

Introduction

The three major components that can be managed in a fishery are anglers, aquatic and terrestrial habitat, and the fish themselves (Kohler and Hubert 1999). Given the complexities associated with the study of fishes, proper management requires a thorough understanding of the ecological requirements of the fish or fishes of interest during a life span and over generations (Matthews 2012; Sass et al. 2017). This is especially true when making decisions regarding fishery regulations. Without quality ecological information, regulations or lack thereof can be detrimental to a species community (e.g., Coble et al. 1990; O'Leary 2011). Understanding ecological components such as demographic information and population dynamics (Schaefer 1954; Hightower and Grossman 1985; Lorenzen 2005), population movement and migrations (Goethel et al. 2011), habitat requirements (Johnson and Zúñiga-Vega 2009; Sass et al. 2017), and trophic linkages within the ecosystem (Walters et al. 2008) will allow managers to set informed and effective regulations.

Demographic information and population dynamics contain vital information for harvest models (e.g., stock structure, mortality; Begley et al. 2018); however, this information also reflects a species life history (Johnson and Zúñiga-Vega 2009). Life-history information offers ecological insight into the environmental conditions under which fish evolved (Magalhães 2003) and their ability to handle future disturbance (Grabowski et al. 2012). Therefore, we can use life-history variability to estimate a portion of the niche partitioning occurring between species and to predict vulnerability of the community to disturbance (Grabowski et al. 2008; Grabowski et al. 2012). A better understanding of variation in species life history allows for more informed management decisions (Winemiller 2005). Information such as this is important as managers

must make increasingly important decisions in the face of climactic variability and increased anthropogenic alteration

Habitat quality and quantity relative to a fish's fundamental niche influences population stability and their susceptibility to extirpation. For example, habitat availability influences stock-recruitment relationships (Hayes et al. 1996). The influence of habitat availability on population dynamics is not always easily discerned as habitat requirements often shift as fish transition to different life stages (Sass et al. 2017). Furthermore, habitat requirements at one life stage may have a greater influence on population biomass than others (Vélez-Espino and Koops 2009). Unfortunately, aquatic habitats face threats due to past and current anthropogenic alteration (Freeman et al. 2001) along with a changing climate (Segurado et al. 2016; Missaghi et al. 2017), which have begun to change community composition (Yeager et al. 2016) and functional diversity (Biswas et al. 2017). Given the uncertainty these ecosystems are facing protecting important habitats should be key component of all aquatic conservation strategies.

Like habitat, fish movement and migrations influence the spatial distribution of fishing effort and harvest (Matthias et al. 2014) and are important to the persistence of fish populations (Auer 1996). Fishes rely on movement for access to resources, intra-species interactions, and colonization of unoccupied habitat patches (Taylor et al. 1993). Coarse-scale movements are instrumental in colonization of unoccupied habitat patches, gene flow, and meeting stage-related life history necessities (Jackson et al. 2001). Migrations act as a way for fishes to find optimal habitat for various life-history stages (e.g., reproduction), avoid unfavorable conditions, and optimize resource consumption (Auer 1996). Migrations also act as a pathway for spatial energy transport between or within systems (e.g., estuary to sea; Deegan 1993). Understanding migrations and movement patterns of fishes provides ecological insight into population

dynamics, predator-prey interactions, community structure, and the effects of habitat fragmentation (Skalski and Gilliam 2000).

Determining how the aquatic community within a system responds to harvest is becoming an increasingly important component of harvest-based management (Pauly et al. 2001; Pritcher and Cochrane 2002). Both ecologists and managers have found that fish harvest has an effect on the trophic structure of an ecosystem (Parsons 1996). To understand how harvest affects trophic structure, we must first estimate how organisms are trophically linked (Christensen and Walters 2004). Once this has been accomplished, it is possible to estimate the effect harvest has on the food web (Pritcher and Cochrane 2002). Innovative approaches, such as this, allow us to intrinsically link management with ecology, resulting in a better understanding of trophic linkages and the effects of harvest within an ecosystem (Christensen 2009). Catostomids (i.e., suckers) are an excellent candidate species with which to simulate trophic dynamics as they are often assumed to have negative impacts on sport fisheries despite little justification to support such an assumption (Holey et al. 1997). Furthermore, little information regarding the influence of harvest on these species and the effects of this harvest have been conducted (Begley et al. 2018).

Most catostomids are understudied across their native range yet are highly sought after by giggers (a type of fishing done with specialized spears; Morgan et al. 2012) across the Ozark Highlands ecoregion. Due to catostomids being understudied, unmanaged, and heavily targeted by anglers in these systems, managers have begun to worry about the effects of harvest on these populations and ultimately the effect on ecosystem health. To address this concern, we will take an ecological approach to model the effects of harvest in the Lake Eucha river-reservoir complex. The overall goal of my dissertation is to further our ecological understanding of

catostomids and provide information useful to developing management options for agencies. The specific objectives of my dissertation are to (1) determine differences in demographic characteristics and population dynamics of different sucker species, (2) determine habitat occupancy of young-of-year suckers, (3) quantify coarse spatial movements and survival probabilities for sucker species, (4) determine trophic linkages and estimate the effects of sucker removal on the river-reservoir complex, and (5) estimate the effects of more restrictive harvest regulations along with potential increased harvest on the sucker population within the river-reservoir complex.

Summary of Catostomid Literature

White sucker, spotted sucker, black redhorse, golden redhorse, and northern hogsucker can be described as moderate to highly fecund generalist that have varying susceptibility to human disturbances (Appendix A). Population stability appears to be mainly influenced by juvenile survivorship, with juvenile habitat availability having the strongest influence on survival prior to maturation. Reproductive potential varies between years as it is unlikely all adults within the population spawn in a given year. In areas where these fish are targeted for either sport or bait purposes, it appears older and presumably larger individuals are the most affected by harvest. Given the lack of information regarding trophic interactions between these individuals and other aquatic organisms, it is unclear the influence their removal may have on the ecosystem (see complete review in Appendix A).

Perceived Benefits

From an ecological standpoint, information derived from these objectives will improve our understanding of the catostomid family. My first objective will increase our understanding of population dynamics associated with suckers in the south-central United States, information that

is lacking within this geographic portion of the range of our species of interest. Furthermore, these dynamics will allow a cursory investigation of niche partitioning between these species (Grabowski et al. 2012). My second objective will attempt to increase our understanding of habitat requirements for YOY suckers, which may help preserve these stream fishes in the face of anthropogenic alteration and climatic variability. Habitat limitations for YOY is the strongest predictor of adult Black Redhorse biomass (Vélez-Espino and Koops 2009); therefore, I hypothesize habitat requirements for of YOY Spotted Sucker, White Sucker, Golden Redhorse, and Northern Hogsucker also have a strong influence on adult biomass. My third objective was selected as movement patterns and subsequent migrations of suckers at the population level remain understudied. Furthermore, individual catostomids can exhibit starkly different movement and migratory behaviors (Booth et al. 2013; Doherty et al. 2010). Additional information regarding movements of these species at the population level has potential to increase our understanding of their habitat preferences at a coarse scale. Furthermore, multi-year observation at this level may alleviate some of the confounding results from past studies. My final objective will attempt to clarify the influence of sucker biomass on the aquatic ecosystem. The trophic linkages between catostomids and other aquatic organisms within aquatic ecosystems remain difficult to discern. Our simulations may better define these linkages along with community responses to changes in sucker biomass. By focusing on these objectives, we hope to increase our understanding of the biological (e.g., growth) and spatial (e.g., movement) variations among these species. This information will then be use in to construct single species harvest models which will allow managers to better understand the influence of sucker removal on the population dynamics of each species. Furthermore, by estimating the influence of sucker

removal on biomass of other functional groups we can better understand potential changes that may occur within the system (e.g., trophic effects).

Suckers are both understudied and undermanaged. Though estimates of fishing effort (see Matheney and Rabeni 1995) and harvest models (Begley et al. 2018) are available, a majority of catostomids remain undermanaged. This lack of management is especially troubling as the popularity of non-angling no-release fisheries has increased (e.g., bowfishing; Lackmann et al. 2019) along with the detrimental effects associated with anthropogenic alteration and climatic variability (Freeman et al. 2001; Missaghi et al. 2017). The important ecological information outlined prior will also serve as inputs for a harvest model aimed at determining the influence of gigging on the system. It is my hope that this single-species model, in conjunction with the community model attained from the mass balance simulation, will allow for the effective management of a long standing and culturally important Ozark gigging fishery. Furthermore, this project can serve as a template for investigating harvest in other non-angling no-release fisheries.

Methods

The River-Reservoir Complex

All work is being conducted in the Spavinaw Creek system upstream of Lake Eucha Dam in northeast Oklahoma and northwest Arkansas. This system includes one reservoir (Lake Eucha) and several interconnected rivers and streams (Figure 1). This river-reservoir complex is situated within the Ozark Highlands ecoregion. The Ozark Highlands has a moderate climate with average high temperatures of 9°C in January and 33°C in July, and an average annual rainfall of ~120 cm (Woods et al. 2005). This area is primarily forest, woodland, and pasture and characterized by its karst topography and numerous springs (Nigh and Shroeder 2002; Woods et al. 2005). The rivers and streams of this ecoregion have a predominantly coarse bed (i.e.,

diameter > 6.5 mm) and carry low sediment loads during baseflow (Nigh and Schroeder 2002).

Within the western portion the ecoregion contains cherty clay soils and underlying karst geology (Woods et al. 2005).

Demographic Characteristics and Population Dynamics

Objective 1: Determine differences in demographic characteristics and population dynamics of different sucker species within the river-reservoir complex.

Spotted sucker, white sucker, golden redhorse, black redhorse, and northern hogsucker will be sampled from each section of the Lake Eucha river-reservoir complex at least once during the fall, winter, summer, and spring. The system was split into six sections defined based on anthropogenic pooling (i.e., reservoir construction) and seasonally observed subsurface flow (i.e., drying; Figure 2). Given the diverse array of system types (e.g., reservoir vs perennial stream), structural habitats (e.g., large woody habitat, rocky shoals), and physical conditions (e.g., water temperatures, water levels, stream discharge) a multi-gear approach will be taken that includes active netting via seine and gill-net seine; passive netting via modified-fyke nets, hoop nets, and gill nets; and backpack, tow barge, and boat electrofishing. Both the conditions during the sampling event and site accessibility will dictate how each sample is taken. For example, deep water that was shallow enough to be sampled via tow barge electrofishing during the last event may have to be sampled via active netting, passive netting, or boat-mounted electrofishing if depth has increased. However, the decision of whether to sample the section using netting or boat-mounted electrofishing may be made based on accessibility (e.g., the boat cannot be transported to the site), conditions (e.g., the water is still too deep to be electrofished successfully), or a combination of both. Sampling gear will be noted during every event and

differences in capture efficiency will be accounted for, if necessary, in the recapture model (described below).

Upon capture, catostomids will be placed into a holding tank until sampling of a section has been completed, or until the number of individuals in the tank is believed to be detrimental to fish health (e.g., fish gulping at surface for air). Sampled individuals will be identified to species and total length (mm) and weight (g) will be collected (though weights will not be collected during spawning season). All live individuals will immediately release and those that have expired will be preserved and taken back to the lab to extract aging structures. Some of the live individuals we capture will be sacrificed to obtain fecundity estimates and to provide additional data for age and growth analyses. However, we will use corpses from gigging tournaments held on the system to minimize the number of individuals we sacrifice. Sacrificed individuals will be immediately dispatched via pithing as suggested by the American Fisheries Society, American Institute of Fishery Research Biologists, and American Society of Ichthyologists and Herpetologists (Nickum et al. 2004).

