lake Sturgeon cruising above the benthos in search of attainable food items. Also, predatory chironomids such as *Coelotanypus, Ablabesmyia, Cryptochironomus,* and *Procladius* spp. may have made themselves available to predation by spending a considerable amount of time outside of their tubes in search of prey items.

Perhaps the most unanticipated aspect of the diet data is the general lack of oligochaetes found in Lake Sturgeon stomachs and/or colons. A review of the literature confirms that oligochaetes can contribute significantly to the relative abundance of Lake Sturgeon diets in other geographical areas. For example, Choudhury et al. (1996) found oligochaetes to be the second most numerous prey item found in Lake Sturgeon stomachs in Lake Winnebago, Wisconsin. Oligochaetes were quite plentiful in Fort Loudoun Reservoir; cooler months saw a relative abundance of 0.44 in the benthos while warmer months maintained a relative abundance of 0.31. In contrast, the cool season saw a total of 2 oligochaetes in sturgeon stomachs and only 1 in the colon. No oligochaetes were found in either of the fish sampled in July 2015. Oligochaetes are the only completely soft-bodied organisms consumed by Lake Sturgeon in Fort Loudoun Reservoir, and are a potentially nutritive prey item. It can be presumed that soft-bodied organisms might be digested more quickly, suggesting that oligochaetes are consumed more regularly by Lake Sturgeon even though they fail to make their way through the entire digestive system relatively intact. But this impression is not befitting when personal observations of live chironomids extracted from sturgeon colons were made on multiple occasions. Furthermore, oligochaetes were found in previous studies to make a considerable contribution to the relative abundance of prey items after they most certainly passed through Lake Sturgeon digestive systems intact. A better explanation could be that the preferred burrowing depths of oligochaete taxa in Fort Loudoun Reservoir put them out of reach of the comparatively small Lake Sturgeons' protrusible mouths. This could mean that oligochaetes are not functionally available to Lake Sturgeon in Fort Loudoun Reservoir.

After inferring that Lake Sturgeon in Fort Loudoun Reservoir prefer to forage from within the benthos (see Figure 7), one might speculate as to why this is so. Seeing as juvenile Lake Sturgeon rely heavily on larval chironomids, ephemeroptera, and annelids, found in soft or gravelly substrate (Kempinger 1996; Chiasson et al. 1997), these prey items can be attained over a flat, expansive, and homogenous environment in Fort Loudoun Reservoir. Novel prey taxa retrieved from our rock cages (i.e., prey taxa found in rock cages but not the benthic grabs) were altogether missing from Lake Sturgeon diets. Though a suitable prey base is available on a variety of hard substrates that include: rip-rap along waterfront properties, bridge pilings and, limestone cliffs; it would be more taxing to pursue these prey items and might provide an explanation as to why the benthos is the preferred habitat for foraging. Also, hard substrate habitats in Fort Loudoun Reservoir tend to be more patchily distributed and are thus encountered with less frequency by Lake Sturgeon.

