

**SPATIOTEMPORAL VARIATION IN LAKE STURGEON
MOVEMENT AND HABITAT SELECTION IN MISSOURI RIVER
TRIBUTARIES:
IMPLICATIONS FOR THE MANAGEMENT AND RECOVERY OF
POPULATIONS AT RANGE MARGINS**

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by

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The undersigned, appointed by the dean of the Graduate School, have examined the
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SPATIOTEMPORAL VARIATION IN LAKE STURGEON MOVEMENT AND
HABITAT SELECTION IN MISSOURI RIVER TRIBUTARIES:
IMPLICATIONS FOR THE MANAGEMENT AND RECOVERY OF POPULATIONS
AT RANGE MARGINS

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ATTRIBUTION

Chapters 1 and 5 follow APA style guidelines. Chapters 2-4 were formatted as independent manuscripts for submission to peer-reviewed journals and therefore there may be content redundancy. We use the pronoun “we” to acknowledge contributions of manuscript coauthors. Some information may be repeated and elements of style may vary among chapters. Chapter 2 adheres to the style guidelines adopted by *Ecohydrology*. Chapter 3 *River Research and Applications*, and Chapter 4 *Restoration Ecology*. Coauthors on these manuscripts include Dr. Craig Paukert, Dr. Thomas Bonnot, Brandon Brooke, Travis Moore, and Seth Owens. Dr. Paukert acquired funding for this project and assisted with study design and manuscript editing. Brandon Brooke helped with study design, data collection and compilation, preliminary analysis, and manuscript editing for all chapters. Dr. Bonnot assisted with spatial-capture-recapture analyses in Chapter 3. Seth Owens collected data and developed GIS map layers used in Chapter 4.

DISSERTATION ABSTRACT

Lake Sturgeon were nearly extirpated from Missouri by the 1970s leading the Missouri Department of Conservation (MDC) to list the species as endangered within the state. Recovery efforts commenced with the publication of the first edition of Missouri's Lake Sturgeon Recovery Plan in 1984. Since, growing populations of mature individuals have been documented; however, information gaps regarding habitat selection and movement in the Missouri River Basin portion of its range hinder MDC's efforts to establish a self-sustaining population. In this project we focused on the following research objectives: (1) elucidate the factors that influence movement patterns of Missouri River Lake Sturgeon, (2) investigate survival and dispersal of stocked age-0 Lake Sturgeon from four stocking locations, (3) define seasonal habitat selection in multiple life stages of Lake Sturgeon and illustrate spatial availability of suitable habitats across the study area. I monitored movements 96 subadult and adult Lake Sturgeon over 3.5 years and 187 age-0 juvenile Lake Sturgeon during the fall/winter of two years. Missouri River tributaries were important habitats for adult and subadult Lake Sturgeon throughout the year. Lake Sturgeon use of the Osage River was greater in all months compared to the Gasconade River. Use of the Osage River was highest in the summer and lowest in the winter, and in the Gasconade River it was lowest in the summer and highest in the spring. In each month tributary occupancy was > 70%. Spring upstream migrations occurred in each tributary and were correlated with above average discharges and temperatures from 13 to 19 °C. Fall migrations only occurred in the Osage River but were also correlated with intermediate temperatures and above-average discharges. A few individuals were detected as far upstream as Bagnell Dam at river km (rkm) 129 in the

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injury in seasonal refugia, promoting resilience under shifting thermal and hydrologic regimes due to climate change, revealing sampling locations for population monitoring or spawning validation, allocating future stocking to suitable habitats, and directing habitat restoration and protection efforts.

CHAPTER 1- GENERAL INTRODUCTION

Reintroduction of rear-edge populations to degraded large river systems

Identifying factors that constrain species' range boundaries is an ongoing priority in ecological research that can inform species reintroduction (Armstrong & Seddon, 2008; Booher & Walters, 2021; Holt, 2003). Natural selection operates through hierarchical abiotic and biotic faunal filters such as climate, physical habitat, or interspecific competition to determine local fish assemblages (Quist, Rahel, & Hubert, 2005). The "abundant-center hypothesis" posits that abiotic conditions may approach a species' optimal values near the geographic center of their distribution leading to greater population abundances and lower probabilities of extirpation there (Brown, 1984; Guo, Taper, Schoenberger, & Brandle, 2005; Sagarin, Gaines, & Gaylord, 2006). In contrast, reestablishing extirpated populations of a species near its distributional margins may be more challenging as abiotic conditions reach physiologically stressful levels approaching the species' niche-limits (Whitney et al., 2016; Woolbright, Whitham, Gehring, Allan, & Bailey, 2014). Furthermore, conservationists are increasingly concerned about what have been coined "rear edge" populations (Hampe & Petit, 2005), as climate change pushes the ranges of coolwater fishes northward (Alofs, Jackson, & Lester, 2014).

In addition to climate, modifications to many other abiotic filters have shaped contemporary fish assemblages in the world's largest rivers. Large rivers are complex socio-ecological systems providing numerous services to humans including water for irrigation, hydroelectric power, inland waterways, construction materials, and flood protection, that often diminish the ecological service they provide as fish habitat (Thoms & Sheldon, 2019). Habitat homogenization due to alterations in sediment and woody

debris transport, channel confinement, and impoundment is common in large rivers (Paukert & Galat, 2010). Ecological consequences of habitat modifications include the disproportionate imperilment of fluvial specialist species that comprise 50% of the total fish species richness in the Missouri River basin (Galat et al., 2005).

Hydrologic regulation for electricity generation, flood control, and irrigation is among the greatest threats to the ecological function of large rivers and conservation of fluvial dependent fishes (Puckridge, Sheldon, Walker, & Boulton, 1998). The serial discontinuity concept explains that dams, levees, and other barriers disrupt longitudinal environmental gradients and block lateral access to floodplain habitats that may be important spawning, foraging, nursery, or resting habitats for fishes (Ward & Stanford, 1995). Alterations in magnitude, duration, and timing of flows downstream of dams also disrupt habitat-forming processes and eliminate seasonal migratory cues (Bunn & Arthington, 2002; Poff et al., 1997). Many large river fishes such as those in the order Acipenseriformes (paddlefish and sturgeons) have evolved periodic reproductive strategies such as large-size, late-maturation, limited parental care, and high fecundity to align with stable seasonal flow patterns (McManamay & Frimpong, 2015; Winemiller & Rose, 1992). However, these reproductive traits are poorly suited for variable flows below hydropeaking dams (Mims & Olden, 2012).

As an alternative to degraded mainstem habitats, tributaries may serve as refugia for large river fishes. Identifiable patterns in stream form and function occur along a stream size continuum (Vannote, 1980). However, these longitudinal gradients are not always smooth and abrupt discontinuities in geomorphology may occur at confluences within a river network (Kiffney, Greene, Hall, & Davies, 2006; Rice, Greenwood, &

Joyce, 2001). Tributaries are sources of water, wood, and sediment that either ameliorate or exacerbate physical degradation in downstream reaches depending on their own degree of hydraulic alteration (Kiffney et al., 2006). Tributary confluences contain complex habitats and may concentrate detritus and nutrients increasing biological diversity and productivity (Benda, Andras, Miller, & Bigelow, 2004; Rice et al., 2001). New sampling methodologies have revealed fish diversity hotspots in tributaries and records of large river fishes using habitats that are not available in mainstem rivers (Dunn, Brooke, Hrabik, & Paukert, 2018). Therefore, habitat management in tributaries may be an effective strategy to conserve fish populations in heavily degraded large river basins (Kiffney et al., 2006).

Lack of suitable habitat for all life stages in mainstems or tributaries can become bottlenecks for successful species reintroductions. When confronted with environmental stressors, organisms have two options: Adapt to local conditions or relocate to more suitable habitats (Holt, 2003). The first is not feasible in many reintroductions because managers are often unable to choose locally adapted source populations and evolutionary adaptation may occur too slowly to track rapid ongoing changes in habitat and climate (Merilä, 2012). The latter strategy where organisms transition among habitat patches to complete life cycles is known as “landscape complementation” (Dunning, Danielson, B. J., & Pulliam, 1992). However, predicted warming temperatures will increase resting metabolic rates of freshwater fishes near southern range boundaries leaving limited aerobic scope to conduct long distance migrations (Whitney et al., 2016) and dams may restrict access to seasonally important habitats (Bunt, Castro-Santos, & Haro, 2012). Therefore, a fundamental question that will determine the effectiveness of a

reintroduction program is whether the dispersal capacity of reintroduced individuals, given the spatiotemporal distribution of suitable habitats and hydrologic conditions, is sufficient to sustain long-term population viability with minimal ongoing stocking. Advancements in telemetry technology have permitted new insights and prompted new questions into adaptive roles of the linked processes of movement and habitat selection in adult and juvenile fishes (Hussey et al., 2015). Presently, some of the most pressing questions include: What abiotic factors drive migratory fish behavior? What is the significance of ontogeny in migration strategies? And how does the spatial distribution of habitat quality affect fish movement? (Lennox et al., 2019).