Length and weight data will be used to construct length-weight regressions and to determine size structure for each species. Length and weight data will be \log_{10} transformed to linearize the data (Ogle 2015). Following this, a simple linear regression will be used to determine the relationship between \log_{10} transformed weight and length. These relationships will then be compared among species. Size structure for each species will be summarized by creating histograms of the total lengths for each species. Size structure will be statistically compared between species using independent Kolmogorov -Smirnov tests (Zar 1999).

Aging structures (i.e., otoliths and spines) will be collected from ~10 individuals in each 10 mm length bin (e.g., ~10 fish between 100 and 110 mm) and aged by 2 readers (using

consensus reads to settle disagreements). Age data will be used to produce an age-length key, which will then be used to assign age estimates to all sampled fish (Coggins et al. 2013; Ogle 2015). Growth curves will be created for each species using the von Bertalanffy growth equation:

$$L_{\infty} = L_t(1 - e^{-k(t-t_0)})$$

where: L_{∞} = asymptotic maximum length, L_t = length at time t , k = Brody growth coefficient, t = time (age), t_0 = theoretical time at which fish length would be zero mm (Kirkwood 1983; Ogle 2015). Growth models will be fit using a frequentist (i.e., maximum likelihood) or Bayesian framework dependent upon data available for each of our study species.

Comparisons between parameter estimates of L_{∞} , k , and t_0 will be made using 95% confidence or credible intervals to determine if significant differences exist between growth characteristics for our study species. We will also assign age estimates to unaged individuals using their total length in a similar manner as described for program AGEKEY by Isermann and Knight (2005). The same Monte Carlo approach will be used to decide ages for fractional fish; however, all calculations will be conducted in program R (Ogle 2016; R Core Team 2020).

Length at maturity will be determined by sampling individuals during spring when gametes are clearly distinguishable. We will attempt to sample 10 individuals from every 10 mm length bin to determine the proportion of mature individuals for each species. Curves which estimate the proportion mature by age or size will be constructed using one of the methods suggested by Trippel and Harvey (1991) based on the maturity distribution we observe. Attempts will be made to identify sexually mature individuals via the expression of gametes; however, a certain number of individuals will need to be sacrificed for maturation determination. These sacrificed individuals will also be used for spawning chronology and fecundity estimation.

Spawning chronology will be determined via histological analysis of ovarian tissue. After collection tissues will be preserved using a 10% formalin solution for analysis in the laboratory. In the laboratory, ovaries will be blotted to remove excess fluid, weighed, and then stored in $\geq 70\%$ ethanol solution (Brewer et al. 2006). Ovaries will then be sent to the Oklahoma State University College of Veterinary Medicine for processing. Following this, slide-mounted sections will be used to classify ovarian stages for each gonad as: early phase, midphase, late phase, maturation phase, resorption phase (Brewer et al. 2006). The physical act of spawning will be determined via the presence of empty follicles within ovary (Brewer et al. 2006). Fecundity will be determined by extracting the ovary from ripe females; calculating the weight of a subsample of 100 eggs per individual, then using that relationship to estimate the number of eggs in the entire ovary (see Grabowski et al. 2012).

Young of Year Habitat Occupancy

Objective 2: Determine how reach scale habitat influences young-of-year sucker occupancy across the river-reservoir complex

To determine habitat influences on young-of-year (YOY) catostomid occupancy, snorkeling will be carried out at 80 reaches throughout the river-reservoir complex during the late summer and early fall (i.e., months August, September, October). At each reach, the stream will be snorkeled at 20x the wetted width during sampling (Leopold et al. 1964). Using visual observation, we will count white sucker, northern hogsucker, and redhorse spp. (golden and black redhorse). At each site, two to three snorkelers (dependent on wetted width at the time of snorkeling) will travel slowly upstream counting all fish in their predetermined lanes. Once snorkelers have reached the end of the site, visibility will be assessed. Following this, snorkelers will wait 1 h in an attempt to allowing any disturbed fishes to redistribute (Brewer and Ellersieck

2011). A second survey will then be conducted; however, snorkelers will switch (two snorkelers) or rotate (three snorkelers) lanes and a second sample will be conducted. YOY catostomids will be counted again and visibility will be assessed a second time. While snorkeling, observers will score observations. At the reach scale we will measure residual pool depth ($\pm 0.01\text{m}$), temperature (estimated over a 2-week period; $\pm 0.1^\circ\text{C}$), groundwater input (gaining or losing), cover (i.e., boulders or large woody habitat [LWH] as 0 – 100% of reach), and vegetation (0 – 100% of reach). At the segment scale, I will estimate drainage area (km^2 ; McKay et al. 2012) and a modified estimate of human disturbance (Brown and Vivas 2005; Mouser et al. 2018).

Occupancy models will be used to estimate occupancy probability of YOY suckers across each site while accounting for imperfect detection. Occupancy models allow us to model detection and occurrence simultaneously as a function of covariates through replicate surveys. A thorough description of the occupancy modeling process is available in MacKenzie et al. (2002, 2005). A simple multinomial likelihood equation that describes occupancy is:

$$\text{logit}(\Psi_i) = \beta x_i^\top \text{ and } \text{logit}(P_{ij}) = \alpha v_{ij}^\top$$

where $\text{logit}(\cdot)$ refers to the logit-link function, Ψ_i is the species occupancy probability of site i , x_i^\top are occupancy covariates for site i , β are the corresponding coefficients for x , P_{ij} is the detection probability for site i during survey j , v_{ij}^\top are detection covariates for site i during survey j , and α are the corresponding coefficients for v (Mollenhauer et al. 2018).

A Bayesian multispecies single season occupancy model will be used to determine the most likely relationship between sucker occupancy and our environmental covariates while allowing us to determine conditions for interspecific independence (Rota et al. 2016). Once correlations between our predictor variables have been determined a series of candidate models will be constructed and compared using DIC (Burnham and Anderson 2001). Within our

candidate model set, Ψ and P will either be assumed constant or vary based on some combination of covariates (i.e., species, cover via boulders or large woody habitat, residual pool depth, temperature, groundwater input, percent vegetation for Ψ , and visibility, cover via boulders or large woody habitat, and percent vegetation for P).

Determining seasonal movement and survival

Objective 3: Quantify coarse spatial movements and survival probabilities for sucker species within the river-reservoir complex.

The river-reservoir complex will be broken into six segments (i.e., states for multi-strata models) based on the natural drying and anthropogenic pooling known to occur within the system. Samples from each segment will be taken using boat or barge mounted electrofishing and passive or active netting (dependent on depth). Sites in each segment will be sampled at least once during each season (i.e., spring, summer, autumn, winter). Shortly (i.e., 1 week maximum) after every site has been sampled across the system, stream sections will be traversed with a mobile PIT antenna to increase detections while attempting to minimize disturbance to individuals. Fixed antennas will also be used to passively monitor the movement of individuals in Beaty, Brush, and Rattlesnake or Dry Creeks.

Upon capture, individuals will be identified, measured. Individuals >250 mm TL will also be tagged with a single 23-mm HDX passive integrated transponder tag (PIT; Oregon RFID) weighing ~ 0.6 g. The PIT tag will be placed into the abdominal cavity and the left pelvic fin will be removed. Fish will be held for ~30 min prior to release to determine if the stress associated with capture and tagging resulted in mortality and then will be released back into the site they were sampled.

Multi-strata models (Nichols and Kendall 1995) will be used to determine transitional, apparent survival, and capture probabilities for our five study species across our six defined states (Figure 2, Figure 3). Though designating six states seems complex, any state where movement is not observed will be removed (see Dieterman and Hoxmeier 2011). Likewise, any strata where tagged fish are not observed will be removed from the final model. Each model component (i.e., transitional, survival, and capture probability) within the final model will be fixed or allowed to vary via measured coefficients (i.e., season (spring, summer, autumn, winter), average discharge from available gauges during that season, average water level from available gauges during that season, average temperature from available gauges during that season, sample year, and species) resulting in several potential candidate models (Table 1). All candidate models will be compared using DIC and the top model will be selected (Spiegelhalter et al. 2002; Albert 2009).

Quantifying the Trophic Effects of Sucker Removal within the System

Objective 4: Estimate trophic linkages and the effects of sucker removal on different predefined trophic groups within the river-reservoir complex.

Simulation will be used to quantify the importance of suckers relative to other groups within the river-reservoir complex based on production and biomass ratios (Christensen and Walters 2004; Langseth et al. 2012). We selected an Ecopath with Ecosim approach for this as it has been used in past studies of marine and freshwater ecosystems (Pine et al. 2007; Langseth 2012). The Ecopath with Ecosim approach is made of an initial mass balance model (Ecopath) using user-defined biotic groups and their associated production and losses in biomass over a user-defined time interval. For the purpose of our simulation, data will be obtained for eight groups. These groups are a modified version of the functional groups used in the Pine et al.

(2007) Ecopath model for eastern coastal rivers (Table 2). Data for these groups will be obtained from the current project along with past published and unpublished data for the system. The Ecopath model will be based on the hypothetical food web in Figure 4. Once the Ecopath model is constructed, a second mass balance model (Ecosim) can be used to vary exploitation of suckers and determine the potential resulting variation in biomass for other fish groups.

To conduct this simulation, I will first build the Ecopath mass balance model for ecosystem production and losses. This model functions using two master equations that are comprised of several smaller equations (see Christensen and Walters 2004). The first master equation defines the total production rate of each group using:

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + M0_i \times B_i$$

where P_i is the total production rate for group i , Y_i is the total fishery catch rate of group i , $M2_i$ is the instantaneous predation rate for group i , B_i is the biomass of group i , E_i is the net migration rate of group i , BA_i is the biomass accumulation rate of group i , and $M0_i$ is the “other mortality” rate for group i (catch all term for mortality not accounted for elsewhere; Christensen and Walters 2004). All parameters for the production rate equation for each group do not need to be known by the user as the Ecosim software allows for the estimation of their values based on available data (Christensen and Walters 2004; Langseth et al. 2012). Following the estimates of parameters for each group’s production equation, the second master equation defines energy balance for each group using:

$$C_i = P_i + R_i + U_i$$

where C_i is the total consumption of group i , P_i is the total production of group i , R_i is the total respiration of group i , and U_i is the total unassimilated food for group i (Christensen and Walters 2004). The formulation for this model and the terms used are based on their description in

Winberg (1956), who defined consumption as the sum of somatic and gonadal growth less metabolic costs and waste (i.e., egestion and excretion). However, Christensen and Walters (2004) noted the energy balance equation differs slightly because Ecopath: 1) estimates losses instead of somatic growth, 2) does not explicitly account for gonadal growth but includes it in the predation term, and 3) estimates respiration as the difference in consumption and the sum of production and unassimilated food.