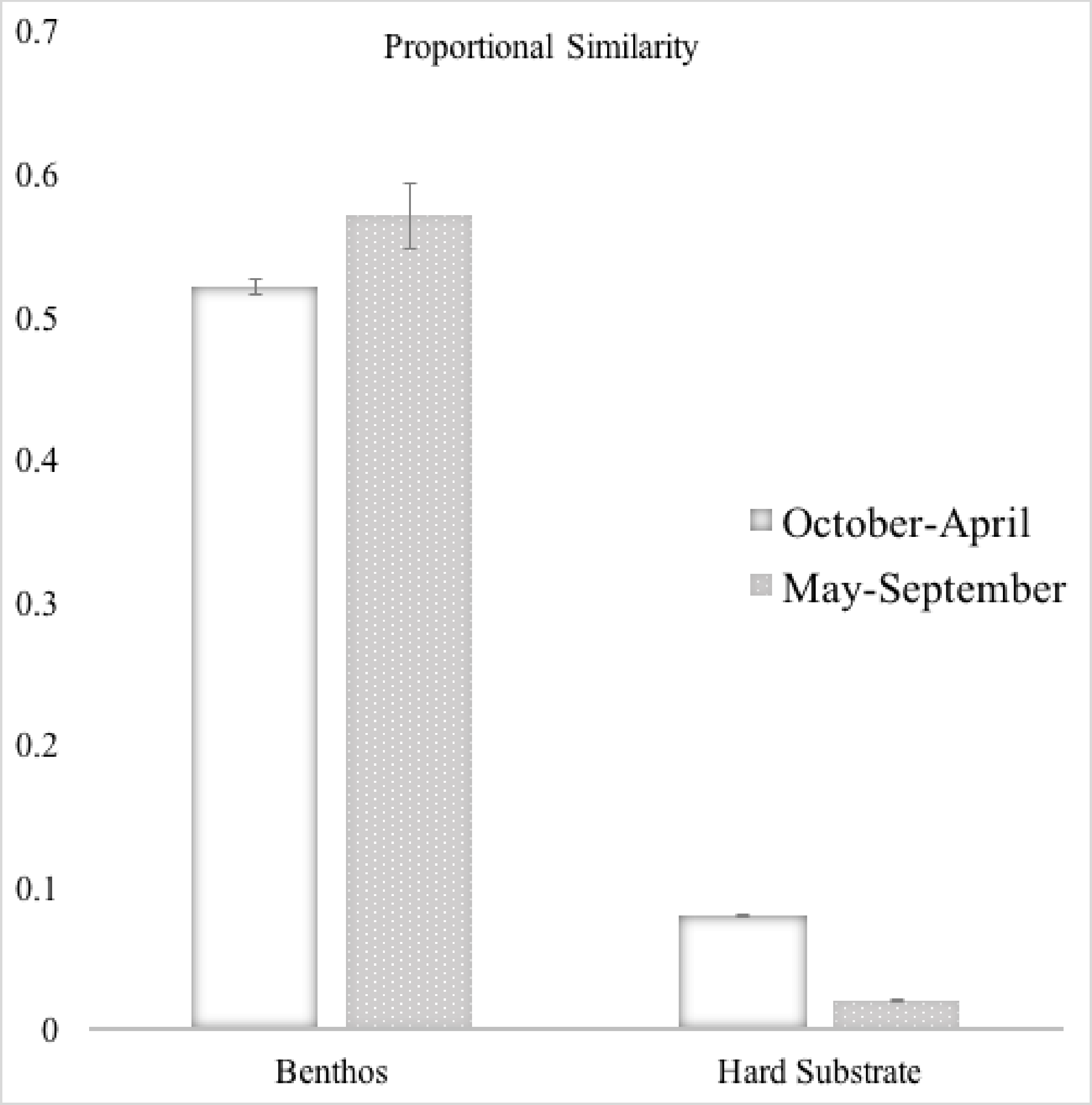

Figure 7. Proportional Similarity (PS) compares the invertebrate taxa composition found in the diet of Lake Sturgeon (Acipenser fulvescens) to the invertebrate taxa composition found in the prey base in Fort Loudoun Reservoir (closer to 0 is less similar, closer to 1 is more similar).

A thorough, quantitative characterization of benthic substrate was not taken into account, though the general composition of each grab was documented. Of the 83 total benthic grabs retrieved, 63 of them were composed of fine silt, 5 contained considerable fine particulate organic material, 5 contained minimal fine particulate organic material, 5 were composed of a mixture of cobble and gravel, 2 were hard-packed clay, 2 were primarily composed of sand, 1 was exposed bedrock, and 1 was an entire boulder approximately 65 cm in diameter.