Lake Sturgeon ecology and reintroduction at the “edge”

Many questions associated with the movement of large river fishes are manifested in our lack of understanding of Lake Sturgeon (*Acipenser fulvescens*) ecology near its southern range margin. Lake Sturgeon are native to portions of the Mississippi, Great Lakes/St. Lawrence, and Hudson Bay drainages from 34 °N to 58 °N (Bruch, Haxton, Koenigs, Welsh, & Kerr, 2016). However, beginning in the late 1800s Lake Sturgeon populations declined. As a result, 21 U.S. states or Canadian provinces consider Lake Sturgeon as endangered, threatened, or a species of conservation concern (Bales & Phelps, 2017) and the Center for Biological Diversity recently petitioned for the Lake Sturgeon’s protection under the Federal Endangered Species Act (Fink, 2018). Lake Sturgeon declines were particularly drastic in southern states where they were extirpated from large portions of the Mississippi, Missouri, Ohio and Tennessee river basins. For example, by 1980, biologists were unable to capture Lake Sturgeon anywhere in the state

of Missouri (Carlson & Pflieger, 1981). Biologists have observed latitudinal differences in growth, aerobic scope, and migratory behavior in Lake Sturgeon populations (Bugg et al., 2020; Moore, Paukert, & Moore, 2020; Power & McKinley, 1997) prompting a need for spatially-explicit studies of Lake Sturgeon ecology to inform ongoing recovery efforts (Wishingrad, Carr, Pollock, Ferrari, & Chivers, 2014). There is additional concern for “rear-edge” populations of this “coolwater” species because physiological stress and reduced growth may occur at temperatures above 28 °C (Lyons & Stewart, 2014). Water temperatures in many southern rivers occupied by Lake Sturgeon already exceed this threshold and temperatures are expected to further increase due to climate change (Bezold & Peterson, 2008; IPCC, 2014).

Many of the anthropogenic abiotic and biotic stressors that caused the homogenized fish communities in North America’s large rivers are implicated in the Lake Sturgeon’s decline. Traits such as long generation times and intermittent reproduction increase the Lake Sturgeon’s vulnerability to overexploitation and habitat degradation (Hayes & Caroffino, 2012). Adults can attain ages of 150 years, weights of 140 kg, and may take 15-25 years to become reproductively mature (Harkness & Dymond, 1961; Scott & Crossman, 1973). Males typically spawn every 1 to 2 years and females every 3 to 4 years with females producing up to 5,000 eggs per pound of body weight (Harkness & Dymond, 1961). Lucrative commercial fisheries in the 1800s that targeted Lake Sturgeon flesh, hides, swimbladders, and roe and annual harvest > 13 million kg/year from Lake Erie and Lake Huron, quickly outpaced the low natural annual recruitment rates (Baldwin, Saalfeld, Ross, & Buettner, 1979). Degradation of foraging, spawning, and nursery habitats hastened population declines and continues to hinder

recovery despite the enactment of harvest moratoriums (Hayes & Caroffino, 2012). Lake Sturgeon inhabit rivers, lakes, and occasionally estuaries, but are classified as fluvial dependent requiring coarse gravel, cobble, or boulder habitats and flowing water to reproduce (Baril, Buszkiewicz, Biron, Phelps, & Grant, 2017). Spawning sites can be degraded by silt deposition or algal growth (Johnson, LaPan, Klindt, & Schiavone, 2006). Mortality is high from the egg stage through the first year of life (Caroffino, Sutton, Elliott, & Donofrio, 2010; Forsythe, Scribner, Crossman, Ragavendran, & Baker, 2013), but increases dramatically with subadult and adult annual survival rates > 85% (Adams, 2004; Vélez-Espino & Koops, 2006). Interstitial spaces in coarse substrate are required to oxygenate eggs and larvae and to protect them from predation (Forsythe et al., 2013; Manny & Kennedy, 2002). Downstream habitat connectivity is also important to permit larval drift into nursery habitats (Auer & Baker, 2002). Tributary use during spawning migrations is well-documented, but Lake Sturgeon may also forage in tributary confluences that can be productive depositional areas (Knights, Vallazza, Zigler, & Dewey, 2002). Lake Sturgeon may be less selective for physical characteristics of foraging habitats, opportunistically preying on various benthic taxa of macroinvertebrate larvae, crayfish, mussels, and fish (Amacker & Alford, 2017; Braun, Phillips, Nanayakkara, & Wissel 2018). Dams can confine populations to short river reaches and unstable flows may negatively affect reproductive migrations (Auer, 1996; McDougall, Blanchfield, Peake, & Anderson, 2013). Southern Lake Sturgeon rivers contain many large hydroelectric dams, but recently there have been efforts to improve ecological flows, promote passage, and reduce entrainment some of these areas (Bednarek & Hart, 2005; McDougall et al., 2013).

Despite the persistent obstacles to southern Lake Sturgeon reintroduction, these populations remain understudied relative to their mid-latitude and northern counterparts (Moore et al., 2020; Saidak, 2015). We are not aware of any studies that have investigated movement and habitat selection of multiple life stages of Lake Sturgeon in these systems. Adult Lake Sturgeon are especially understudied as early stocked cohorts in reintroduced southern populations have just recently attained reproductive maturity. Lake Sturgeon in the Missouri River basin offer an excellent opportunity to study ontogenetic shifts in and seasonal movement and habitat selection of a reintroduced Lake Sturgeon population near its southern range margin.

Lake Sturgeon management in the study area

The Lake Sturgeon recovery program in Missouri began in the early 1980's, and since then > 420,000 Lake Sturgeon fingerlings or fry have been released in Missouri waters (Moore, 2021). Increasing angler reports in Missouri River tributaries as well as the first documented Lake Sturgeon spawning in 2016 in the tailwaters of Melvin Price Lock and Dam in West Alton, MO (Buszkiewicz, Phelps, Tripp, Herzog, & Scheibe, 2016), suggest that adult populations are increasing in Missouri. Despite these milestones, recovery successes will not be sustainable if habitats needed for survival and recruitment are limiting. Successful spawning has not been documented in the Missouri River basin nor is it known if suitable spawning habitat exists. Further, it is likely that strains native to the Missouri River have been replaced by reintroduced individuals sourced from further north in Wisconsin (Berkman, Anderson, Herzog, Moore, & Eggert, 2020). The potential loss of local adaptation to warmer lotic environments may further

reduce fitness in reintroduced populations (Eliason et al., 2011). Identifying important habitat requirements and mapping their occurrence will help managers recommend strategies to reduce degradation, fragmentation, and make flow release recommendations from upstream dams.

The core study area for this project is centered at a latitude of 39 °N near the species' southwestern range margin and encompasses two of the larger tributaries of the lower Missouri River the Osage and Gasconade rivers. These rivers have been the source of the most sightings of Lake Sturgeon in Missouri in recent years and may be important year-round habitats for the species (Moore, 2021). Through collaborations with agency partners, we can also monitor coarse scale movement portions of the lower Missouri River, the middle and lower Mississippi River in Missouri and Iowa, as well as other tributaries such as the Chariton, Grand, Lamine, Moreau, and Salt (Mississippi tributary) rivers (Figure 2.1).

Lower Missouri River Lake Sturgeon populations have access to thousands of km of lotic habitats downstream of mainstem and tributary dams. In its natural state, the Missouri River accumulated large amounts of sediments from highly erodible lands in the Great Plains, producing a braided channel and high turbidity (Galat et al., 2005). Today, the lower one-third of the river has been channelized for flood protection, navigation, irrigation, and electricity generation (Galat et al., 2005). Upstream impoundment has homogenized downstream flow regimes by reducing the magnitude of spring flood pulses and increasing summer and autumn base-flows (Pegg, Pierce, & Roy, 2003). Large tributaries contribute 50% of the lower Missouri River's total discharge and greatly influence the characteristics of the river (Galat et al., 2005). Therefore, tributaries like the

Osage and Gasconade rivers which are themselves large rivers, may provide critical habitat for many fluvial specialist and dependent fishes (Pracheil, McIntyre, & Lyons, 2013).

The entirety of the Gasconade River and much of the Lower Osage River occurs within the Ozark Plateau physiographic region and are the major tributaries to the lower Missouri River within this physiographic region. The 8th Strahler order Osage River has a watershed area 3 times larger than the 6th order Gasconade River. Ozark rivers are characterized by coarser bed loads of primarily gravel substrate as compared to sand and silt dominated rivers of the plains ecoregions. Only 40 km separates their confluences with the Missouri River. The geology of both watersheds is primarily dolomite and sandstone and karst geology is common (Blanc, 2001; Benke & Cushing, 2005; Schubert, 2001). The lower 19 km of the Osage River and lower 15 miles of the Gasconade River is almost entirely pool habitat due to low channel gradients and backflow from the Missouri River (Lobb & Lueckenhoff, 2013).