Once a viable (i.e., “balanced”) Ecopath has been constructed for our system, we will simulate the potential influence of increased and decreased sucker harvest (via gigging) and the response of each group (i.e., increased or decreased biomass) using the Ecosim model. This is done using a series coupled differential equations (see Walters et al. 1997, 2000). The Ecosim equations are derived from the total production master equation for the Ecopath model and the new master equation takes the form:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (M0_i + F_i + e_i) \times B_i$$

where: $\frac{dB_i}{dt}$ represents the growth rate during time interval dt of group i in terms of its biomass B_i , g_i is the net growth efficiency of group i , Q_{ji} defines consumption rates for group i given predatory group j based on the foraging arena concept (see Walters et al. 1997), I_i is the immigration rate for group i (assumed constant over time), $M0_i$ is the non-predation (“other”) natural mortality rate estimated for group i , F_i is the fishing mortality rate for group i , e_i is the emigration rate for group i , and B_i is the biomass of group i (Christensen and Walters 2004).

Determining the Influence of Tournament Harvest on Suckers

Objective 5: Estimate the effects of more restrictive harvest regulations along with potential increased harvest on sucker populations within the river-reservoir complex.

I will use either an age- or length-based harvest model to determine the influence of gigging harvest on the sucker species in the river-reservoir complex. We will use a Ricker or Beverton-Holt recruitment process within a Leslie matrix-based model framework (Begley et al. 2018). The model will project the change in yield through time (e.g., 50 years) under the current harvest regulation (i.e., no regulation) and under more restrictive management strategies (e.g., creel limits) and using the current harvest regulation under increased harvest levels to determine at what point unrestricted gigging may be an issue.

All variables required for the Begley et al. (2018) excluding mortality estimates have been defined in prior subsections of the methods; therefore, only mortality equations will be explained below. Natural mortality will be estimated using the an updated Pauly (1980) formula. This method was recommended by Then (2015) for estimating natural mortality when the maximum age is unknown for the species. The updated form of the equation is:

$$M_{est} = 4.118 \times K^{0.73} \times L_{\infty}^{-0.33}$$

where M_{est} is the resulting estimation of natural mortality, K is the growth coefficient from the von Bertalanffy growth equation, and L_{∞} is the asymptotic maximum length from the von Bertalanffy growth equation (Then 2015). Following this, instantaneous natural mortality will be estimated using a modification of an estimator in Miranda and Bettoli (2007):

$$Z_{est} = \frac{0.693K}{\left(-\log_e\left(1 - L_{median}/L_{\infty}\right)\right) - \left(-\log_e\left(1 - L_x/L_{\infty}\right)\right)}$$

where Z_{est} is the estimated instantaneous natural mortality, K is the growth parameter from the von Bertalanffy growth equation, L_{median} is the median length of a fish above which all fish are vulnerable to capture gear, L_{∞} is the asymptotic maximum length from the von Bertalanffy growth equation, and L_x is the length at which all fish are estimated to be vulnerable to capture

gear (Hoenig et al. 1983). This estimator was selected as median length estimates are more robust to variable recruitment and growth across year classes) when compared to estimators based on mean length (see Beverton and Holt 1956; Hoenig et al. 1983) and variability in our instantaneous mortality rate (Z_{est}) is easily determined via bootstrapping (Efron and Tibshirami 1998; Haddon 2001). Finally, the instantaneous rate of fishing mortality (F_{est}) will be determined using modification of an estimator presented Miranda and Bettoli (2007):

$$F_{est} = \left(\frac{T_G}{T_N} \right) \times \left(\frac{M_{est}}{\left(\frac{M_{est}(1 - e^{-Z_{est}})}{Z_{est}} \right)} \right)$$

where F_{est} is the instantaneous rate of fishing mortality, T_G is the number of tags recovered from giggers during a tournament, T_N is the number of tags present in the river-reservoir complex adjusted for apparent survival, M_{est} is the estimation of natural mortality, and Z_{est} is the estimated instantaneous natural mortality.

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Tables

Table 1. Potential coefficients for apparent survival (ϕ), transition probabilities (ψ), and capture probabilities (p) with the associated number of parameters that will need to be estimated.

| Model component | Coefficient | Parameters* | |
|-----------------------------------|-----------------------------------|---------------------------------|----|
| Apparent Survival (ϕ) | - | 6 | |
| | Season | 24 | |
| | Average discharge across gauges | 24 | |
| | Average water level across gauges | 24 | |
| | Average temperature across gauges | 24 | |
| | Year | 24 | |
| | Species | 36 | |
| | Transition Probability (ψ) | - | 22 |
| | | Season | 88 |
| | | Average discharge across gauges | 88 |
| Average water level across gauges | | 88 | |
| Average temperature across gauges | | 88 | |
| Year | | 88 | |
| Species | | 132 | |
| Capture Probability (p) | - | 6 | |
| | Season | 24 | |
| | Average discharge across gauges | 24 | |
| | Average water level across gauges | 24 | |
| | Average temperature across gauges | 24 | |
| | Year | 24 | |
| | Species | 36 | |

* The number of parameters is calculated based on complete use of the coefficient across all strata; however, applying the coefficient to a subset of strata (e.g., only states 1 and 2) will result in the number of parameters varying between the no coefficient estimate (-) and the full estimate.

Table 2. Group designations for different species and genus combinations known to occur in the Spavinaw-Eucha river-reservoir complex (modified from Pine et al. 2007).

| Group Designation | Family (Genus or Species Qualifier) |
|----------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Piscivore | Ictaluridae (<i>Ictalurus</i> spp., <i>Pylodictis olivaris</i>) Centrarchidae (<i>Microperus</i> spp., <i>Pomoxis</i> spp.) Moronidae (<i>Morone chrysops</i>) Salmonidae (<i>Oncorhynchus mykiss</i>) |
| Omnivore | Percidae (<i>Etheostoma</i> spp., <i>Percina</i> spp.) Aphredoderidae (<i>Aphredoderus sayanus</i>) Cyprinidae (<i>Nocomis</i> spp., <i>Cyprinus</i> spp., <i>Semotilus</i> spp.) Clupeidae (<i>Dorosoma</i> spp.) |
| Insectivore | Centrarchidae (<i>Lepomis</i> spp.) Poeciliidae (<i>Gambusia</i> spp.) |
| Giggable Sucker* | Catostomidae (<i>Minytrema melanops</i> , <i>Catostomus commersoni</i> , <i>Moxostoma erythrurum</i> , <i>Moxostoma duquesnei</i> , <i>Hypentelium nigricans</i>) |
| Non-giggable Sucker* | Catostomidae (<i>Minytrema melanops</i> , <i>Catostomus commersoni</i> , <i>Moxostoma erythrurum</i> , <i>Moxostoma duquesnei</i> , <i>Hypentelium nigricans</i>) |
| Invertebrates | |
| Plankton | |
| Detritus | |

*Separate designations due to theorized differences in harvest potential

Figures

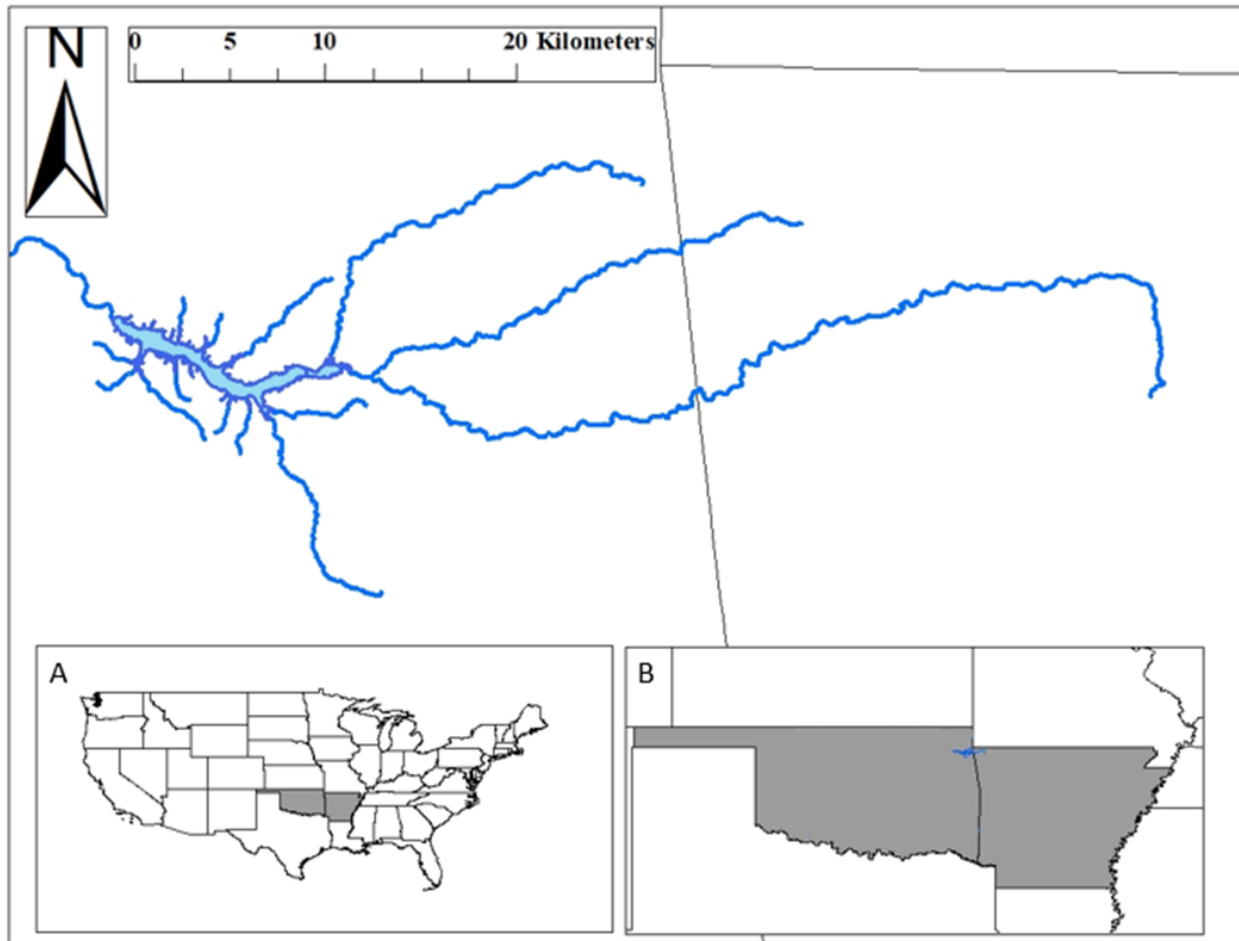


Figure 1. Spavinaw-Eucha river-reservoir complex, including rivers and streams that are currently the focus of catostomid sampling efforts. Inset A shows the states which contain the Lake Eucha river -reservoir complex in reference to the contiguous United States. Inset B shows the location of the of the Lake Eucha river-reservoir complex within Oklahoma and Arkansas.