Previous studies have investigated Lake Sturgeon diet in the northern reaches of this species' expansive range; generally, these studies have concluded that *A. fulvescens* is an opportunistic benthic feeder (Chiasson et al. 1997, Nilo et al. 2006) that preys on a wide variety of taxa (see Table 4). However, it is important to note that few of these studies compared Lake Sturgeon diet to the relative abundance of prey taxa available in the resource base, making it difficult or impossible to properly discern foraging patterns. Furthermore, even fewer diet studies have identified chironomid larvae to the genus/species level. I believe that, in addition to a systematic assessment of prey availability, identifying chironomid larvae to genus/species is the main driver in accurately determining foraging mode for suction-feeding, benthic invertivores (Alford and Beckett 2007), especially when larval chironomids are consumed so disproportionately to other prey items.

Table 4. Results from previous Lake Sturgeon (Acipenser fulvescens) diet studies conducted in northern areas with well-studied populations

Study area	***Commonest food items***	***Principal investigator(s)***	***Year***
Oneida Lake, NY	Amphipods Snails Zebra Mussels	J.R. Jackson et al.	2002
Lake Winnebago, WI	Chironomidae Oligochaeta	A. Choudhury et al.	1996
Winnipeg River, Canada	Trichoptera Diptera Ephemeroptera	C.C. Barth et al.	2013

The reintroduction of Lake Sturgeon into the Upper Tennessee River Basin has caused some concern regarding the possibility of Lake Sturgeon consuming native mussels in the family Unionidae. Those species of unionid mussels that have been able to survive and prosper in anthropogenic-induced lacustrine conditions are available to be preyed upon. However, I conjecture that Lake Sturgeon in Fort Loudoun Reservoir are too small and thus gape-limited in regard to adult unionid mussel consumption (though they would certainly be capable of preying upon juveniles, which tend to be small for several years). While available prey items in the phylum Mollusca include zebra mussels (*Dreissena* sp.), fingernail clams (*Musculium* sp.), Asian clams (*Corbicula* sp.), hornsnails (*Pleurocera* sp.), and bladder snails (*Physa* sp.), only fingernail clams and Asian clams were found in the stomach and/or colon of sampled Lake Sturgeon. Of the 36 *Corbicula* clams consumed by Lake Sturgeon during cooler months (none were consumed by the 2 fish sampled during the summer), 33 of them were found in 2 fish, which happened to be the third and fourth largest fish. It is noteworthy that they were the same weight (3.2 kg) and had nearly identical lengths (70.5 cm TL and 71.0 cm TL respectively). However, neither the first nor the second largest fish had consumed any mollusks. It may be possible that larger Lake Sturgeon specimens found downstream of Fort Loudoun Reservoir could consume native mussels that tend to also be larger, but this could only be investigated with future diet studies in other reservoirs that contain larger fish. Though previous studies have found evidence of Lake Sturgeon feeding upon both adult and age-0 fish (J.R. Jackson et al. 2002), I found no evidence of piscivory exhibited by Lake Sturgeon in Fort Loudoun Reservoir, which would come in the form of fish scales, otoliths, or identifiable body parts or whole organisms. I did, however, regularly find considerable amounts of fine sediment in the colons of sampled Lake Sturgeon. This could provide an opportunity for toxins to bioaccumulate in Lake Sturgeon over the length of their considerable life spans, and is worthy of further study.

Of the 32 fish sampled across seasons, the gastric lavage technique was not administered to a total of 8 fish (6 during cool seasons, 2 during the summer). The colonic flush technique was not administered on 2 fish, both during the cool season. The fish sampled during the summer were intentionally not sampled for stomach content due to a perceived threat to the fishes' physiology, primarily because of elevated water temperatures. Failure to administer either technique on the remaining occasions was due to either a sensitivity to fish stress or technical malfunctions.