Hydrologic regimes differ greatly in these two rivers. The most precipitation and highest flows in the Gasconade and Osage rivers occur during April and May (Benke & Cushing, 2005; Figure 2.2A). The impassible Bagnell Dam impounds the Osage River ~ 128 km upstream of its confluence with the Missouri River forming Lake of the Ozarks. The practice of “peaking” at this 45 m tall hydroelectric facility produces rapid changes in flow and river levels up to 2 m per day (E. Pherigo, U.S. Fish and Wildlife Service, unpublished data). Flow regulation is also linked to channel widening and bank erosion in the Osage River (Mohammed-Ali, Mendoza, & Holmes Jr, 2020). Lallaman (2012) suggests that this flow variability may hinder Paddlefish reproduction in the lower Osage

River. An additional low-head dam is present on the Osage River at river kilometer 19 which restricts the distribution of big river fish species Flathead Catfish (*Pylodictis olivaris*), Longnose Gar (*Lepisosteus osseus*), and Skipjack Herring (*Alosa chrysochloris*), during low water periods (Pherigo, 2019) and may also affect Lake Sturgeon seasonal distribution. In contrast, the lower Gasconade River lacks major dams to impede Sturgeon movements and reports exist of Lake Sturgeon captured as far upstream as Jerome, MO, over 160 kilometers from the confluence with the Missouri River (Pflieger, 1997). Temperature regimes also differ between these two tributaries. Bagnell Dam is a bottom release hydroelectric structure, which has moderating effect on thermal regime of the Osage River. Downstream temperatures in the Osage tend to be warmer in the winter and cooler in the summer than the Gasconade (Pherigo, 2019). Due to its smaller size and absence of moderating effects of upstream impoundment the Gasconade River exhibits greater diel fluctuations in water temperatures, warms faster in the spring, and cools faster in the fall (E. Pherigo, unpublished data). Relative to the Gasconade and Missouri rivers, the Osage River will warm more slowly in the spring and cool more slowly in the fall (Figure 2.2B).

Management goals and research questions

This study was designed in conjunction with the Missouri Department of Conservation to fulfill information needs outlined in their Lake Sturgeon Recovery Plan. Originally published in 1992, the plan was updated in 2007 (Todd, 2007), and is currently being finalized in 2021 (Moore, 2021). The latest iteration outlines four goals for Lake Sturgeon recovery:

- 1) Identify and address barriers to establishment of a self-sustaining Lake Sturgeon population
- 2) Manage Missouri's Lake Sturgeon populations and preferred habitats to promote further population growth
- 3) Ensure stakeholder awareness of Lake Sturgeon recovery efforts
- 4) Develop a strategic plan for recreational Lake Sturgeon catch-and-release and harvest seasons

In support of the first two goals, MDC provided funding to conduct a four-year telemetry study of movement and habitat use of multiple life stages of Lake Sturgeon and outlined three specific research priorities for the project:

- 1) Determine distribution, movement, and site fidelity of adult Lake Sturgeon.
- 2) Determine habitat selection of adult Lake Sturgeon in the Osage and Gasconade rivers.
- 3) Determine dispersal of stocked Lake Sturgeon.

Building off the three objectives and connecting them to broader questions regarding species reintroduction, tributary ecology, and habitat suitability for southern Lake Sturgeon populations, I developed the following 4 chapters:

Chapter Two: Lake Sturgeon seasonal movements in two rivers with differing degrees of hydrologic regulation

Chapter Three: Does where they start affect where they finish? A multi-method investigation of the role of stocking location on survival and dispersal of hatchery-reared Lake Sturgeon in Missouri River tributaries

Chapter Four: Habitat selection in a southern Lake Sturgeon population: Implications of temporal, spatial, and ontogenetic variation for restoration

Chapter Five: Summary and implications for the management of Missouri Lake Sturgeon populations

References

Adams Jr, W. E. (2004). *Lake Sturgeon biology in Rainy Lake, Minnesota and Ontario*.

[Master's thesis, South Dakota State University, Brookings, South Dakota].

Retrieved from https://ijc.org/sites/default/files/50_Adams-Jr-Wells-Eugene-MS-2004.pdf

Alofs, K. M., Jackson, D. A., & Lester, N. P. (2014). Ontario freshwater fishes demonstrate differing range-boundary shifts in a warming climate. *Diversity and Distributions*, 20(2), 123-136. <https://doi.org/10.1111/ddi.12130>

Amacker, T. M., & Alford, J. B. (2017). Selective predation by reintroduced juvenile Lake Sturgeon (*Acipenser fulvescens*) in Ft. Loudoun reservoir, Tennessee (USA). *Environmental Biology of Fishes*, 100(10), 1301-1314. <https://doi.org/10.1007/s10641-017-0643-9>

Armstrong, D. P., & Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in Ecology & Evolution*, 23(1), 20-25. <https://doi.org/10.1016/j.tree.2007.10.003>

- Auer, N. A. (1996). Response of spawning Lake Sturgeons to change in hydroelectric facility operation. *Transactions of the American Fisheries Society*, 125(1), 66-77.
[https://doi.org/10.1577/1548-8659\(1996\)125<0066:ROSLST>2.3.CO;2](https://doi.org/10.1577/1548-8659(1996)125<0066:ROSLST>2.3.CO;2)
- Auer, N. A., & Baker, E. A. (2002). Duration and drift of larval lake sturgeon in the Sturgeon River, Michigan. *Journal of Applied Ichthyology*, 18(4-6), 557-564.
- Baldwin, N. S., Saalfeld, R. W., Ross, M. A., & Buettner, H. J. (1979). *Commercial fish production in the Great Lakes 1867–1977*. Great Lakes Fisheries Commission. Ann Arbor, Michigan, Tech. Rep. No. 3, 187.
- Bales, K., & Phelps, Q. (2017). Current status of Lake Sturgeon (*Acipenser fulvescens*) throughout their range. Unpublished draft.
- Baril, A. M., Buszkiewicz, J. T., Biron, P. M., Phelps, Q. E., & Grant, J. W. (2018). Lake Sturgeon (*Acipenser fulvescens*) spawning habitat: a quantitative review. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(6), 925-933.
<https://doi.org/10.1139/cjfas-2017-0100>
- Bednarek, A. T., & Hart, D. D. (2005). Modifying dam operations to restore rivers: ecological responses to Tennessee River dam mitigation. *Ecological Applications*, 15(3), 997-1008. <https://doi.org/10.1890/04-0586>
- Benda, L. E. E., Andras, K., Miller, D., & Bigelow, P. (2004). Confluence effects in rivers: interactions of basin scale, network geometry, and disturbance regimes. *Water Resources Research*, 40(5), 1-15. <https://doi.org/10.1029/2003WR002583>
- Benke, A. C., & Cushing, C. E., (Eds.). (2005). *Rivers of North America*. Academic Press.

- Berkman, L. K., Anderson, M. R., Herzog, D. P., Moore, T. L., & Eggert, L. S. (2020). A Genetic assessment of Missouri's Lake Sturgeon after 30 years of restoration Releases. *North American Journal of Fisheries Management*, 40(3), 700-712. <https://doi.org/10.1002/nafm.10430>
- Bezold, J., & Peterson D. L. (2008). Assessment of Lake Sturgeon reintroduction in the Coosa River system, Georgia–Alabama. In *American Fisheries Society Symposium* (Vol. 62, pp. 1-15).
- Blanc, T. J. (2001). *Gasconade River Watershed inventory and assessment*. Missouri Department of Conservation. Report, Sullivan, Missouri.
- Booher, E. C., & Walters, A. W. (2021). Biotic and abiotic determinants of Finescale Dace distribution at the southern edge of their range. *Diversity and Distributions*, 27(4), 696-709. <https://doi.org/10.1111/ddi.13227>
- Braun, D. P., Phillips, I. D., Nanayakkara, L., & Wissel, B. (2018). Diet characterization and a preliminary investigation into trophic niche placement for an endangered Lake Sturgeon (*Acipenser fulvescens*) population in the Saskatchewan River, SK, Canada. *PloS one*, 13(11), e0206313. <https://doi.org/10.1371/journal.pone.0206313>
- Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, 124(2), 255-279.
- Bruch, R. M., Haxton, T. J., Koenigs, R., Welsh, A., & Kerr, S. J. (2016). Status of Lake Sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. *Journal of Applied Ichthyology*, 32, 162-190. <https://doi.org/10.1111/jai.13240>

- Bugg, W. S., Yoon, G. R., Schoen, A. N., Laluk, A., Brandt, C., Anderson, W. G., & Jeffries, K. M. (2020). Effects of acclimation temperature on the thermal physiology in two geographically distinct populations of Lake Sturgeon (*Acipenser fulvescens*). *Conservation Physiology*, 8(1), coaa087.
<https://doi.org/10.1093/conphys/coaa087>
- Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental management*, 30(4), 492-507. <https://doi.org/10.1007/s00267-002-2737-0>
- Bunt, C. M., Castro-Santos, T., & Haro, A. (2012). Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, 28(4), 457-478. <https://doi.org/10.1002/rra.1565>
- Buszkiewicz, J. T., Phelps, Q. E., Tripp, S. J., Herzog, D. P., & Scheibe, J. S. (2016). Documentation of Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817) recovery and spawning success from a restored population in the Mississippi River, Missouri, USA. *Journal of Applied Ichthyology*, 32(6), 1016-1025.
<https://doi.org/10.1111/jai.13211>
- Carlson, D. M., & Pflieger, W. L. (1981). *Abundance and life history of the Lake, Pallid and Shovelnose sturgeons in Missouri*. Final Report. Endangered species project SE-1-10. Missouri Department of Conservation, Jefferson City, MO.
- Caroffino, D. C., Sutton, T. M., Elliott, R. F., & Donofrio, M. C. (2010). Predation on early life stages of Lake Sturgeon in the Peshtigo River, Wisconsin. *Transactions of the American Fisheries Society*, 139(6), 1846-1856.
<https://doi.org/10.1577/T09-227.1>

- Dunn, C. G., Brooke, B. L., Hrabik, R. A., & Paukert, C. P. (2018). Intensive sampling reveals underreported use of great-river tributaries by large-river fishes in Missouri. *Southeastern Naturalist*, *17*(3), 512-520.
<https://doi.org/10.1656/058.017.0316>
- Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 169-175.
<https://doi.org/10.2307/3544901>
- Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., ... & Farrell, A. P. (2011). Differences in thermal tolerance among Sockeye Salmon populations. *Science*, *332*(6025), 109-112.
<https://doi.org/10.1126/science.1199158>
- Fink, M. (2018). *Petition to list U.S. populations of Lake Sturgeon (Acipenser fulvescens) as endangered or threatened under the endangered species act*. Center for Biological Diversity. <https://www.biologicaldiversity.org/species/fish/pdfs/Lake-Sturgeon-petition-5-14-18.pdf>
- Forsythe, P. S., Scribner, K. T., Crossman, J. A., Ragavendran, A., & Baker, E. A. (2013). Experimental assessment of the magnitude and sources of Lake Sturgeon egg mortality. *Transactions of the American Fisheries Society*, *142*(4), 1005-1011. <https://doi.org/10.1080/00028487.2013.790847>
- Galat, D. L., Berry, C. R., Gardner, W. M., Hendrickson, J. C., Mestl, G. E., Power, G. J., Stone, C. & Winston, M. (2005). Spatiotemporal patterns and changes in Missouri River fishes. *American Fisheries Society Symposium*, *45*, 249-291.