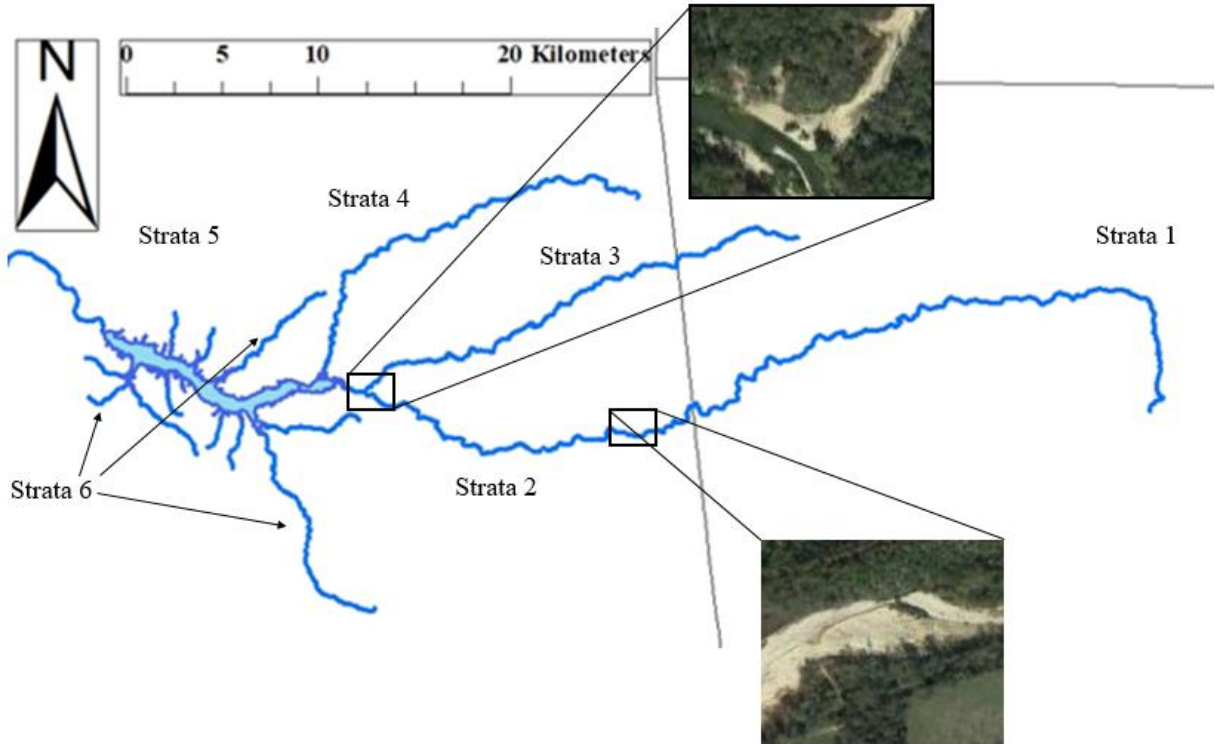


Figure 2. Spavinaw-Eucha river-reservoir complex including the designations of each strata separated based on reservoir locations and natural stream drying (indicated by pop-outs). Note that strata 5 is the reservoir and 6 included a series of perennial streams that terminate in the reservoir.

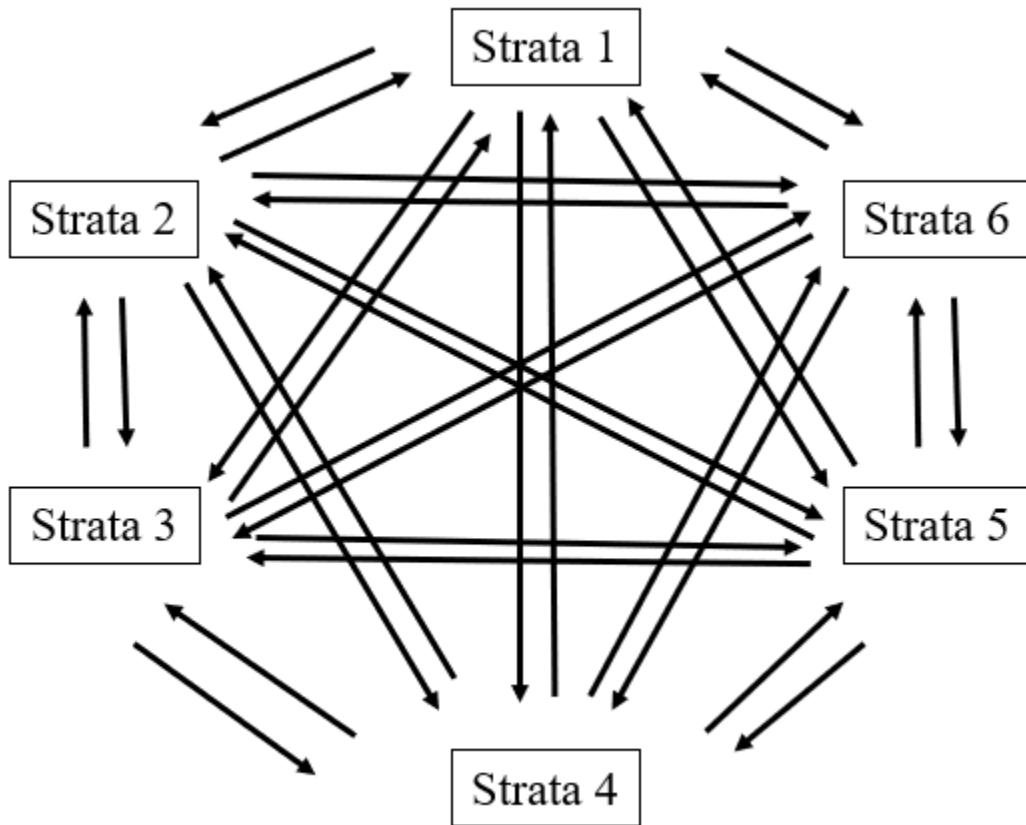


Figure 3. Illustration simplifying the possible transition probabilities (ψ) between each strata using arrows. Both apparent survival (ϕ) and capture probabilities (p) will be estimated within or across each strata.

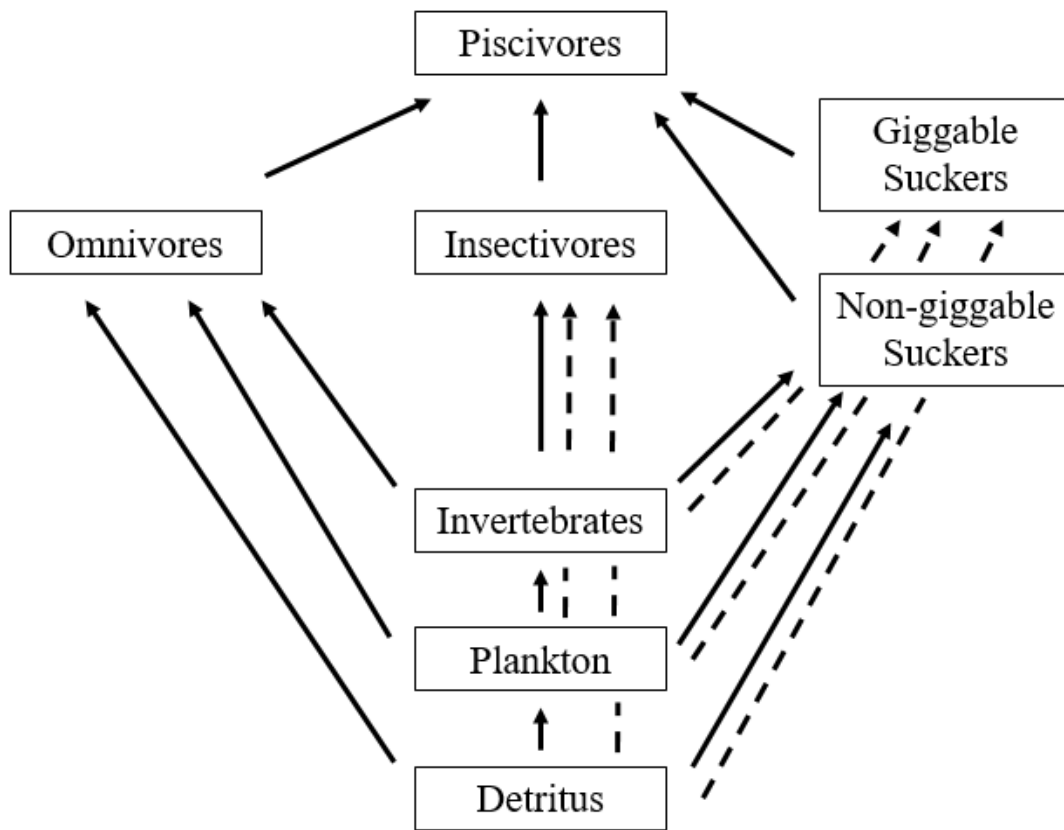


Figure 4. Simplified food web diagram showing the linkages among taxa with shared trophic dynamics in the Spavinaw-Eucha river-reservoir complex (adapted from Pine et al. 2007). Vertical positioning indicates coarse trophic positions. Dotted arrows were used to increase interpretability.

Appendix A. A coarse review of the family Catostomidae, including a specific review focusing on the species that will be studied during the dissertation.

The Family Catostomidae

The family Catostomidae comprises 76 extant species, with 75 of these occurring in North America (Bagley et al. 2018). The 75 species in North America make up 7 – 8% of the freshwater ichthyofauna for the continent (Harris and Mayden 2001; Bagley et al. 2018). Despite being the third largest freshwater fish clade and having one of the largest native-geographic ranges of freshwater fish, only two species occur outside of North America (Jacquemin and Doll 2015; Bagley et al. 2018). The Chinese sucker *Myxocyprinus asiaticus* only occurs in the Minjiang and Yangtze rivers of China (Gao et al. 2008) and the longnose sucker *Catostomus catostomus* co-occurs in Siberia and northern North America (Page and Burr 2011). Fossil record combined with molecular analysis suggest that catostomids originated in Asia and dispersed to North America via Beringia; following this the longnose sucker migrated back to Asia and all native Asiatic suckers except the Chinese sucker went extinct (Darlington 1957; Chang et al. 2001; Bachevskaya et al. 2014). Despite their diversity and geographic range, recent estimates suggest ~35% (~27 species) of catostomids are threatened or endangered (Warren et al. 2014; Bagely et al. 2018).

The majority of species within the Catostomidae family were first described and studied in the late 1700s and early 1800s (Jordan and Gilbert 1877; Jordan 1885; Cope 1878; Cox 1897). Fishes within the family Catostomidae have cycloid scales covering the entire body except their fins and heads, toothless fleshy subterminal mouths with protrusible premaxille and large lips (excluding the bigmouth buffalo *Ictiobus cyprinellus* and harelip sucker *Moxostoma lacerum*),

and comb or molarlike pharyngeal teeth (Page and Burr 2011). They have a single dorsal fin with nine or more rays, an anal fin set far back on the body, and abdominal pelvic fins (Page and Burr 2011). Despite being studied for ~200 years, there is still debate regarding the number of species (e.g., southeastern blue sucker *Cycleptus meridionalis*, Burr and Mayden 1999) and subspecies (e.g., dwarf white sucker *Catostomus commersoni utawana*; Beamish and Crossman 1977) within the family. Furthermore, Cooke et al. (2005) estimated that ~10 species of catostomids have yet to be fully described.

Due to the diversity and distribution of the family Catostomidae, this review will focus on the species that occur within the Lake Eucha river-reservoir complex. These species are the white sucker *Catostomus commersoni*, spotted sucker *Minytrema melanops*, golden redhorse *Moxostoma erythrurum*, black redhorse *Moxostoma duquesnei*, and northern hogsucker *Hypentelium nigricans*. Reference to other catostomids will be made when pertinent, or when published information for a genus or species is scarce but information on a related species is known.