There were occasions when stomach and/or colon contents were empty. On 11 occasions stomach contents were empty, while on 4 occasions Ifound empty colons. It is possible that a specimen could have recently defecated (in the case of an empty colon) or not foraged recently (in the case of an empty stomach). More likely, the unusual physiological stress of remaining sedentary for extended periods of time on trotlines induced vomiting in certain individuals. Though several sturgeon biologists have suggested this as a possibility, it remains unproven and is nearly impossible to observe directly.

When handling a threatened species, it is important to support the fish properly as they are prone to spinal injuries. Biologists should also remain vigilant of signs of stress (lethargy, body rolling, excessive opercular pumping, etc.). After processing a Lake Sturgeon specimen, it should be fully resuscitated (in an oxygenated tank and/or by hand in river water) in order to reverse the sedative properties of MS-222 before being released. All 32 of the Lake Sturgeon that I sampled during our study swam away vigorously after being processed. A total of 2 fish were resuscitated and released without being processed due to perceived stress by those biologists present; they swam away vigorously.

Concern was expressed about sampling fish during summer months, and this was not taken lightly. The gastric lavage technique was waived in favor of the colonic flush technique, as it is generally a quicker process and less stressful for Lake Sturgeon specimens. After a three-day sampling effort in July, two fish were caught on trotlines using the aforementioned technique. Diet data was gained from both fish and was quite valuable; to our knowledge, Lake Sturgeon diet had not been assessed during summer months in the extreme southern range of its Holarctic distribution. This helped to dispel the notion that Lake Sturgeon avoid feeding during the summer months, even though prey availability is lesser than that available during cooler months. However, having only sampled two fish during warmer months, it is difficult to infer patterns regarding Lake Sturgeon ecology or behavior during summer months. I suggest further research be conducted on Lake Sturgeon diet during both cool and warm months in the Upper Tennessee River System. Specifically, assessing diet of and prey availability for Lake Sturgeon in reservoirs further downstream (perhaps Nickajack or Guntersville Reservoir) which could account for the most valuable insights. Ongoing research and monitoring efforts indicate that larger fish tend to move downstream and congregate in the previously mentioned reservoirs. Noting that Fort Loudoun Reservoir tends to harbor Lake Sturgeon on the smaller end of the spectrum, foraging habits of larger fish downstream could yield noticeably distinctive results.

Chapter 4

Summary and Suggestions

This study seems to support the argument set forth by Pollock et al. (2015) claiming that many Lake Sturgeon ecological traits are plastic and can vary significantly among populations. As we continue research on Lake Sturgeon in the extreme southern reaches of their range, especially in disciplines that are being investigated for the first time (diet, habitat selection, spawning, etc.), it is important that managers exercise caution in transferring knowledge from the literature to our recently reintroduced population.

As such, it is significant to present results of the first comprehensive diet assessment of Lake Sturgeon in the Upper Tennessee River Basin. I conclude that larval chironomids in their abundance are fundamental in providing Lake Sturgeon with nutritive values that contribute to their sustenance and growth. Though organisms in the family Chironomidae dominate both the prey base and Lake Sturgeon prey items, certain genera are more important than others. Namely, chironomid larvae in the genera *Chironomus* (subfamily Chironominae) and *Coelotanypus* (subfamily Tanypodinae) tend to dominate the benthos, the preferred foraging habitat for Lake Sturgeon in Fort Loudoun Reservoir.

Sturgeon are one of the most threatened groups of species in the world. Consequently, we could not expect the resiliency of these organisms to persist indefinitely when dams are operated solely as income-generating or power-producing ventures (Pollock et al. 2015). However, I applaud the Tennessee Valley Authority for operating their dams as structures that consider the environment; beginning in the early 1990's, the Tennessee Valley Authority began improving the quality and quantity of dam releases (Higgins et al. 1999), creating a benthic habitat with improved dissolved oxygen levels and thus an environment more suitable for the colonization of macroinvertebrates.