- Guo, Q., Taper, M., Schoenberger, M., & Brandle, J. (2005). Spatial-temporal population dynamics across species range: from centre to margin. *Oikos*, *108*(1), 47-57. <https://doi.org/10.1111/j.0030-1299.2005.13149.x>
- Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology letters*, *8*(5), 461-467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>
- Harkness, W. J. K., & Dymond, J. R. (1961). *The Lake Sturgeon*. Ontario Department of Lands and Forests, Toronto, Ontario.
- Hayes, D. B., & Caroffino, D. C. (2012). *Michigan's Lake Sturgeon rehabilitation strategy*. Michigan Department of Natural Resources, Fisheries Division Special Report, 62.
- Holt, R. D. (2003). On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research*, *5*(2), 159-178.
- Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., ... & Whoriskey, F. G. (2015). Aquatic animal telemetry: a panoramic window into the underwater world. *Science*, *348*(6240). <https://doi.org/10.1126/science.1255642>
- IPCC (2014). *Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]*. IPCC, Geneva, Switzerland.
- Johnson, J. H., LaPan, S. R., Klindt, R. M., & Schiavone, A. (2006). Lake Sturgeon spawning on artificial habitat in the St Lawrence River. *Journal of Applied Ichthyology*, *22*(6), 465-470. <https://doi.org/10.1111/j.1439-0426.2006.00812.x>

- Kiffney, P. M., Greene, C. M., Hall, J. E., & Davies, J. R. (2006). Tributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(11), 2518-2530. <https://doi.org/10.1139/f06-138>
- Knights, B. C., Vallazza, J. M., Zigler, S. J., & Dewey, M. R. (2002). Habitat and movement of Lake Sturgeon in the upper Mississippi River system, USA. *Transactions of the American Fisheries Society*, 131(3), 507-522. [https://doi.org/10.1577/1548-8659\(2002\)131<0507:HAMOLS>2.0.CO;2](https://doi.org/10.1577/1548-8659(2002)131<0507:HAMOLS>2.0.CO;2)
- Lallaman, J. (2012). *Factors affecting paddlefish reproductive success in the lower Osage River*. [Doctoral dissertation, University of Missouri, Columbia, Missouri]. Retrieved from <https://mospace.umsystem.edu/xmlui/handle/10355/33041>
- Lennox, R. J., Paukert, C. P., Aarestrup, K., Auger-Méthé, M., Baumgartner, L., Birnie-Gauvin, K., ... & Cooke, S. J. (2019). One hundred pressing questions on the future of global fish migration science, conservation, and policy. *Frontiers in Ecology and Evolution*, 7, 1-16. <https://doi.org/10.3389/fevo.2019.00286>
- Lyons, J., & Stewart, J. S. (2014). Predicted effects of future climate warming on thermal habitat suitability for Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in rivers in Wisconsin, USA. *Journal of Applied Ichthyology*, 30(6), 1508-1513. <https://doi.org/10.1111/jai.12543>
- Manny, B. A., & Kennedy, G. W. (2002). Known Lake Sturgeon (*Acipenser fulvescens*) spawning habitat in the channel between lakes Huron and Erie in the Laurentian Great Lakes. *Journal of Applied Ichthyology*, 18(4-6), 486-490.

- McDougall, C. A., Blanchfield, P. J., Peake, S. J., & Anderson, W. G. (2013). Movement patterns and size-class influence entrainment susceptibility of Lake Sturgeon in a small hydroelectric reservoir. *Transactions of the American Fisheries Society*, *142*(6), 1508-1521. <https://doi.org/10.1080/00028487.2013.815659>
- McManamay, R. A., & Frimpong, E. A. (2015). Hydrologic filtering of fish life history strategies across the United States: implications for stream flow alteration. *Ecological Applications*, *25*(1), 243-263. <https://doi.org/10.1890/14-0247.1>
- Merilä, J. (2012). Evolution in response to climate change: in pursuit of the missing evidence. *BioEssays*, *34*(9), 811-818. <https://doi.org/10.1002/bies.201200054>
- Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, *93*(1), 35-45. <https://doi.org/10.1890/11-0370.1>
- Mohammed-Ali, W., Mendoza, C., & Holmes Jr, R. R. (2020). Influence of hydropower outflow characteristics on riverbank stability: case of the Lower Osage River (Missouri, USA). *Hydrological Sciences Journal*, *65*(10), 1784-1793. <https://doi.org/10.1080/02626667.2020.1772974>
- Moore, M. J., Paukert, C. P., Moore, T. M. (2020). Effects of latitude, season and temperature on Lake Sturgeon movement. *North American Journal of Fisheries Management Special Section: Mississippi-Yantze River Basins Symposium*, 1-13. <https://doi.org/10.1002/nafm.10416>
- Moore, T. M. (2021). *A continuing plan for recovery and management of Lake Sturgeon in Missouri*. Missouri Department of Conservation Management Plan Unpublished Draft.

- Paukert, C. P., & Galat, D. L. (2010). Warmwater rivers. In W. A. Hubert, & M. Quist (Eds.), *Inland Fisheries Management in North America* (pp. 699-736). American Fisheries Society, Bethesda, Maryland.
- Pegg, M. A., Pierce, C. L., & Roy, A. (2003). Hydrological alteration along the Missouri River basin: a time series approach. *Aquatic Sciences*, 65(1), 63-72.
<https://doi.org/10.1007/s000270300005>
- Pflieger, W. L. (1997). *The fishes of Missouri, 2nd edition*. Missouri Department of Conservation, Jefferson City, Missouri.
- Pherigo, E. K. (2019). *Seasonal fish community and reproductive biology of fishes in two tributaries of the lower Missouri River, USA*. [Master's thesis, University of Missouri, Columbia, Missouri]. Retrieved from
<https://mospace.umsystem.edu/xmlui/bitstream/handle/10355/70159/PherigoEmilyResearch.pdf?sequence=1&isAllowed=y>
- Pracheil, B. M., McIntyre, P. B., & Lyons, J. D. (2013). Enhancing conservation of large-river biodiversity by accounting for tributaries. *Frontiers in Ecology and the Environment*, 11(3), 124-128. <https://doi.org/10.1890/120179>
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., ... & Stromberg, J. C. (1997). The natural flow regime. *BioScience*, 47(11), 769-784.
<https://doi.org/10.2307/1313099>
- Power, M., & McKinley, R. S. (1997). Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. *Transactions of the American Fisheries Society*, 126(4), 549-558. [https://doi.org/10.1577/1548-8659\(1997\)126<0549:LVLSS>2.3.CO;2](https://doi.org/10.1577/1548-8659(1997)126<0549:LVLSS>2.3.CO;2)

- Puckridge, J. T., Sheldon, F., Walker, K. F., & Boulton, A. J. (1998). Flow variability and the ecology of large rivers. *Marine and freshwater research*, 49(1), 55-72.
<https://doi.org/10.1071/MF94161>
- Quist, M. C., Rahel, F. J., & Hubert, W. A. (2005). Hierarchical faunal filters: An approach to assessing effects of habitat and nonnative species on native fishes. *Ecology of Freshwater Fish*, 14(1), 24-39. <https://doi.org/10.1111/j.1600-0633.2004.00073.x>
- Rice, S. P., Greenwood, M. T., & Joyce, C. B. (2001). Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(4), 824-840.
<https://doi.org/10.1139/f01-022>
- Sagarin, R. D., Gaines, S. D., & Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution*, 21(9), 524-530. <https://doi.org/10.1016/j.tree.2006.06.008>
- Saidak, C. (2015). *Determination of dispersal patterns and characterization of important habitats for Lake Sturgeon restoration in the upper Tennessee River system*. [Master's thesis, University of Tennessee, Knoxville, Tennessee]. Retrieved from https://trace.tennessee.edu/utk_gradthes/3604/
- Schubert, A. L. S. (2001). *East Osage River Watershed inventory and assessment*. Missouri Department of Conservation. Report, Clinton, Missouri.
- Scott, W. B., & Crossman, E. J. (1973). *Freshwater fishes of Canada*. Fisheries Research Board of Canada Bulletin 184.