Sexual Dimorphism

Outside of the spawning season, males and females of the species that occur within the Lake-Eucha river-reservoir complex are remarkably similar. However, morphometric differences have been suggested for each species. Mature female white suckers and spotted suckers are often larger than male white suckers (Reighard 1920; Grabowski et al. 2007). The anal, pectoral, and lower lobe of the caudle fin is also often longer in male white suckers than females (Reighard 1920). However, these findings have been refuted by later studies. For example, Spoor (1935) stated that only the shape of the pelvic fins (females rounded, and males squared) was reliably different based on species from Wisconsin lakes. These findings were confirmed by Stanley

(1988), though they were not able to determine sex with 100% accuracy. No information was available related to sex-specific differences in golden or black redhorse growth rates, though the anal and pectoral fins are generally longer in male redhorse spp. (Reighard 1920). Raney et al. (1947) suggested northern hogsucker females began to grow larger than males around four years old. However, Grabowski et al. (2007) found no difference in growth rates between northern hogsucker sexes in the Savannah River, South Carolina and Georgia. Stanly (1988) found that northern hogsucker exhibit pelvic fin dimorphism similar to white sucker (i.e., females rounded, and males squared).

During the spawning season, males and females are easier to distinguish; however, there is debate regarding which characteristics are sex specific. Both male and female spotted sucker can develop a pinkish-red dorsal band and have tubercles on the anal fin; however, these characteristics are typically more prominent on males (Mcswain and Gennings 1972). Only male spotted suckers develop breeding tubercles on their head (Mcswain and Gennings 1972). Conversely, only male white suckers have breeding tubercles on their anal and caudle fins (Reighard 1920). Reighard (1920) noted that not all males will develop breeding tubercles. Both male and female redhorse spp. have tubercles on the head; however, males also develop tubercles on the caudle peduncle, caudal fin, and anal fins (Reighard 1920). Conversely, Kwak and Skelly (1992) stated that tubercles were present on the head of male black and golden redhorse but absent on females. Breeding tubercles are present in similar areas on both sexes of northern hogsucker, but male tubercles are often more prominent (Reighard 1920). One explanation for the varying descriptions of tubercle expression between sexes is that development in catostomids may be linked to abiotic conditions. For example, McMaster et al. (1991) found that bleached

kraft mill effluent can reduce the degree to which secondary sexual characteristics are displayed in white suckers.

Reproduction

White and spotted suckers, black and golden redhorse, and northern hogsuckers spawn during spring (Page and Johnston 1990). These fish often migrate from lakes and large rivers to spawning areas within tributaries (Raney and Webster 1942; Olson and Scidmore 1963). However, spawning within large rivers has been documented for populations of spotted sucker and northern hogsucker (Grabowski and Isely 2007). It is likely this phenomenon occurs with other “large river” catostomids. However, focused study (see Grabowski and Isely 2007) would be required to confirm this hypothesis. Individuals inhabiting smaller streams make their way to spawning areas within those specific streams (Page and Johnston 1990). In the absence of a lotic connection, in-lake populations generally spawn on lake shorelines (Page and Johnston 1990; Wakefield and Beckman 2005). It is unclear if in-lake populations will still spawn along shorelines when a significant lotic connection is available.

Information regarding how catostomids select, or find, their spawning locations is understudied. The prevailing theory is that olfaction aids navigation and migratory behavior (Dence 1956). Werner and Lanoo (1994) suggested white sucker use olfactory cues to return to the locations where they hatched. However, it is unclear if their olfactory system is developed enough prior to drifting to imprint on the exact location (Werner and Lanoo 1994). The olfactory lobe of *Catostomus* spp. responds to select prostaglandins (released during ovulation) but not maturational hormones (released pre-ovulation; Cardwell et al. 1991). This suggests suckers may be able to differentiate between species on a spawning ground via olfaction, however olfaction may not aid migration prior to an act of reproduction. An equally probable hypothesis is that

migration is random in catostomids and their formation of loose aggregations aids in navigation to suitable spawning locations, as shoal size is inversely related to navigational error (see Larkin and Walton 1969). It is currently unknown how spotted sucker, black redhorse, golden redhorse, or northern hogsucker find their spawning grounds.

Sex ratios of fish present at spawning sites vary throughout the spawning season as most male suckers arrive near spawning grounds prior to females. However, the number of males on a spawning ground should be relatively consistent as they remain throughout the majority of the breeding season. Spawning aggregations of black and golden redhorse are male dominated (Reid 2006a). Spawning aggregations of white sucker are typically male dominated but may be dominated by females within certain years (Trippel and Harvey 1990; McManamay et al. 2012). Interestingly, 1:1 sex ratio have been observed for spawning white suckers (Corbett and Powles 1983) and spotted suckers (Mcswain and Gennings 1972); however, sex ratios of spawning aggregations may vary between years because not all fish spawn in a given year (Quinn and Ross 1985). This theory is supported by the fact that some females have been observed harboring eggs after the spawning season, which suggests the eggs are reabsorbed or expelled after they break down (Trippel and Harvey 1990). It is unknown if this behavior occurs because individuals decided not to reproduce or if they were unsuccessful finding a mate.

Agnostic behavior between males while on a spawning shoal seems to vary by species. During the spawning period, male spotted suckers establish and defend loosely-defined territories within spawning grounds (Mcswain and Gennings 1972). Golden redhorse also establishes territories, which they defend in a more aggressive manner (Kwak and Skelly 1994). Kwak and Skelly (1994) noted that dominant golden redhorse would physically injure subordinate males who ventured too close to their territories by ramming them with their

tubercles. Based on current literature, golden redhorse appear to exhibit the most aggressive behavior of any catostomid while spawning. Male white sucker, black redhorse, and northern hogsucker congregate and generally do not actively defend territories (Reighard 1920; Kwak and Skelly 1994). However, territoriality was observed for black redhorse within Big Piney River, Missouri (Bowman 1970). The reason for variation in agnostic behavior between populations of the same species of catostomids is unknown (Page and Johnston 1990).

Observational studies have documented ritualized reproductive behavior (see Diana 2003) within most members of the catostomidae family. For spotted and white suckers along with black and golden redhorse, spawning is initiated when one or more males approach a female and begin bumping or nuzzling her. If the female does not swim away, the pair or group begin “vibrating” and gametes are released (Reighard 1920; Mcswain and Gennings 1972; Kwak and Skelly 1992; Dion et al. 1994). Northern hogsucker exhibit similar behavior, however it is unknown if the spawning group “vibrates” prior to the release of gametes or just the male(s) (Reighard 1920; Raney and Lachner 1946). The basic spawning orientation for most catostomids is two males positioned along each side of a single female (Page and Johnston 1990). However, the number of individuals within the group may be highly variable (e.g., 1-12 individuals; Reighard 1920; Kwak and Skelly 1992) and the sex ratio within groups is often estimated via speculative sexually-dimorphic features (e.g., pigmentation; Page and Johnston 1990). The act of spawning may be interrupted via cursory males trying to disrupt the spawning group or attempting to join the act of spawning (i.e., “sneak spawn”; Page and Johnston 1990; Kwak and Skelly 1994). This disruptive behavior has only been observed with spotted sucker, golden redhorse, black redhorse, and northern hogsucker (Bowman 1970; Page and Johnston 1990). Spawning may also be halted by the female when a procedural misstep by the adjacent males

occurs (Kwak and Skelly 1994) or when females select against some trait the males display. If a female spotted sucker swims away from the male(s), they will actively pursue her; however, reproduction is unlikely (Mcswain and Gennings 1972). If a female white sucker or black redhorse swims away from the male(s), they will not chase her (Bowman 1970; Dion et al. 1994). Pairings are not permanent and both polygyny and polyandry have been observed in all species described above (Reighard 1920; Mcswain and Gennings 1972; Kwak and Skelly 1994).

Most catostimids are broadcast spawners and do not exhibit parental care following fertilization (Lane et al. 1996). It is debated whether catostomids construct nests prior to, or during, the act of spawning, or if some eggs become buried unintentionally as the substrate is disturbed during deposition (Page and Johnston 1990). For example, Breder and Rosen (1966) said suckers bury their eggs under coarse substrates (based on observations that sucker eggs had become covered with substrate), which was refuted by Kwak and Skelly (1994). Bridglip sucker *Catostomus columbianus* is the only catostomids known to actively engage in substrate digging and egg burying (Murdoch et al. 2005). Within our species of interest, it is likely any “burying” that occurs is an artifact of body position when suckers deposited eggs (Mcswain and Gennings 1972; Kwak and Skelly 1992; Dion et al. 1994). Eggs that are not actively buried would then settle between interstitial spaces, be transported to other presumably less suitable habitats, or be eaten by predators.

Hybridization has been observed between some catostomids (e.g., longnose sucker × white sucker; Nelson 1973). However, when hybridization occurs, it is generally in low levels relative to the population size (Nelson 1973; Dauble and Buschborn 1981). Interestingly, live backcrosses have never been documented for catostomid populations (Bangs et al. 2017). The isolating mechanisms for hybrid sucker have never been explained, suggesting backcrosses exist

or existed within most populations at extremely low densities (Mock et al. 2006; Bangs et al. 2017). This agrees with theories of Dowling et al. (2016), which suggests introgressive hybridization and reticulate evolution have and may still be occurring within the family. Currently no hybridization has been documented between white sucker, black redhorse, golden redhorse, northern hogsucker, or spotted sucker. The most likely mechanism for isolation between our species of interest is spatial or temporal partitioning spawning habitat based on selection for different abiotic conditions (Curry and Spacie 1984; Kwak and Skelly 1992; Grabowski and Isley 2007).

Maturity and Fecundity

Estimated age and size at maturity have been used to compare life-history strategies between catostomids, monitor populations, and outline recovery plans for catostomid species (Grabowski et al. 2008; Vélez-Espino and Koops 2009; Fite 2018). However, estimates of when catostomids mature are often coarse and may be regionally specific. Spotted suckers reach sexual maturity between three to six years of age in the Apalachicola River, Florida (Grabowski et al. 2012). However, male and female spotted suckers have been documented as mature at 2-5 years of age, respectively, in the Savannah River, South Carolina and Georgia (Grabowski et al. 2008). In general, white suckers mature at 3-4 years old with males maturing at smaller sizes and younger ages than females (Scott and Crossman 1973; Wakefield and Beckman 2005). However, maturity in white suckers is energy dependent and both age- and length-at-maturity show large variations within and among populations (Beamish 1973; Trippel and Harvey 1989, 1991; Chen and Harvey 1994). Chen and Harvey (1994), suggesting length at maturity is a function of juvenile growth rates. However, abiotic conditions, especially those related to water quantity (e.g., acidity), also affect size at maturity (Trippel and Harvey 1987; Chen and Harvey 1999).