While it may not be necessary to suggest further management recommendations in Fort Loudoun Reservoir, I must stress the need to investigate macroinvertebrate assemblages in reservoirs further downstream in the upper Tennessee River Basin. A similar composition/abundance of macroinvertebrate taxa may very well yield similar foraging patterns among resident Lake Sturgeon, but a noticeably different prey base could yield interesting and distinctive results, and might warrant a separate diet study.

Though it is more time consuming and labor intensive, this study shows the importance of identifying larval chironomids to genus/species level when they are a principal food item for a particular species of fish. Furthermore, when determining the foraging modes of aquatic predators, it can be misrepresentative to strictly assess the diet. One must also take into account the prey items available in the prey base in order to draw a sounder conclusion when considering sturgeon foraging modes. This is something that many previous Lake Sturgeon diet studies have failed to take into account.

Works Cited

Alford, J.B., and D.C. Beckett. 2007. Selective predation by four darter (Percidae) species on larval chironomids (Diptera) from a Mississippi stream. Environmental Biology of Fish 78:353-364

Barth, C.C., W.G. Anderson, S.J. Peake, and P. Nelson. 2013. Seasonal variation in the diet of juvenile Lake Sturgeon, Acipenser fulvescens, Rafinesque, 1817, in the Winnipeg River, Manitoba, Canada. Journal of Applied Ichthyology 29(4):721-729.

Bezold, J., and D.L. Peterson. 2008. Assessment of lake sturgeon reintroduction in the Coosa River system, Georgia–Alabama. American Fisheries Society, Symposium 62, Bethesda, Maryland.

Brower JE, Zar JH, von Ende CN (1997) Field and laboratory methods for general ecology, 4th ed. McGraw-Hill, Boston

Bruch, R.M. 1999. Management of Lake Sturgeon on the Winnebago System - long term impacts of harvest and regulations on population structure. Journal of Applied Ichthyology 14(4):142–152.

Chiasson, W.B., D.L. Noakes, and F.W. Beamish. 1997. Habitat, benthic prey, and distribution of juvenile lake sturgeon (Acipenser fulvescens) in northern Ontario rivers. Canadian Journal of Fisheries and Aquatic Sciences 54(12): 2866-2871

Chipps, S.R., and J.E. Garvey. 2007. Assessment of food habits and feeding patterns; analysis and interpretation of freshwater fisheries data. Pages 502-514 in M. Brown, editor. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Choudhury, A., R. Bruch, and T.A. Dick. 1996. Helminths and food habits of lake sturgeon Acipenser fulvescens from the Lake Winnebago System, Wisconsin. American Midland Naturalist 135(2):274-282.

Drauch, A. M., and O. E. Rhodes, Jr. 2007. Genetic evaluation of the Lake Sturgeon reintroduction program in the Mississippi and Missouri rivers. North American Journal of Fisheries Management 27:434–442.

Everett, S.R., D.L. Scarnecchia, G.J. Power, and C.J. Williams. 2003. Comparison of age and growth of Shovelnose Sturgeon in the Missouri and Yellowstone Rivers. North American Journal of Fisheries Management 23(1):230-240.

Finnoff, D., and J. Tschirhart. 2003. Protecting an endangered species while harvesting its prey in a general equilibrium ecosystem model. Land Economics 79(2):160-180.

Harkness, W.J.K. 1923. The rate of growth and the food of the Lake Sturgeon (Acipenser rubicundus LeSueur). Ontario Fisheries Research Laboratory 24(18):15-42.

Harkness, W.J.K., and J.R. Dymond. 1961. The Lake Sturgeon. Ontario Department of Lands and Forests, Toronto.

Haxton, T. 2011. Depth selectivity and spatial distribution of juvenile Lake Sturgeon in a large, fragmented river. Applied Ichthyology 27(2):45–52

Hershey, A.E. 1987. Tubes and foraging behavior in larval Chironomidae: implications for predator avoidance. Oecologia 73:236-241.