- Thoms, M., & Sheldon, F. (2019). Large rivers as complex adaptive ecosystems. *River Research and Applications*, 35(5), 451-458. <https://doi.org/10.1002/rra.3448>
- Todd, B. (2007). *A Plan for Recovery of the Lake Sturgeon in Missouri*. Missouri Department of Conservation.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1), 130-137. <https://doi.org/10.1139/f80-017>
- Vélez-Espino, L. A., & Koops, M. A. (2009). Recovery potential assessment for Lake Sturgeon in Canadian designatable units. *North American Journal of Fisheries Management*, 29,1065-1090. <https://doi.org/10.1577/M08-034.1>
- Ward, J. V., & Stanford, J. A. (1995). The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers: Research & Management*, 10(2-4), 159-168. <https://doi.org/10.1002/rrr.3450100211>
- Whitney, J. E., Al-Chokhachy, R., Bunnell, D. B., Caldwell, C. A., Cooke, S. J., Eliason, E. J., ... & Paukert, C. P. (2016). Physiological basis of climate change impacts on North American inland fishes. *Fisheries*, 41(7), 332-345. <https://doi.org/10.1080/03632415.2016.1186656>
- Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(10), 2196-2218. <https://doi.org/10.1139/f92-242>
- Wishingrad, V., Carr, M. K., Pollock, M. S., Ferrari, M. C., & Chivers, D. P. (2014). Lake Sturgeon geographic range, distribution, and migration patterns in the

Saskatchewan River. *Transactions of the American Fisheries Society*, 143(6), 1555-1561. <https://doi.org/10.1080/00028487.2014.954052>

Woolbright, S. A., Whitham, T. G., Gehring, C. A., Allan, G. J., & Bailey, J. K. (2014). Climate relicts and their associated communities as natural ecology and evolution laboratories. *Trends in Ecology & Evolution*, 29(7), 406-416. <https://doi.org/10.1016/j.tree.2014.05.003>

CHAPTER 2- LAKE STURGEON SEASONAL MOVEMENTS IN TWO RIVERS WITH DIFFERING DEGREES OF HYDROLOGIC REGULATION

Abstract

Spatiotemporal shifts in the distribution of aquatic organisms are a key component of many ecological processes. However, dams have fragmented large river systems blocking migrations and altering the hydrologic and thermal regimes that drive movement behavior of freshwater fishes. Many recovering southern Lake Sturgeon populations occur in large river systems with hydroelectric dams and little research has been done to assess the impact of hydrologic alteration on their seasonal movements. We conducted a three-year telemetry study of 96 adult and subadult Lake Sturgeon to compare their migratory responses to temperature and flow variables in adjacent regulated and unregulated tributaries of the lower Missouri River. Year-round tributary use by Lake Sturgeon in this population was among the greatest documented for the species. Differences in flow and thermal regimes in the regulated Osage River may have contributed to the later initiation, more frequent directional changes, and longer duration of spring migrations compared to the unregulated Gasconade River. Lake Sturgeon made spring upstream migrations at similar temperatures of 13 to 19 °C and elevated discharges in both rivers. However, Osage River migrants appeared less responsive to measured changes in discharge or temperature during spring migrations especially those that overwintered at upstream locations. Fall tributary migrations occasionally occurred in the Osage River at rising or high discharges but did not occur frequently in the

Gasconade River. Information on tributary use and response to flow and temperature variables may help manage key habitats and establish flow management plans to promote ongoing recovery of migratory fishes.

Introduction

Movement allows fish to exploit disparate habitats for feeding, reproduction, and avoidance of physiological stress (Schlosser & Angermeier, 1995). Migrations also distribute energy throughout ecosystems supporting numerous ecological, recreational, cultural, and subsistence services (Lennox et al., 2019; Wilcove & Wikelski, 2008). Natural annual cycles of temperature and flow often synchronize species migrations (Bunn & Arthington, 2002; McManamay, Bevelhimer, & Frimpong, 2015). Yet these cycles have been disrupted by the construction of an estimated 58,000 large (> 15 m high) dams globally that generate 24% of the global electricity supply (Mulligan, van Soesbergen, & Sáenz, 2020). Dams increase short-term flow variability when generating electricity and decrease seasonal flow variability by regulating flood pulses (Poff et al., 2010). Impoundments can also affect downstream water quality and temperature during periods of reservoir stratification (Olden & Naiman, 2009). Hydrologic regulation can disrupt movement cues, increase energy expenditures, and inhibit access to critical habitats, thereby favoring the establishment of generalist or nonnative species (Baras & Lucas, 2001). For example, large dams on the Yangtze River have led to the extirpation of 76 native fishes including charismatic megafauna such as the Chinese Paddlefish (*Psephurus gladius*) (Liu, Qin, Xu, Ouyang, & Wu, 2019). Research has long emphasized the harmful impacts of dams on diadromous migrations (McIntyre et al.,

2016). However, dams have also led to the decline of potadromous species whose migrations are confined to freshwater environments and the environmental drivers of their movements remain relatively unstudied (Hayden et. al., 2014). Therefore, an improved understanding of the external drivers of movement has been identified as a primary need to confront a conservation crisis for migratory fishes caused by interacting impacts of hydrologic alteration, fragmentation, and climate change (DeInet et al., 2020; Lennox et al., 2019).

The Lake Sturgeon (*Acipenser fulvescens*) is a potadromous species native to the Mississippi River, Great Lakes and Hudson Bay basins of North America that can live for over 150 years and attain weights in excess of 100 kg (Bruch, Haxton, Koenigs, Welsh, & Kerr, 2016). Lake Sturgeon require specific temperatures, flows, and access to substantial lengths of river to complete their life history (Auer, 1996b; Smith, Smokorowski, & Power, 2017; Struthers et al., 2017). Triggered by temperatures and flows, reproductive adults may migrate up to 150 km to reproduce at rocky rapids in tributaries that oxygenate their adhesive demersal eggs (Auer, 1996a; Auer, 1996b; McKinley, Kraak, & Power, 1998; Shaw, Chipps, & Windels, 2013; Smith et al., 2017) and subsequently retreat downstream to lakes or larger rivers (Peterson, Vecsei, & Jennings, 2007). Water temperatures above 28 °C in southern populations may cause thermal stress, periods of inactivity, and arrested growth (Bezold & Peterson, 2008; Lyons & Stewart, 2014; Moore, Paukert, & Moore, 2020), whereas Lake Sturgeon also often remain sedentary in deep waters in colder months (Hay-Chmielewski, 1987; Rusak & Mosindy, 1997).

In addition to overharvest, dams blocked migrations, degraded spawning habitat, and disrupted migratory cues resulting in the extirpation of Lake Sturgeon from many southern U.S. rivers by the mid-1900s (Auer 1996b; Barnickol & Starrett, 1951; Thiem et al., 2011). A 1999 census identified over 30,000 small and large dams in the Mississippi River basin that comprises the southern portions of the Lake Sturgeon's native range (Graf, 1999). Despite harvest restrictions, these persistent threats to riverine habitats prompted the filing of a petition for listing the Lake Sturgeon under United States Endangered Species Act that is currently under review (Fink, 2018). In 1984, Missouri became the first of at least five southern states to reintroduce Lake Sturgeon and has produced a reproductively mature population in the lower Missouri River Basin. However, little was known about Lake Sturgeon distribution, whether reproductive migrations were occurring, and how Lake Sturgeon responded to hydrologic regulation. Given the growing recognition of population-specific variability in movement behavior in Lake Sturgeon, research into the movement ecology of southern populations is needed to inform conservation planning (MacKenzie, 2016; Moore et al., 2020; Moore, 2021). Furthermore, studies of species movement in comparable unregulated river reaches are rare (e.g., Harvey-Lavoie, Cooke, Guénard, & Boisclair, 2016), but serve as valuable controls to provide evidence supporting flow-ecology relationships to improve flow management to benefit migratory fishes (Murchie et al., 2008; Jacobson & Galat, 2008).

In response, we sought to determine the influences of flow and temperature conditions on tributary use and movements of Lake Sturgeon in adjacent regulated and unregulated tributaries to the lower Missouri River. We predicted that Lake Sturgeon would primarily occupy Missouri River tributaries during the spring spawning season and

that a greater proportion would occupy the larger, regulated Osage River than the smaller unregulated Gasconade River during other seasons. We expected individuals would use large habitat extents (> 100 km of river length) with the greatest movement occurring during spring. Finally, we predicted that upstream migrations during spring and fall would be primarily associated with temperature but that discharge metrics would also play a role. We expected Lake Sturgeon to respond similarly to flow and temperature variables in both rivers, but the timing of suitable migration conditions would differ due to hydrologic regulation in the Osage River. Our results can be used to spatially direct habitat restoration efforts, predict the timing of spawning for monitoring efforts, and develop ecological flows for the conservation of fluvial fishes (Knight, Murphy, Wolfe, Saylor, & Wales, 2014; Viers, 2011).

Methods

Study Site Description

The 8th Strahler order Osage and 6th order Gasconade are large Ozark rivers separated by just 40 km of the mainstem Missouri River (Mississippi River Basin) in central Missouri USA. These rivers contain Lake Sturgeon near the southern edge of the species' native range (Figure 2.1). Mean channel width is ~200 m in the Osage River, and ~90 m in the Gasconade River. Substrate in both systems consists primarily of gravel and cobble which may provide Lake Sturgeon with suitable spawning habitat. Large boulders occur along bluffs and fine sediments dominate depositional areas near each river's confluence with the Missouri River (Chapter 3 this dissertation).