Anthropogenic pollution also plays a role as bleached kraft mill effluent increases age and length at maturity in white sucker (McMaster et al. 1991; Gagnon et al. 1994). Both male and female northern hogsucker appear to mature at age three in the Savannah River, South Carolina and Georgia (Grabowski et al. 2008). Black redhorse attain sexually maturity between 170- and 355-mm total length (TL; Bowman 1970; Reid 2006a). Estimated age-at-maturity for black redhorse is thought to be between 2-6 years old over much of their range (Bowman 1970; Jenkins and Burkhead 1993; Howlett 1999). However, sexually mature black redhorse from the Grand River, Ontario and Muskegon River, Michigan were 5-13 years old (Reid 2006a). Mature female golden redhorse are significantly larger than males; with females ranging in size from 292-mm to 500-mm TL and males ranging between 250-mm to 443-mm TL (Reid 2006a). Jenkins and Burkhead (1993) stated that golden redhorse mature between 3-5 years of age. However, Smith (1977) determined that both male and female golden redhorse in Clear Creek, Ohio did not mature until age five or older.

Fecundity of catostomids offers insight into their life history and helps determine potential reproductive output for each related species (Grabowski et al. 2008; Vélez-Espino and Koops 2009; Fite 2018). Overall, catostomid fecundity has been less studied than age/size at maturity. Published fecundity estimates are coarse and lack spatial variability. Mean \pm SE fecundity of spotted suckers is $30,418 \pm 9,466$ eggs (Grabowski et al. 2012). Black redhorse produce approximately 1,3000 to over 11,000 eggs per female (Bowman 1970; Smith 1977; Kott and Rathman 1985). Golden redhorse produce approximately 5,000 to over 12,000 eggs per female (Smith 1977). Fecundity in both black and golden redhorse increases non-linearly with fork length (FL; Smith 1997). Though no fecundity information is available for northern hogsucker, analysis of eastern stream fishes (east of the 100th meridian) by Mendor and Brown

(2014) suggested that eastern suckers have high fecundity relative to their body size. White sucker produce approximately 2,000 to 31,000 eggs with fecundity increasing with age and length (Stewart 1920; Bureau of Reclamation 1992; McPhee 2007). Egg production is highly variable in white suckers (Johnston 1997). This variable fecundity is likely due to the propensity of white suckers to skip spawning events or due to environmental constraints, but may also be driven by water quality as pollution has been documented to limit fecundity in the species. Munkittrick and Dixon (1988) found Copper and Zinc limit egg size and fecundity of white suckers. Furthermore, bleached kraft mill effluent reduces egg production and create lower more variable fecundity (McMaster et al. 1991; Gagnon et al. 1994).

Early Life History

A primary focus of early-life-history study for catostomids is quantifying young-of-year abundance and timing of their drift. Within lotic ecosystems, larvae of all target species drift at some point during development (Brown and Armstrong 1985). However, larval sucker occupancy is negatively related to water velocity due to their limited swimming capabilities (Ivasauskas 2017). Interestingly, Dutterer et al. (2013) found a positive relationship between spring and summer discharge and recruitment of spotted sucker. White sucker, northern hogsucker, and spotted sucker larvae drift primarily at night (Geen et al. 1966; Gale and Mohr 1978; Wiltz 1983; Muth and Schmulbach 1984; Johnson and Mckenna 2007). No information is currently available regarding the drift timing of black or golden redhorse. Though most information comes from lotic systems, in Wisconsin lakes, larval white sucker are associated with the littoral zone, though some appear to enter the limnetic zone during nighttime (Faber 1967). It is unclear if this pattern holds true for other larval catostomids in lentic systems.

Hatch timing and development have received almost as much attention as young-of-year abundance and drift timing. Despite this, several gaps in our knowledge exist regarding these processes *in situ*, and several species remain understudied. White sucker hatch between 6.2 and 24.1 °C but appear to prefer temperatures ranging from 9.0 to 17.2 °C (McCormick et al. 1977). Hatching and developmental times are largely thermally regulated in white sucker (McElman and Balon 1980), though compensatory responses (i.e., faster development) in cooler systems have been observed (Hamel et al. 1997). White sucker ranged from 9 to 11 mm at emergence and prolarvae remained in the substrate 11 to 13 days post-hatch before beginning to drift (Corbett and Powles 1983). In controlled environments, swim-up for larval white sucker appears to be 5-8 days post fertilization, with fins, mouth, and gill arches developing around 13 to 14 days post-fertilization (Hart and Werner 1987; McMaster et al. 1992). The development of these parts coincides with the switch to planktivorous feeding (Hart and Werner 1987). Interestingly, Hart and Werner (1987) found that mortality of larval white suckers is greatest during the yolk sac phase. Hogue and Buchanan (1977) observed vertical movements of larval spotted sucker 5-6 days post-hatch when fish averaged 10-mm TL. Following a few hours of vertical movement, larval spotted sucker became free swimming (Hogue and Buchanan 1977). Scales become fully formed on spotted sucker between 30- and 33-mm TL, which also marks the average length when larvae become juveniles (White 1977). At hatch, larval northern hogsucker were ~9.0- to 10.66-mm TL and become fully formed juveniles between 21.2- and 27.8-mm TL (Buynak and Mohr 1978; Kay et al. 1994; Ivasauskas 2017). Egg development in larval black redhorse occurs at temperatures ≥ 11 °C, however the upper thermal limit is unknown (Bunt et al. 2013a). In controlled environments, eggs hatch in 9-16 and 11-25 days at temperatures of 17 and 20 °C, respectively (Bunt et al. 2013a). Black redhorse become fully formed juveniles between 24- and

76-mm TL (Bunt et al. 2013a; Ivasauskas 2017). Little information is available regarding golden redhorse early life history. However, golden redhorse become fully formed juveniles between 21.3- and 69.0-mm TL (Fuiman and Whitman 1979; Ivasauskas 2017).

Habitat Use

Catostomids generally use lotic habitats for egg deposition. In the absence of lotic connections in-lake egg deposition may occur, but this has never been formally documented. Within lotic ecosystems, white sucker, northern hogsucker, spotted sucker, black redhorse, and golden redhorse all spawn over riffle habitat (Raney and Lachner 1946; Mcswain and Gennings 1972; Corbett and Powles 1986; Kwak and Skelly 1992; Aadland 1993). Spatial and temporal habitat partitioning allow multiple species to use similar spawning locations (Kwak and Skelly 1992; Grabowski and Isely 2007). Spawning habitat partitioning has been documented for the majority of our species of interest. For example, Curry and Spacie (1984) documented northern hogsucker and white sucker spawning in similar water velocities; however, northern hogsucker spawned in deeper habitats (i.e., 35-45 cm) than white sucker (i.e., 20-25 cm). Similar habitat partitioning was observed for golden and black redhorse in Stony Creek, Illinois (Kwak and Skelly 1992) and both temporal and spatial habitat partitioning was observed for catostomid species in the Savannah River, Georgia and South Carolina (Grabowski and Isley 2007).

Body size and available habitat within a system appear to influence the location of egg deposition within the same species of catostomid. For example, Curry and Spacie (1984) found “larger” redhorse staged and spawned in “deeper” water in Indiana streams. This spatial segregation by members of the same species may reduce intraspecific competition and help buffer variations in recruitment should survival vary spatially (e.g., shallow areas become dewatered). However, it is just as likely smaller individuals are unable to compete with larger

individuals for the most suitable habitat, which is consistent with the observation of agnostic behaviors directed at smaller individuals (Mcswain and Gennings 1972; Kwak and Skelly 1992). Both hypotheses may explain why, catostomid egg deposition has also been documented in obscure places such as the edge of pools (Raney and Lachner 1946) and wetland features (i.e., submergent and emergent vegetation; Brazner 1997). It is also important to note that spawning habitat used by catostomids will be constrained by the systems they inhabit. In the Detroit River, Detroit and Ontario, white sucker spawning occurred at depths of 1.9 to 6.0 m, velocities between 3.0 and 34.0 cm/s, and substrates containing a mix of silt/clay, sand, shells, and coarse substrates (Manny et al. 2010), whereas in Illinois tributary streams, white suckers spawning occurs at depths of 0.2 to 0.3 m, velocities between 50.0 and 59.0 cm/s, and medium gravel substrates. This variation is most likely the result of differences in available habitat within each system.

Upon hatching it is unknown how long most catostomids remain benthically oriented prior to drifting. White sucker are the only species of interest for which we were able to obtain a field-based observation. Corbett and Powles (1986) sampled yolk sac larvae of white sucker on the spawning ground 11 to 13 d after peak hatch using surber samplers. Interestingly, laboratory observations show suckers are able to remain suspended in the water column after two days (Stewart 1920). It is likely that this difference is due to variation in the thermal regimes between studies. *In vitro* observations of larval development for northern hogsucker suggest they remain benthically oriented for ~8 d post hatch at 17.4 °C. Larval spotted sucker in laboratories initiated vertical movements 5 to 6 d post hatch at temperatures between 16.1 and 20.0 °C. Northern hogsucker hatched in approximately 10 days after fertilization and became free swimming ~18 days after hatching (Buynak and Mohr 1978).

Following swim up, catostomids appear to passively drift downstream to nursery habitat (Corbett and Powles 1983, 1986). White sucker and other catostomid larvae (i.e., redhorse spp., Quillback *Carpoides cyprinus*) appear to prefer drifting during low light periods (Gale and Mohr 1978; Corbet and Powles 1983). This agrees with negative phototaxis observed for spotted sucker larvae in laboratory settings (Hogue and Buchanan 1977). Along with optical habitat conditions, thermal (McCormick and Jones 1977; Hamel et al. 1997) and chemical (Oseid and Smith 1971; Siefert and Spoor 1973) conditions also influence survival and development. Furthermore, information from white sucker suggest that larval suckers have varying tolerance to different pollutants (McMaster et al. 1992; Colavecchia et al. 2006). Despite documenting the influences of various physical and chemical habitats on larval sucker survival, it is unclear if larval catostomids are able to physically select for optimal conditions *in vivo*. It is likely, their ability to select for different habitats is primarily dictated by hydraulic conditions prior to becoming juveniles.

Larval and post-larval suckers appear to select low-velocity environments. White sucker, spotted sucker, redhorse spp. and northern hogsuckers have all been caught in backwaters and off-channel habitats (Corbett and Powles 1983; Sheaffer and Nickum 1986; McDonald et al. 2014). White sucker, northern hogsucker, and redhorse spp. are also found in interfaces between fast- and low-velocity water (Aadland 1993; McDonald et al. 2014). Bunt et al (2013b) found larval black redhorse in backwaters, pools, runs, and riffles. Interestingly, they determined black redhorse were most abundant in runs with low to moderate flows and sand- to cobble-size substrates (Bunt et al. 2013b). Cover and sparse aquatic vegetation are also important to White sucker, northern hogsucker, and redhorse spp. (Leslie and Moor 1985; Aadland 1993; Tanner et al. 2004).

Juvenile catostomids appear to select habitats with aquatic vegetation. In the Great Lakes, young-of-year white sucker, northern hogsucker, and golden redhorse have an affinity for submergent vegetation (Lane et al. 1996). Interestingly, black redhorse have a high affinity for emergent vegetation (Lane et al. 1996). Brazner (1997) also determined juvenile golden redhorse and white sucker use wetlands for nursery habitat within Lake Michigan. It is likely that this vegetative preference is really fish selecting for structure to increase predator avoidance and limit predator encounters (Schlosser 1987).