Higgins, J., and W. Brock. 1999. Overview of reservoir release improvements at 20 TVA dams. Journal of Energy Engineering 125(1):1-17

Jackson, J.R., A.J. VanDeValk, T.E. Brooking, O.A. VanKeeken, and L.G. Rudstam. 2002. Growth and feeding dynamics of Lake Sturgeon, Acipenser fulvescens, in Oneida Lake, New York: results from the first five years of a restoration program. Journal of Applied Ichthyology 18(4-6):439-443.

Kempinger, J.J. 1996. Habitat, growth, and food of young Lake Sturgeon in Lake Winnebago System, Wisconsin. North American Journal of Fisheries Management 16:102-114.

Krebs, C.J. 1989. Ecological Methodology. Harper and Row, New York.Lebreton, G.T.O., and F.W. Beamish. 2005. Growth, bioenergetics and age. Fish and Fisheries Series 27:195-216.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 237-240.

Liem, K.F., W.E. Bemis, W.F. Walker, Jr, and L. Grande. 2001. Functional anatomy of the vertebrates: an evolutionary perspective. Harcourt Brace College, Orlando.

Manly, B.F.J., L.L. McDonald, and D.L. Thomas. 1993. Resource Selection by Animals:Statistical Design and Analysis for Field Studies. Chapman and Hall, London.

Nilo, P., S. Tremblay, A. Bolon, J. Dodson, P. Dumont, and R. Fortin. Feeding ecology of juvenile Lake Sturgeon in the St. Lawrence River System 135(4):1044-1055.

Peterson, D.L., and P. Vecsei. 2004. Sturgeons and paddlefish of North America. Kluwer Academic Publishers, The Netherlands.

Peterson, D.L., P. Vecsei, and C.A. Jennings. 2007. Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Reviews in Fish Biology and Fisheries 17(1):59-76.

Pinder, L.C.V. 1995. The habitats of chironomid larvae. Page 123 in Armitage, P., P.S. Cranston, and L.C.V. Pinder, editors. The Chironomidae. Chapman & Hall, London.

Pollock, M.S., M. Carr, N.M. Kreitals, and I.D. Phillips. 2015. Review of a species in peril: what we do not know about Lake Sturgeon may kill them. Environmental Reviews 23(1):30-43.

Saidak, C.G. 2015. Determination of dispersal patterns and characterization of important habitats for Lake Sturgeon restoration in The Upper Tennessee River System. Master's thesis. University of Tennessee, Knoxville, Tennessee.

Scott, W.B., and E.J. Crossman. 1973. Fishes of Canada. Bulletin of the Fisheries Research Board of Canada, Ottawa.

Southeastern Lake Sturgeon Working Group. 2013. Lake sturgeon management plan for the Tennessee and Cumberland Rivers. U.S. Fish and Wildlife Service, Asheville, NC.

Sulak, K.J., and M. Randall. 2002. Understanding sturgeon life history: enigmas, myths, and insights from scientific studies. Journal of Applied Ichthyology 18(4):519-528.

Van der Klaauw, C.J. 1948. Ecological studies and reviews, IV: ecological morphology. Biotheory 4:27-111.

Vander Zanden, M.J., B.J. Shuter, N.P. Lester, and J.B. Rasmussen. 2000. Within-and among-population variation in the trophic position of a pelagic predator, Lake Trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 57(4):725-731.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37(1):130-137.