The hydrology of the Osage River has been heavily regulated by the construction of multiple dams for hydroelectric generation, navigation, and flood control. Bagnell Dam is a large hydropeaking dam responsible for rapid fluctuations in discharge and establishes an impassible barrier for fishes at river km (rkm) 130 (hereafter refers to upstream distance from Missouri River confluence). The Osage River also contains a non-operational navigation lock and dam (L&D#1) at rkm 19 that impedes fish passage when combined Osage and Missouri River discharges are $< \sim 2,900 \text{ m}^3/\text{s}$ (Lallaman, 2012). In contrast, the Gasconade River watershed contains no major impoundments and retains a more natural flow regime. Storage capacity of upstream reservoirs reduces the amplitude of downstream flood peaks in the Osage River, occasionally allowing the Gasconade River to surpass its discharge. During the study period, discharges ranged from $29 \text{ m}^3/\text{s}$ to $2,231 \text{ m}^3/\text{s}$ in the Osage River and from $12 \text{ m}^3/\text{s}$ to $5,380 \text{ m}^3/\text{s}$ in the Gasconade River (Figure 2.2A). The maximum recorded 15-minute gage height change in the Osage River was 1.2 m (Bagnell, MO: 0692600, rkm 129) compared to only 0.2 m in the Gasconade River (Rich Fountain, MO: 06934000, rkm 80). Impoundment and river size also influence thermal regimes. Bottom-releases from Lake of the Ozarks contribute to the Osage River being warmer in the winter and colder in the summer than the Gasconade River. Temperatures ranged from 0.3°C to 32.0°C in the Osage River and 0°C to 33.2°C in the Gasconade River. Spring warming and fall cooling often progresses 2 to 4 weeks faster in the Gasconade River compared to the Osage River (Figure 2.2B).

Data Collection

We captured Lake Sturgeon in the lower Osage and Gasconade rivers using trotlines and gillnets during March 2015, March 2016, March to April 2017, October to November 2017, February to March 2018, and March 2019. Trotlines consisted of 60 m lead core rope with 40 dropper lines equipped with 8/0 stainless steel Shaughnessy non-offset hooks baited with nightcrawlers. Gillnets were usually deployed overnight parallel to the current and measured 50–150 ft long (~ 15–50 m) by 2.5 to 3.5 m high with 101 to 152 mm bar mesh. We calculated catch per unit effort as the number of Lake Sturgeon per hook-night or the number of fish per 30 m net night for each sampling trip (Appendix 2.1). We examined Lake Sturgeon for missing scutes, coded wire, Passive Integrated Transponder (PIT), or T-bar tags that may indicate hatchery origin or a previous capture and measured fork length (FL) in mm and total weight in kg (Appendix 2.2).

During transmitter implantation, the fish's gills and skin were irrigated with water. We sterilized all surgical equipment using a 50-50 mixture of 70% to 90% isopropyl alcohol and an aqueous 10% povidone-iodine solution (Betadine). We implanted Vemco V16-4H (Halifax, Nova Scotia, Canada) acoustic transmitters in all Lake Sturgeon larger than 2.4 kg so as to not exceed 2% of the fish's body weight (Bridger & Booth, 2003). We made a ~ 3–4 cm incision on the ventral surface anterior to pelvic girdle and ~ 2 cm off the ventral midline, inserted the transmitter, then sealed incisions with three to four interrupted stitches. Fish recovered in an aerated tank before being released. Tags began transmitting immediately with an expected battery life of 4.2 years. Sex or maturity could not be determined confidently by examining gonads through the incision in 40% of individuals and therefore is not considered in analyses (Appendix 2.2).

We monitored movements of tagged Lake Sturgeon from May 2017 to July 2020 with Vemco VR2W and VR2Tx stationary receivers mounted on bridge pilings or concrete anchors, (hereafter; passive tracking) and monthly boat tracking (hereafter; manual tracking). The core study area included the lower 130 km of the Osage River and lower 150 km of the Gasconade River (Figure 2.1). We established 7 Osage and 8 Gasconade stationary receiver stations in early 2017–2018 which remained in place for the duration of the study. Receivers were also deployed in other large Missouri River tributaries including the Lamine (1), Moreau (1), Grand (2), and Chariton (1) rivers (Figure 2.1). We deployed additional receivers primarily beginning in October 2018 to provide better coverage of the core study area. The change in movement monitoring resolution applies primarily to the 2018 spring migration data in the Osage River. In total, 33 receiver stations were used to track fish in Missouri River tributaries (Figure 2.1, Appendix 2.3). Detections were also obtained from 6 Missouri and ~25 Mississippi River basin receiver stations maintained by the Missouri Department of Conservation, Iowa State University, and from active tracking in the Missouri River by U.S. Fish and Wildlife Service and U.S. Geological Survey. Movement data outside of the Osage and Gasconade rivers were only incorporated in monthly movement rates and were excluded from tributary upstream migration analyses. We conducted a range test at rkm 4 of the Osage River in 2017 and detection efficiency was 70% to 80% at 300 m and > 45% at 500 m. At stations with channel widths > 250 m, one receiver was deployed on each side of the channel. Missed station passages by tagged sturgeon were rare, corroborating that receiver detection range covered channel widths under most conditions.

We attempted to locate each tagged sturgeon known to occupy the Osage and Gasconade rivers once monthly by manual tracking from May 2017 to May 2020. Reaches were typically tracked in the same order to keep the between tracking event intervals of reaches relatively consistent. We detected fish using a Vemco VR-100 omnidirectional hydrophone while traveling between 6 and 10 km/h and pinpointed the fish's location until transmission level reached 95–105 decibels using a rotating bow-mounted directional hydrophone and the “ground-zero method” (Boase, Diana, Thomas, & Chiotti, 2011; Holland, Lowe, Peterson, & Gill, 1992; Jadot, Ovidio, Voss, 2002). We estimated our tracking accuracy to be < 30 m by relocating hidden V16 transmitters prior to start of the study. Manual tracking typically took 10 to 14 days per month. Fish were considered to have perished following > 3 months of consecutive manual relocations within 30 m.

Statistical Analysis

In order to compare movement patterns in the two rivers, we conducted a preliminary step to describe the timing and extent of seasonal tributary migrations. In step 2, we use generalized additive mixed models (GAMMs) to quantitatively compare relationships between a suite of flow and temperature metrics and upstream movement during migratory periods (as defined in step 1) in both tributaries.

Step 1: Describing seasonal movement patterns that define migratory behaviors

We assessed monthly tributary residency (T. Res %) as the average percent of tagged individuals occupying Missouri River tributaries over, n , weekly study periods within the 12 months of the year, m , calculated as:

$$\text{T. Res (\%)}_m = \left(\frac{100 * \text{sturgeon in trib.}_{1,w}}{\text{active tags}_{1,w}} \right) + \left(\frac{100 * \text{sturgeon in trib.}_{2,w}}{\text{active tags}_{2,w}} \right) + \dots + \left(\frac{100 * \text{sturgeon in trib.}_{n,w}}{\text{active tags}_{n,w}} \right) / n \quad (1)$$

Individuals were considered tributary residents in a given week if they were detected at least once there or were believed to be occupying tributary reaches between receiver stations based on previous detections.

Next, we developed monthly kernel density utilization estimates (KDEs) for Lake Sturgeon in the Osage and Gasconade rivers to identify the location of overwinter or oversummer refugia from which migrations originated. The KDEs were calculated using the *adehabitatHR* package (Calenge, 2006) in R (R Development Core Team, version 3.2.3). We selected a bandwidth of 650 and a grid resolution of 3000 to produce multimodal utilization distributions rather than using common home range analysis estimators such as least squares cross validation (Glitzen & Millsbaugh, 2003).

We also determined the percentage of Lake Sturgeon occupying reaches containing these refugia identified by the KDE (R.Res(%)). The percentage of tagged individuals residing in a selected reach, a , during each week, w , was calculated as:

$$\text{R. Res (\%)}_w = 100 * \left(\frac{\text{sturgeon in reach}_{aw}}{\text{active tags}_w} \right) \quad (2)$$

Finally, we analyzed monthly movement rates to determine when fish were migrating. We combined receiver and manual detections obtained from May 2017 to May

2020 of 96 sturgeon to include a single daily detection per transmitter, per receiver station. Minimum distance traveled (MDT) of movement events between successive locations of an individual were calculated using the *gdistance* package (van Etten, 2017). Fish detected at receivers were assigned the coordinates of that receiver station. Movement paths followed the shortest distance of the river channel. We chose to retain movement events up to 45 days in length since monthly intervals between monthly manual tracking of occupied reaches sometimes slightly exceeded 30 days. Movement event duration was calculated as the whole day difference between dates of successive locations. Next, we aggregated all movement events within individuals by the month that they ended. Mean movement rates in m/day (MDPD) for each individual, i , within each month, j , was calculated by dividing the sum of the MDT by the sum of durations for all events:

$$MDPD_{ij} = \frac{\sum_{ij} Distance}{\sum_{ij} Days} \quad (3)$$

We used generalized linear mixed models (GLMMs) in the *glmmTMB* package in R (Brooks et al., 2017) to compare differences in movement rates among months. We used a negative binomial distribution to account for overdispersion (Lindén & Mäntyniemi, 2011) and discarded all 0 distance events. Predictor variables included a random intercept (α) for TagID, i , 11 dummy variables for month, k , with January, which had the lowest movement rates, set as the reference factor level. P -values for monthly β estimates indicate whether mean movement rates in a given month were significantly different than the reference level. We also included a fixed effect for the number of days