Within aquatic systems, juvenile catostomids have been observed in a variety of habitats. Young northern hogsucker inhabited shallow riffles and riffle margins (Larimore et al. 1952; Funk et al. 1953). Juvenile white sucker inhabit deep pools with sand and gravel substrates (Banks 2009). Young golden redhorse inhabit slow moving water with soft bottoms (Larimore et al. 1952; Meyer 1962). Conversely, Martin and Cambell (1953) found young golden redhorse in deep fast water near riffles in Missouri, similar to observations of juvenile black and golden redhorse near riffle margins in the Black River, Missouri (Funk et al. 1953). It is possible that these contrasting observations are due to juvenile catostomid plasticity, or other coarse scale factors that were not accounted for. For example, Bunt et al. (2013b) found juvenile black redhorse occupied backwaters, pools, riffles, and runs but show a strong preference for runs. It is also possible that the use of shallower habitats is a predator avoidance strategy. The use of riffles and their margins limits aquatic predator access and the probability of encountering aquatic predators (Schlosser 1987). Juvenile suckers may also be selecting for something other than the channel unit. Groundwater contributions to that reach may be the primary factor catostomids are selecting for (Bunt et al. 2013b).

Adult suckers appear to be best adapted for stream habitats and modification of these habitats may be detrimental to the population. This may be due to dams limiting upstream movements, creating isolated populations (Hastings et al. 2016). The influence of dams and resulting river fragmentation reduces the number of redhorse spp. in stream systems (Reid et al. 2008a; Reid et al. 2008b). Interestingly, Reid et al. 2008a found fragmentation had negligible effects on occupancy of stream reaches, which they attributed to source-sink dynamics and barrier permeability (Reid et al. 2008a). This suggests barriers that are modified with fish passage structures reduce the effect of fragmentation on catostomids; however, dams have other effects on catostomids besides population fragmentation. The upstream effects of dams such as reservoir creation and pooling of water may also reduce suitable habitat (Hastings 2014). For example, Meyer (1962) found golden redhorse to be better adapted for riverine systems compared to lakes or reservoirs. Additional threats to catostomids in anthropogenically altered stream systems are pollution (Tsai 1970; McMaster et al. 1991) and thermal changes (Eaton and Scheller 1996).

Suckers are not evenly distributed throughout all river systems. For example, Rahel and Hubert (1991) found white sucker were most abundant in upper to middle sections of Horse Creek, Wyoming and relatively rare in lower sections. The fragmentation of these population along with the reduction of suitable habitat likely results in abundance reductions and in extreme cases may cause localized extinctions. This would explain the variation in catostomid species presence and abundances observed by Miranda et al. (2017) in the serially impounded Tennessee River. This suggests a thorough understanding of each species' ecological requirements is necessary to fully understand their vulnerability across modified lotic systems.

At coarse spatial scales (i.e., segment or coarser), our species of interest exhibit differential spatial partitioning. White sucker appears to use smaller streams to a higher degree (Creque et al. 2005). Furthermore, they appear more likely to inhabit “cooler” (undefined) water and lots of coarse woody habitat (Hubert and Rahel 1989; Eaton and Scheller 1996). Black redhorse occupancy is positively associated with moderately sized streams with higher channel stability and available cover (Reid 2006b; Reid et al. 2008a). Golden redhorse occupancy is positively associated with large, low-gradient streams containing coarse substrates and large pools (Reid 2006b; Reid et al. 2008a). Spotted sucker are most abundant in lower gradient streams (Miranda et al. 2017).

At finer spatial scales (i.e., finer than segment), our species of interest exhibit variable habitat selection. Black and golden redhorse are more likely to be found in large-deep pools and areas of coarse substrates (Reid 2006b; Reid et al. 2008a). Black redhorse also uses large-rifles (Reid 2006b; Reid et al. 2008a) and golden redhorse are associated with runs habitat containing cover (Aadland 1993). Adult northern hogsucker and white sucker appear to use similar habitat as both are primarily associated with run and pool habitat with cover (Aadland 1993; Banks 2009). However, Finger (1982) stated white sucker primarily use pool habitat whereas adult northern hogsucker are associated with transitional zones. This variation in habitat use could have been due to differences in body size (Schlosser 1987), time of year (Brown et al. 2001), or physicochemical conditions (Matheney and Rabeni 1995).

It is well documented our species of interest can inhabit reservoir or lake systems (Hastings et al. 2016; Miranda et al. 2017). Within lentic systems, white sucker shifts their spatial distribution to offshore areas during the warmer months (i.e., June, July, August; Tremblay and Magnan 1991). These change in habitat use may be system specific. In two

montane lakes, white sucker occupied shallower areas of lakes during June-October and in deeper water during the late fall (Bureau of Reclamation 1992). Given the lack of published information regarding lentic or modified-lotic systems, this variation can be attributed to numerous factors. For example, Reighard (1913) observed suckers across a variety of depths year-round, but generally found them below the thermocline in midsummer.

Feeding and Diet

Along with the majority of freshwater ichthyofauna, larval suckers first consume their yolk sac as their mouths develop (Stewart 1927). This first ontogenetic shift from endogenous to exogenous feeding is thought to occur 27 to 30 days post fertilization, with the yolk sac becoming fully absorbed after 30 days (McMaster et al. 1992). White sucker larvae then begin feeding on rotifers along with copepod nauplii and *cyclops bicuspidatus* (Siefert 1972). A similar pattern is observed for spotted sucker, who begin feeding between 12- and 15-mm TL and consume zooplankton and diatoms (White and Haag 1977). No published information on the larval diets of black redhorse, golden redhorse, or northern hogsucker was located, though it is likely they are planktivorous to some degree.

As larval suckers transition into juveniles, it is unlikely they undergo a true ontogenetic feeding shift and more likely that they acquire a more generalist diet. For example, Nurnberger (1928) found white sucker consumed algae, rotifers, insects and their associated larvae. Furthermore, juvenile white suckers from different systems consumed primarily daphnia (Olson 1963; Schneidervin and Hubert 1987). Interestingly, white sucker juveniles often engage in detritivory (Ahlgren 1990a). Detritivory is thought to be a compensatory response to scarce or nutritionally poor food as it bolsters growth (Ahlgren 1990b). No published information on the

juvenile diets of spotted sucker, black redhorse, golden redhorse, or northern hogsucker was located.

All our species of interest are primarily benthivorous as adults. Chen and Harvey (1995) determined food availability within the benthos is positively correlated with growth of white sucker. Though commonly thought of as generalists, selective feeding has been observed in many catostomid genera (White and Haag 1977; Saint-Jacques et al. 2000). Resource partition appears to take place when different catostomids occupy the same system (Saint-Jacques et al. 2000; Spiegel et al. 2011). Spiegel et al. (2011) attributed this to differences in gill raker morphology. It is also possible temporal feeding patterns limit competition between catostomid species. Kwak et al. (1992) observed golden redhorse exhibit discontinuous feeding, with a majority of activity occurring at night. It is unknown if other catostomids exhibit different or similar feeding patterns.

As adults, our species of interest exhibit varying diets. Across their range, adult white sucker eat mollusks, fish eggs, detritus, periphyton, zooplankton, insects, and insect larvae (Schneberger 1977; Barton 1980; Tremblay and Magnan 1991; Bureau of Reclamation 1992; Swift-Miller et al. 1999; Murphy et al. 2005). However, white sucker exhibit variation in diet items. For example, Olson (1963) determined they primarily feed on insects and mollusk's; whereas, Swift-Miller et al. (1999) found no evidence of mollusk consumption. Adult spotted suckers primarily consume Cladocera (Bur 1976). Golden redhorse diets consist of immature insect larvae; generally, chironomids, Ephemeroptera, and tricoptera (Meyer 1962; Bur 1976; Spiegel et al. 2011). Black redhorse consume Diptera, Copepoda, Cladocera, and Ephemeroptera (Bowman 1970) and northern hogsucker primarily choromimid pupae and larva (Spiegel et al. 2011). Due to a lack of study, it is unclear if these species of interest also exhibit variation in

prey choice. If they do, it is likely due to variation in food availability as observed for white sucker (Bureau of Reclamation 1992). However, it is also possible differences in selection are due to sampling bias as individual suckers may exhibit differential diet choice within the same system (Dence 1942).

Age and Growth

Validation of ages estimates from hard structures using known age fish should be conducted prior to using those ages for growth estimates; however, relatively few studies do so (~65%; Beamish and McFarlane 1983). Spurgeon et al. (2015) showed that the number of validation studies had increased since the “call for validation work” by Beamish and McFarlane (1983). Unfortunately, for several fish families, validation studies have not been conducted for all species (Spurgeon et al. 2015). The razorback sucker *Xytauchen texanus* is only species, and therefore genus, where annual increments have been validated via known age fish within the family Catostomidae. Validation for this species was possible as to known age broodstock were used. McCarthy and Minckley (1987) validated annual increments for ages 1 to 6 using sectioned sagittal otoliths from razorback sucker. Daily increments have been validated via known age fish for razorback sucker (1-49 d for lapilli; Bundy and Bestgen 2001), Chinese sucker (1-90 d for lapilli and sagita; Song et al. 2007), and shortnose sucker *Chasmistes brevirostris* (1-30 d for lapilli; Hoff et al. 1997). No validation using known age fish has been conducted for any of our species of interest.

Marginal increment validation is a form of annulus validation which compares the increment width at the edge of a structure to a regular sampling interval (e.g., month; Isely and Grabowski 2007). Increment validation has been used to confirm annulus formation in lapilli otoliths for spotted sucker (Strickland and Middaugh 2015), white sucker (Thompson and

Beckman 1995), golden redhorse, and black redhorse (Beckman and Howlett 2013). We were unable to find validation work for *Hypentellium* spp. (colloquially: “Hogsucker’s”). Increment validation is described as “less robust” when compared to other age validation techniques as: 1) it is difficult to measure growth when the edge increment is thin, 2) failure to capture individuals representing all ages present within the population may bias age estimates, and 3) variation in increment formation among years or spatial locations has been observed (see Beckman and Wilson 1995; Campana 2001) and these issues can make annuli unsuitable for aging fish, but increment-formation studies would not identify this problem. The variation in growth trajectories based on age has been documented in white suckers as the first annulus forms between July and September and subsequent annuli form between May and July each year (0-18 years; Thompson and Beckman 1995; Beckman and Calfee 2014). This suggests estimates should be shifted 0.5 years based on the month a fish was sampled (Beckman and Calfee 2014). Spotted sucker (1-10 years), black redhorse (1-10 years), and golden redhorse (0-12 years) also form annuli between May and June each year (Beckman and Howlett 2013; Strickland and Middaugh 2015). It is unclear if the trend (i.e., initial annulus forms after 0.5 years) exists for our other species of interest as the sample size for the age 0 year class of golden redhorse was low (i.e., $n < 5$) and the sample size for the age 1 year classes of all species was similarly low (i.e., $n \leq 6$).

Otoliths are often considered the “gold standard” for suckers given they are the only structure validated for the family Catostomidae and several species have been validated using marginal increment analysis (information for other species not presented). For this reason, the validity of non-lethal structures (i.e., scales, pectoral rays) is assessed via comparison to otoliths using one or more metrics (e.g., precision, coefficient of variation; Sylvester and Berry 2006). For our species of interest, information regarding between-structure comparisons were only

available for white sucker. Scales appear to be the least viable option of all nonlethal structures (MacCrimmon 1979; Bureau of Reclamation 1993). Scales tend to underestimate the age of white sucker after age 3 with a maximum difference of 5 years when compared to lapillus otoliths (Sylvester and Berry 2006). They may be the result of within structure variability, as scales taken from different body locations have resulted in different age estimates for the same fish (Quist et al. 2007). Pectoral fin rays appear to be a better nonlethal aging structure than scales for catostomids (MacCrimmon 1979; Quist et al. 2007). Sylvester and Berry (2006) determined fin rays began to disagree with lapillus otoliths after age 6 with a maximum difference of 3 years. This disagreement may be due to variation in annulus formation (Douglas Zentner, unpublished data) or the interpretability of annuli (Scidmore and Glass 1953) from sections taken along the fin ray.