Wolda, H. 1981. Similarity indices, sample size and diversity. Oecologia 296-302

Appendix

Appendix A. Raw data table including invertebrate taxa consumed by Lake Sturgeon (*Acipenser fulvescens*), the method used to retrieve invertebrate taxa from Fort Loudoun Reservoir, Tennessee, and the invertebrate taxa retrieved from the prey base (cool season, October-April); an asterisk denotes a chironomid taxon

Invert. Taxon	***Total***	***Flush***	***Lavage***	***Grab***	***Cage***
Chironomus*	4,608	4536	102	260	9
Coelatanypus*	1,130	1094	36	26	0
Ablabesmyia*	175	173	2	17	0
Procladius*	73	72	1	3	1
Cryptochironomus*	120	118	2	6	0
Ceratopogonidae	18	17	1	0	0
Chaoboridae	54	52	2	0	0
Hexagenia	73	68	5	26	2
Pupa	77	74	3	3	0
Musculium	18	14	4	6	7
Corbicula	36	35	1	1	0
Nematoda	1	1	0	0	0
Oligochaeta	3	1	2	276	1
Goeldichironomus*	0	0	0	0	1
Cladotanytarsus*	0	0	0	0	1
Rheotanytarsus*	0	0	0	0	1
Glyptotendipes*	0	0	0	0	1
Cardiocladius*	0	0	0	0	2
Chironominae*	0	0	0	0	2
Chaetocladius*	0	0	0	0	3
Tvetenia*	0	0	0	0	1
Zalutschia*	0	0	0	0	1

Metriocnemus*	0	0	0	0	1
Eukiefferiella*	0	0	0	0	4
Pseudochironominae*	0	0	0	0	1
Cricotopus*	0	0	0	0	4
Orthocladius*	0	0	0	0	3
Beardius*	0	0	0	0	1
Neozavrelia*	0	0	0	0	1
Odonata	0	0	0	0	4
Clitellata	0	0	0	0	6
Pleurocera	0	0	0	1	9
Sialidae	0	0	0	0	1
Gammaridae	0	0	0	0	19
Heptageniidae	0	0	0	0	51
Taeniopterygidae	0	0	0	0	2
Dreissenidae	0	0	0	0	1
Physidae	0	0	0	0	9

Appendix B. Raw data table including the frequency of occurrence for each invertebrate taxon in the diet of Lake Sturgeon (*Acipenser fulvescens*), benthic grab, and rock cage samples from Fort Loudoun Reservoir, Tennessee (cool season, October-April); an asterisk denotes a chironomid taxon

Invert. Taxon	***Diet***	***Grabs***	***Cages***
Chironomus*	72.2%	41.6%	6%
Coelatanypus*	17.7%	4.1%	0
Ablabesmyia*	3%	2.7%	0
Procladius*	1%	<1%	1%
Cryptochironomus*	2%	1%	0
Ceratopogonidae	<1%	0	0
Chaoboridae	1%	0	0
Hexagenia	1%	4.1%	1.3%
Pupa	1%	<1%	0
Musculium	<1%	1%	4.7%
Corbicula	1%	<1%	0
Nematoda	<1%	0	0
Oligochaeta	<1%	44.2%	1%
Goeldichironomus*	0	0	1%
Cladotanytarsus*	0	0	1%
Rheotanytarsus*	0	0	1%
Glyptotendipes*	0	0	1%
Cardiocladius*	0	0	1.3%
Chironominae*	0	0	1.3%
Chaetocladius*	0	0	2%
Tvetenia*	0	0	1%
Zalutschia*	0	0	1%

Metriocnemus*	0	0	1%
Eukiefferiella*	0	0	2.7%
Pseudochironominae*	0	0	1%
Cricotopus*	0	0	2.6%
Orthocladius*	0	0	2%
Beardius*	0	0	1%
Neozavrelia*	0	0	1%
Odonata	0	0	2.7%
Clitellata	0	0	4%
Pleurocera	0	<1%	6%
Sialidae	0	0	1%
Gammaridae	0	0	12.7%
Heptageniidae	0	0	34%
Taeniopterygidae	0	0	1.3
Dreissenidae	0	0	1%
Physidae	0	0	6%

Appendix C. Raw data table including invertebrate taxa consumed by Lake Sturgeon (*Acipenser fulvescens*), the method used to retrieve invertebrate taxa from Fort Loudoun Reservoir, Tennessee, and the invertebrate taxa retrieved from the prey base (warm season, May-September); an asterisk denotes a chironomid taxon, a double-asterisk conveys that the gastric lavage technique was not attempted