(1–45 days) used in an individual’s monthly movement rate calculation, to control against underestimating movement rates from longer duration events (Horton & Guy, 2004).

$$\log(\text{MDPD}_{ik}) = \alpha_i + \beta_1 * \text{Days}_{ik} + \beta_k * 1 \quad (4)$$

Results from step 1 that are presented in more detail in the results, suggested that upstream tributary migrations from seasonal refugia occurred from January 1st to July 23rd in both rivers and from September 1st to December 1st in the Osage River only. Therefore, we used these date ranges to define a “spring” and a “fall” migration period during which we modeled upstream movement separately. As periodic spawners, we did not expect individual Lake Sturgeon to migrate in all years (Peterson et al., 2007) and therefore we only model migration by individuals during years in which they met migration criteria. Migration criteria were specific to three migration groups. For Gasconade River migrations, group 1 (hereafter, G1) began their migrations in the lower Gasconade River or mainstem Missouri River. Group 2 (hereafter, O2) began migrations in the 19 km downstream of L&D#1 on the Osage River or the mainstem Missouri River, and group 3 (hereafter O3) began migrations in the Osage River upstream of L&D#1. An individual who migrated in both rivers in a season would start as a G1 migrant then would transition to the O2 migrant group during a subsequent Osage River migration. Gasconade River spring or fall migrations were defined as upstream movements upriver of rkm 20. Osage River spring or fall migrations for O2 individuals were defined as upstream movement upriver of rkm 16, or for O3 individuals, upstream movement upriver of rkm 37.

Step 2: Comparison of timing and environmental conditions associated with spring and fall migrations upstream of refugia in the Osage and Gasconade rivers

A fish's migration duration was defined as the number of days from the first date it met migration criteria to the date of its farthest upstream detection in that season. We also compared the average number of detected directional reversals (upstream to downstream movement) during the seasonal migrations in each river.

Next, we used gaussian GAMMs to investigate non-linear relationships between an individual's longitudinal location (i.e., rkm of an individual Lake Sturgeon) and environmental predictors (Zuur, Saveliev, & Ieno, 2009). We retained the final (latest time) daily manual or passive detection of each individual from January 2018 to July 2020 and assigned longitudinal river km positions during spring or fall migratory periods (defined above) in both tributaries in ArcMap 10.6 (ESRI, Redlands, CA.). An individual's most recent known position was carried forward until its next detection (Shao & Zhong, 2003; Vine, Holbrook, Post, & Peoples, 2019). Periods of > 1 month between detections of an individual at the downstream most tributary receiver indicated that the individual had likely vacated the river and were removed from the dataset.

Next, we identified a set of flow and water temperature predictors we hypothesized would explain sturgeon migratory behavior (Forsythe et al., 2012; Vine et al., 2019). We obtained average daily discharge and average daily temperature data from the United States Geological Survey (USGS) gage stations in both the Osage (St. Thomas MO: 06926510, rkm 54) and the Gasconade rivers (Rich Fountain, MO: 06934000, rkm 80). In previous studies Lake Sturgeon reproduction and physiology was driven by temperature and we hypothesized the effects of migratory flow cues would depend on

temperatures being appropriate for migration. Therefore, we included main effects and interactions of 3-day daily average water temperature (temperature) with all other variables. We also chose a previous 3-day temporal resolution for: average discharge (discharge), change in daily average discharge (Δ discharge), or change in temperature (Δ temperature). We standardized discharge using the within river mean and standard deviation to account for river size. We applied an additional 1-day lag to all environmental metrics to account for the position of gage stations ~25–60 km upstream of primary overwintering or oversummering refugia in each river. Models assumed a normal distribution for response and error terms, therefore we implemented a square-root transformation of the response variable to stabilize variance and improve normality. Despite a risk of taking on negative values, Zuur (et al., 2012) suggests that normal distributions are appropriate for modeling exclusively positive response variables when the observed values are not close to 0 as was the case with rkm observations during upstream migration. We used a first order autoregressive (AR1) covariance structure to account for correlation between consecutive daily positions (Kleinbaum, Kupper, Nizam, & Rosenberg, 2008). We used smoother-factor interactions to compare responses to environmental variables in different rivers (G1 vs. O2 and O3) as well as different migration groups within the Osage River (O2 vs. O3). Collinearity among predictors was not strong enough to warrant their removal ($r < 0.7$). Interactions were fit using tensor product smoothers (Zuur et al., 2012). We included random intercepts for an individual's river-year migrations. The basis dimension, K, dictates the “wiggleness” of a smoother line with higher K indicating more complex non-linear relationships. We implement the double penalty approach (Marra & Wood, 2011), which applies smoothing penalties to a

in both the range and null spaces to effectively remove the influence of insignificant smoother components from the model in a single step. We fit the following global model for the spring and fall seasons using restricted maximum likelihood in the `mgcv` package in R (Wood, 2004) that predicts the rkm location of an individual, j , on day, t .

We examined p-values to determine if within group predictor smoothers were significantly different than a flat horizontal line (i.e., $K = 0$) that would indicate no relationship. We developed contour plots to illustrate interactive effects between water temperature and other environmental predictors on longitudinal position in using the `visreg` (Breheny & Burchett, 2017) and `ggplot2` packages (Wickham, 2016).

Results

We monitored movements of 96 telemetry tagged Lake Sturgeon (mean 1,118 mm FL, range 737–1,510 mm FL) captured in the Osage River (62) and Gasconade River (34). Mean fork length was not significantly different between fish tagged in each river ($t(93) = -1.66, p = 0.10$). Four tags were stationary over extended periods of time in the Osage River and two in the Gasconade River, indicating mortality or tag expulsion. The status of an additional sturgeon that was not detected for over two years is unknown.

Describing seasonal movement patterns that define migratory behaviors

Lake Sturgeon spent a majority of time in the Osage and Gasconade rivers occupying these two rivers during 78% of the study period. Individuals were rarely detected in other monitored tributaries including the Grand ($n = 4$), Lamine ($n = 3$), Chariton ($n = 1$), and Moreau ($n = 10$) rivers (Figure 2.1). Lake Sturgeon occupied at

least one tributary during 80% of the 3-year study period and weekly tributary use was high during spring months of March to May with 55% to 64% of tagged individuals occupying the Osage River and 19% to 21% occupying the Gasconade River. Lake Sturgeon Osage River residency peaked during July and August, (68%–74%). However, Lake Sturgeon generally avoided the Gasconade River in July and August (9%–11%) when average daily water temperatures exceeded 28 °C (Figure 2.2B). More Lake Sturgeon emigrated into the Missouri River during the winter but proportional use remained high in the Osage River (51%) relative to the Gasconade River (16%–19%) for the months of December to February.

KDE plots were constructed using 1,883 manual relocations of 78 individuals in the Osage River and 460 manual relocations from 43 individuals in the Gasconade River. Kernel density plots highlight distinct summer (July–September) and winter (December–February) non-migratory refugia in both tributaries (Figure 2.3, Figure 2.4). During these periods ~ 94% of individuals in the Osage River occupied two river reaches that contained a ~ 16 m deep gravel dredging pool at rkm 35, which is > 4 meters deeper than all other pools, and the lower 19 rkm of the Osage River (Figure 2.3). Similarly, 95% of individuals within the Gasconade River were confined to the lower 17 rkm during the same period (Figure 2.4). These analyses also showed that most Lake Sturgeon reached the upstream apex of their spring migrations in both tributaries from April to early June. The maximum annual upstream apex during spring was rkm 129 (near Bagnell Dam) in the Osage River and was > rkm 241 in the Gasconade River. Median migration apexes were similar in both rivers, rkm 55.0 in the Osage River and rkm 65.5 in the Gasconade River. In the Osage River 46% of migration apexes were between rkm 50 and rkm 80,

and similarly, manual detections of Lake Sturgeon in the Osage River during May were primarily concentrated from rkm 48 to 65. In the Gasconade River, spring migration distances were variable with no large aggregations identified. For example, in 2020, 5 sturgeon passed a receiver at rkm 200 when only 1 sturgeon passed rkm 148 in 2018 and 2019 combined.

We calculated average monthly movement rates from 2,653 individual-month movement events of 96 tagged Lake Sturgeon. The greatest movement rates occurred during spring and fall migratory periods at intermediate temperatures of 10 to 20 °C in May (median = 910 m/day, $z = 14.54$, $p < 0.0001$) and October (median = 747 m/day, $z = 3.44$, $p < 0.0001$). Movement rates were lowest when water temperatures reached their annual maxima of 27 to 30 °C in the Osage River or 29 to 32 °C in the Gasconade River in August (median = 235 m/day, $z = 3.97$, $p < 0.0001$) or their annual minima of < 9 °C in January (median = 248 m/day) or February (median = 197 m/day, $z = 0.38$, $p = 0.71$) (Figure 2.5). Eighty-seven percent of G1 spring migrations originated downstream of Gasconade rkm 17 (a few fish overwintered in backwater habitats further upstream in the Gasconade River), 100% of O2 migrations originated downstream of Osage rkm 19 (by definition), and 88% of O3 migrations originated in a deep pool where gravel dredging occurred at rkm 35 (Figure 2.3, Figure 2.4).