Variation in longevity between species from different climates has been observed in suckers (i.e., white sucker; Schneberger 1977) along with variation between species in the same climate (e.g., Grabowski et al. 2012), so longevity should be estimated for each system independently when possible. A comparative study of longevity using our species of interest has never been conducted. Based on the available literature, longevity appears to be relatively similar (i.e., < 3 years difference) between our species of interest within “similar” climactic ranges; however, certain species exhibited anomalous longevity relative to the other estimates. For example, within midwestern systems (i.e., Iowa and Missouri) longevity estimates of golden redhorse (7-8 years), black redhorse (10 years), and northern hogsucker (7 years) were similar (Meyer 1962; Bowman 1970; Quist and Spiegel 2012), whereas white sucker had slightly higher longevity estimates (11 to 18 years; Thompson and Beckman 1995; Wakefield and Beckman 2005; Sylvester and Berry 2006). In other systems variation in longevity estimates was not

observed. For example, in Ontario white sucker and black redhorse exhibited similar longevity (16 and 17 years respectively; Reid 2009; Begley et al. 2017). The variation in longevity observed between and within our species of interests suggests longevity should be estimated for each system independently whenever possible.

Growth rates are important to the fisheries management process (Isely and Graboweki 2007). Unfortunately, early estimates of catostomid growth were obtained using age information from scales (e.g., Stewart 1926; Spoon 1938; Raney and Webser 1942); however, the accuracy of these ages has long been called into question (see Dence 1948; Ovchynnyk 1965; Geen et al. 1966). Therefore, our overview of growth will be constrained to more recent studies using otoliths or spines. Growth rates for our species of interest appear to be slower in “cooler” climates based on studies of white sucker (Schneberger 1977) and black redhorse (Reid 2009). Growth rates are constrained by population size and food abundance (Chen and Harvey 1995). Growth rates in lotic systems is also related to discharge (Quist and Spiegel 2012; Grabowski et al. 2012). Pollution, specifically bleached kraft mill effluent, appears to slow growth rates (McMaster et al. 1991).

Alternative forms of age estimation (e.g., length-frequency, mark-recapture; Isely and Grabowski 2007) have not been frequently attempted for on suckers. The only published record found for our species of interest using alternative age-estimation methods determined the length-frequency method does not provide good estimates of age after years one and two in white suckers (Priegel 1976). Prior to these findings, it had been used intermittently on other members of the family (e.g., mountain sucker *C. platyrhynchus*; Hauser 1968). No published information regarding growth rates from mark-recapture data was located for our species of interest; however, studies with other species (e.g., Sonora sucker *C. insignis*; Bestgen et al. 1987;

razorback sucker; Modde et al. 1996) suggest the method is could be used to increase our understanding of growth rates.

Marking and Tagging

Chemical marks and fin modification (i.e., removal or scarring) are the main marking methods that have previously been used with our species of interest. Beckman and Schulz (1996) recommended chemical marking for larval white sucker be done in 200 to 300 mg/L of Alizarin red S for 12 to 24 hr as it had a low mortality rate (i.e., 2.6%) and resulted in clear readable marks on the otolith. However, studies with other members of the family suggest that alternative chemicals and thermal marking also work (see Muth and Meisner 1995; Song et al. 2008). The most commonly used marking technique has been the removal or clipping of fins (Olson 1963; Dion et al. 1994). The frequent use of fin ray removal is likely due to the fact that it has little effect on sucker behavior (Dence 1942). Furthermore, the use of alternative methods such as scarring of fins is difficult to interpret (Welch and Mills 1981). Fin clips are easy to identify (Douglas Zentner, unpublished data) and have been used in conjunction with tags to estimate tag loss rates (Bulow et al. 1998).

Our species of interest have been studied using anchor (Quinn and Ross 1982, 1985; Dion et al. 1994), Passive Integrated Transponder (PIT; Castro-Santos 2004), and both radio- and acoustic-telemetry tags (Matheney and Rabeni 1995; Doherty et al. 2010). Based on published literature, the retention rate for anchor tags was relatively low for “rough fish”, which included black and golden redhorse among other species (average 75% after 8 months; Bulow et al. 1988); however, the exact retention rate for each species was not provided. Conversely, tag retention of PIT (30 d) and radio-telemetry tags (1 year) appears to be 100% based on observations of white sucker and northern hogsucker (Matheney and Rabeni 1995; Ficke et al.

2012). Survival (30 d) of juvenile white suckers (100-172 mm, TL) implanted with 23- and 12.5-mm PIT tags into their body cavity was 44.4 and 31.6% respectively (Ficke et al. 2012). This suggests PIT-tag-induced mortality may be high for juvenile suckers. Interestingly, Ficke et al. (2012) noted no changes in swimming performance for tagged juvenile suckers, which suggests survival cannot be discerned clearly from behavior. Matheney and Rabeni (1995) estimated ~13.6% mortality for radio tagged northern hogsuckers that met the 2% body weight recommendation for tagging (see Winter 1983).

Movement and Migrations

Past studies of group and individual movements for our species of interest suggest suckers movement is highly variable at the individual level. Funk (1957) estimate that 47.4 % of golden and 60.0% black redhorse exhibited little movement in Missouri streams based on angler tag returns. However, the ~ 40-53% of fishes that did move were recaptured 11.3 to 55.0 km from their last known location (Funk 1957). Though a coarse comparison, these findings suggests sucker populations exhibit stark variations movement behavior. Shorter temporal observations have suggested suckers are crepuscular and move to feeding areas during the night (Matheney and Rabeni 1995). Matheney and Rabeni (1995) noted that movements were greatest during the summer and lowest during the winter. During periods of increased discharge, northern hogsucker move to the edges of the streams where currents are reduced (Matheney and Rabeni 1995). Under reduced flows and water levels, Meyer (1962) noted golden redhorse showed significant downstream movement and hypothesized they were seeking out larger systems that maintained consistently flowing water.

Patterns of spawning-season migrations appear highly variable, likely due to non-annual spawning by individual suckers. White and spotted suckers, black and golden redhorse, and

northern hogsuckers are generally thought to migrate from lakes and large rivers to spawning areas within tributaries (Raney and Webster 1942; Olson and Scidmore 1963). However, spawning may also occur within the same large rivers, lakes, or small streams they were already inhabiting (Page and Johnston 1990; Wakefeild and Beckman 2005; Grabowski and Isely 2007). Doherty et al. (2010) observed white suckers making significant migrations during the spawning period. Across their range, our species of interest spawn during the spring, presumably in response to increasing water temperature and discharge (when associated with a lotic environment; Barton 1980; Page and Johnston 1990). White suckers have been observed making spawning migrations during the day (Dence 1948) and night (Webster 1942), suggesting no clear diel pattern for spawning migration activity. However, Doherty et al. (2010) hypothesized non-annual spawning may influence results obtained from spawning-migration studies as they observed no movement by all but one of their white suckers during the last year of their tracking study.

Harvest

Harvest effects on the catostomid family has received little attention. Though qualitative in nature, several reports document the long-standing practice of gigging suckers in the Ozark Highlands (e.g., Everts-Boehm 1996; Morgan et al. 2012). However, few studies have quantified gigging effort or harvest within this ecoregion. The only quantitative published record of Ozark Highlands sucker gigging reported a 50% increase in harvest effort for Current River, Missouri from 1980 to 1987 (Matheney and Rabeni 1995). However, the Ozark Highlands are not the only ecoregion where sucker are harvested. For example, the commercial harvest of catostomids has been occurring for years across the United States (Schneberger 1977; Brant and Schreck 1975; Begley et al. 2017). Harvest decreased the density of white sucker older than age 10 in Main

lakes (Begley et al. 2018) and was the main cause of population collapse of lost river sucker (Cooke et al. 2005; Janney et al. 2008). The size at which suckers are removed from the population may determine the population-level effects as the removal of “small” bodied catostomid for bait had little effect on Rich Creek, Virginia (Brant and Schreck 1975). Given the broad geographic range of suckers in North America, further study of harvest effects is required. This is especially true harvest can be highly variable between systems (Quin 2010).

Trophic Linkages and Community Responses

Trophic interactions for all species of sucker have been poorly studied. The majority of suckers can be described as planktivores early in life (Siefert 1972; McMaster et al. 1992) and primarily benthivores as adults (Chen and Harvey 1995; Spiegel et al. 2011). Though diet overlap has been suggested for suckers and other sportfish for ~90 years (e.g., Harkness and Ricker 1929), no clear evidence for resource competition has been found (Holey et al. 1979). Similarly, suckers have been observed consuming sportfish eggs (Atkinson 1931; Greeley 1932; Keenleyside 1972); however, no studies have shown that it is detrimental to a stock (Holey et al. 1979; Cooke et al. 2005). There is some evidence suckers act as a forage base for game species. Members of the sucker family occur in the diets of piscivores such as muskellunge *Esox masquinongy* (Bozek et al. 1999), northern pike *E. lucius* (Lawler 1965), and largemouth bass *Micropterus salmoides* (Pilger et al. 2008), along with omnivores such as Channel Catfish *Ictalurus punctatus* (Tyus and Nikirk 1990). Suckers may also constitute a portion of the diet of Smallmouth Bass *Micropterus dolomieu* (Waters et al. 1993) and White Bass *Morone chrysops* (Belk et al. 2001), though this is anecdotal and has not been corroborated with actual diet data.

Similar to trophic interactions, community responses to changes in the biomass or density of catostomids are lacking. The information available regarding community responses to changes

in the catostomid community are limited to removal studies (e.g., Andrews 1973). Holey et al. (1979) reviewed several early removal studies and concluded that select studies showed increases in sportfish catch rates (Johnson 1977) and increased growth in specific age groups of some sportfish (Campbell 1973); however, Holey et al (1997) suggested these results were confounded and inconclusive. Holey et al.'s (1997) findings were supported by long-term studies that showed no discernable effects of sucker removal (Rawson and Elsey 1950; Flick and Webster 1975). More recent sucker removal literature suggests a reduction in the sucker population may increase niche breath of yellow perch *Perca flavescens*, increase invertebrate abundance (Hayes et al. 1992), and improve somatic energy reserves of yellow perch (Hayes and Taylor 1994). However, Hayes et al. (1992) and Hayes and Taylor (1994) are inconclusive because their study lacked replication. Furthermore, Hayes and Taylor (1994) used a Before-After-Control-Impact design, but decided to include some of their post-removal data (i.e., collected after treatment) in the pretreatment group (i.e., before treatment). Brodeur et al. (2001) removed suckers from five lakes at varying densities and concluded age 1 brook trout *Salvelinus fontinalis* biomass increased but white sucker growth rates and age-at-maturity decreased, potentially increasing the spawning stock. Despite the lack of evidence that sucker removal benefits sportfish, Begley et al. (2018) noted that the practice still occurs with little justification.