Invert. Taxon	***Total***	***Flush***	***Lavage*****	***Grabs***	***Cages***
Chironomus*	79	79	0	206	0
Coelatanypus*	18	18	0	18	0
Cryptochironomus*	25	25	0	5	0
Ablabesmyia*	32	32	0	3	0
Ablabesmyia sp. II*	0	0	0	0	11
Glyptotendipes*	0	0	0	0	294
Dicrotendipes*	0	0	0	0	1
Endochironomus*	0	0	0	0	3
Glossiphoniidae	0	0	0	0	1
Coleoptera	1	1	0	0	0
Oligochaeta	0	0	0	119	0
Odonata	0	0	0	0	5
Clitellata	0	0	0	0	1
Hexagenia	2	2	0	16	0
Pupa	7	7	0	2	6
Pleurocera	0	0	0	4	5
Musculium	0	0	0	8	1
Sialidae	0	0	0	0	1
Corbicula	0	0	0	1	0
Gammaridae	0	0	0	0	28
Heptageniidae	0	0	0	0	69

Taeniopterygidae	0	0	0	0	2
Dreissenidae	0	0	0	0	74
Physidae	0	0	0	0	7
Planorbidae	0	0	0	0	1

Appendix D. Raw data table including the frequency of occurrence for each invertebrate taxon in the diet of Lake Sturgeon (*Acipenser fulvescens*), benthic grab, and rock cage samples from Fort Loudoun Reservoir, Tennessee (warm season, May-September); an asterisk denotes a chironomid taxon

Invert. Taxon	***Diet***	***Grabs***	***Cages***
Chironomus*	47.9%	52.6%	0
Coelatanypus*	10.9%	4.7%	0
Cryptochironomus*	15.1%	1.3%	0
Ablabesmyia*	19.4%	<1%	0
Ablabesmyia sp. II*	0	0	2.2%
Glyptotendipes*	0	0	56.3%
Dicrotendipes*	0	0	1%
Endochironomus*	0	0	<1%
Glossiphoniidae	0	0	<1%
Coleoptera	<1%	0	0
Oligochaeta	0	31.1%	0
Odonata	0	0	<1%
Clitellata	0	0	<1%
Hexagenia	1%	4.2%	0
Pupa	4.2%	<1%	1%
Pleurocera	0	1%	1%
Musculium	0	2%	<1%
Sialidae	0	0	<1%
Corbicula	0	<1%	0
Gammaridae	0	0	5.5%
Heptageniidae	0	0	13.5%
Taeniopterygidae	0	0	<1%

Dreissenidae	0	0	14.5%
Physidae	0	0	1%
Coleoptera	<1%	0	0
Planorbidae	0	0	<1%

Appendix E. Below are the results from an experimental rock cage deployment in Fort Loudoun Reservoir, Tennessee in the winter of 2015. While our experimental design called for a one month deployment of rock cages, this deployment lasted for three months. Note the proliferation of zebra mussels (*Dreissena polymorpha*) which showed a 55% increase over any other winter sample. This sample also contained the only crayfish (*Oronectes* sp.) specimen from the entire sampling effort.

Family	***Genus***	***No. indiv.***
Dreissenidae	*Dreissena*	56
Pleuroceridae	*Pleurocera*	9
Sphaeriidae	*Musculium*	1
Corduliidae	*Neurocordulia*	2
Coenagrionidae	*Argia*	7
Heptageniidae	*Stenacron*	1
Cambaridae	*Oronectes*	1

Vita

Todd Michael Amacker is a lifelong student of natural history and spends his free time stalking small creatures in forests and streams. As a published professional photographer, writer, and film-maker, he has covered stories about natural history, science, and conservation. He resides in East Tennessee with his wife and daughter.