Comparison of timing and environmental conditions associated with upstream migrations

Sixty percent of Lake Sturgeon completed spring migrations in multiple years (35% all 3 years, 25% two years) whereas 18% migrated in one and 23% did not migrate. There was not a significant difference in mean fork length of those fish that did not

complete spring upstream migrations versus those that did at least once ($t(93) = -0.01, p = 0.92$). On average, Lake Sturgeon spring migrations in the Osage River began 15 days later on April 10th and ended 28 days later on May 26th, compared to Gasconade River migrations. During the longer duration Osage migrations, we also detected more directional reversals (maximum = 5), than during Gasconade spring migrations (maximum = 2). Multi-tributary migrations during spring of the same year were common with 25% to 53% of Gasconade migrants completing a subsequent upstream migration in the Osage River. However, no individuals migrated in the Gasconade River following an Osage River spring migration within the same year. A total of four Gasconade River fall migrations occurred over the three years of study providing insufficient data to model fall migrations there. Fall migrations were more common in the Osage River but exhibited substantial interannual variation with 0 in 2017, 30 in 2018, and 17 in 2019.

Our spring tributary migration dataset included 4,287 G1, 14,178 O2 and 6,652 O3, daily longitudinal locations of tagged Lake Sturgeon (Figure 2.6A). The global spring GAMM indicated a strong association between longitudinal position and water temperature in all three migratory groups across both rivers with sturgeon predicted to reach peak rkm from 13–19 °C, with rapid retreats downstream when temperatures approached 20–22 °C (Figure 2.7; Table 2.1). Above average discharge was significantly positively associated with upstream movement at peak migration temperature in all migration groups (Figure 2.7A; Table 2.1). Δ discharge was only linked to upstream movement in G1 migrations, with rkm weakly positively associated with near steady or declining discharge (Figure 2.7B, Table 2.1). Δ temperature was significantly associated with only G1 and O2 migrations (Figure 2.7C, Table 2.1). In both the G1 and O2,

upstream migrations were weakly positively associated with 3-day temperature increases of 0–6 °C (Figure 2.7C).

The fall dataset included 3,104, O2, and 736 O3 daily longitudinal locations of tagged Lake Sturgeon (Figure 2.6B). Over 83% of the fall migrations (39/47) were characterized as O2 (i.e., beginning downstream of L&D#1 in the Osage River or in the mainstem Missouri River). Osage River fall migrations were an excellent predictor of migration in the following spring with 95% (37/39) of O2 fall migrants also either migrating in the Osage the following spring or overwintering upstream of areas where spring sturgeon aggregations occurred (i.e., rkm 48–65). Additionally, in 33% (13/39) of fall migrations individuals passed and overwintered upstream of L&D#1, potentially closer to spring destinations. In the global fall GAMM smoothers for all variables, average and Δ temperature and flow, were significant for O2 migrations. In contrast, no smoothers were significant for O3 (Figure 2.8; Table 2.2). O2 smoothers suggested Lake Sturgeon were more likely located further upstream when temperatures were < 18 °C (Figure 2.8), at above average discharges (Figure 2.8A) and during increasing discharges (Figure 2.8B).

Discussion

Lake Sturgeon exhibit population-level differences in migratory behavior (e.g., Moore et al., 2020), but to our knowledge this is the first study to directly compare Lake Sturgeon movement in two rivers with varying degrees of hydrologic regulation within a single population. Lake Sturgeon exhibited distinct seasonal patterns of residency and upstream migration in two Missouri River tributaries. Annual tributary residency in the

Missouri River Basin was high, averaging over 75% across all seasons. Lake Sturgeon were generally sedentary during the winter and summer in seasonal tributary refugia. Activity increased during intermediate temperatures that coincided with spring or fall upstream migrations. More fish migrated and for longer durations in the spring and fall in the Osage River than in the Gasconade River. Lake Sturgeon responded similarly to temperature across all spring migration groups. However, migration timing, as well as the influence of discharge and temperature change variables, differed among rivers and seasons and may be related to hydrologic alterations in the Osage River.

Lake Sturgeon used the Osage and Gasconade rivers in all seasons, in contrast to our hypothesis that Lake Sturgeon would use tributaries primarily in the spring (which is their spawning season). However, as expected, tributary use outside the spring was greater in the larger regulated Osage River. Year-round tributary use by Lake Sturgeon is uncommon in other populations. Of 36 Lake Sturgeon telemetry studies reviewed by Moore et al., (2020), only seven documented likely unconfined year-round tributary residency including populations in the: Rainy River, ON (based on 1 fish; Rusak & Mosindy, 1997), St. Clair-Detroit River complex, MI (river resident subgroups; Kessel et al., 2018); Wisconsin River, WI (< 20% spring tributary use; Knights et al., 2002), Namakan River (lacustrine habitat available within Namakan River system, ON; Welsh & McLeod, 2010), lower Niagara River, NY/ON (unconfirmed; Hughes, 2002), St. Mary's River, MI (unconfirmed with winter tracking; Gerig, Moerke, Greil, & Koproski, 2011), and Kettle River, MN (tributary exclusive population; Borkholder et al., 2002). Furthermore, use of tributaries by Lake Sturgeon in the nearby Mississippi River is rarer (Buszkiewicz, Phelps, Tripp, Herzog, & Scheibe, 2016). Low-velocity habitats have been

reduced by channelization in the mainstem Missouri River (Jacobson, Johnson, & Dietsch, 2009), possibly increasing the importance of tributaries in this watershed. Lower summer tributary residency in the Gasconade River may be due to limited availability of pools > 10 m deep and warmer temperatures. Deep, low-velocity pools may reduce the stranding risk, metabolic costs and exposure to sunlight or predators, during physiologically demanding conditions (Carr, Lacho, Pollock, Watkinson, & Lindenschmidt, 2015; Thayer, Ruppert, Watkinson, Clayton, & Poesch, 2017). Our study suggests that southern Lake Sturgeon populations may rely on stable low-velocity refugia available in tributaries such as deep bluff pools, tributary confluences, and dredged pools in the summer and winter.

As we had expected, Lake Sturgeon exhibited large scale movements exceeding 100 km in the Missouri River basin. For example, one individual traveled 188 km in 37 hours from the Grand River to the Osage River and one individual was detected > 1000 km from their tagging location in the Osage River to Gavin's Point Dam on the Missouri River in Yankton, SD. However, most Lake Sturgeon exhibited fidelity to areas of the Missouri River Basin near the Osage and Gasconade rivers. The factors explaining variability in minimum home range size for Lake Sturgeon remain poorly understood. Originally, Lake Sturgeon were believed to require 250–300 km of open habitat to complete their life cycle (Auer 1996a), however sustainable populations have been discovered in reservoirs < 10 km long (McDougall et al., 2017), and the Osage River has 130 km of fluvial habitat below Bagnell Dam. Location of preferred spawning habitat and occurrence of barriers likely determines migration distances in sturgeon with 70% of Lake Sturgeon spawning sites in other populations occurring within 10 km of upstream

barriers (Baril, Buszkiewicz, Biron, Phelps, & Grant, 2018). However, impassable barriers do not appear to be commonly associated with Lake Sturgeon spring migration apexes in the Osage River. Only 12 spring migrations and 3 fall migrations reached Bagnell Dam (rkm 130). Lake Sturgeon were prevented from passing L&D#1 at rkm 19 in the Osage River during low flows in March and April of 2019 but resumed migrations at higher flows in May. In contrast, most of the Paddlefish (*Polyodon spathula*) that passed L&D#1 in the Osage River approached within 2 rkm of Bagnell Dam, during spawning conditions (Lallaman, 2012). Maximum tributary upstream migration distances in the barrier-free Gasconade River were greater (up to 241 km). However, only 11 of 41 Gasconade Spring migrations surpassed rkm 125 (approximately the upstream distance of Bagnell in the Osage River), further suggesting that Lake Sturgeon may not be space-limited by barriers in either tributary.

Our expectation that Lake Sturgeon movement rates would be greatest in the spring, and lowest in summer and winter was affirmed and is similar to other riverine populations (e.g., Knights, Vallazza, Zigler, & Dewey, 2002). Sedentary behavior we observed at temperatures < 10 °C is likely due to slow metabolic rates at low water temperatures (Deslauriers et al., 2018) and limited movements at these temperatures has been observed in other studies (Carr et al., 2015; Thayer et al., 2017). Lake Sturgeon in both of our study rivers generally ceased upstream migrations at temperatures > 20° C and retreated to downstream summer refugia, a pattern that was also observed at cooler temperatures of 14 °C in the Manistee, MI (Lallaman et al., 2008). Water temperatures 24-28 °C may cause thermal stress (Bezold & Peterson, 2008; Bugg et al., 2020; Lyons and Stewart, 2014), and our results showed that Lake Sturgeon were primarily sedentary

in the three summer refugia when water temperatures were $> 28^{\circ}\text{C}$, which occurred in both rivers. Water temperature had a greater impact than flow on spring upstream movement in both rivers. This result is consistent with McDougall, Blanchfield, & Anderson, (2014) for a hydrologically regulated Canadian reservoir, but our results found this was consistent between two rivers within the same population of Lake Sturgeon. Lake Sturgeon reached migration apexes at similar temperatures of 13-19 $^{\circ}\text{C}$ in all groups in the Gasconade and Osage rivers. This is consistent with average spawning water temperatures of 16.4 $^{\circ}\text{C}$ in the Mississippi River Basin (Baril et al., 2018), and may suggest that Lake Sturgeon in the Osage and Gasconade rivers are migrating to spawn. These temperatures were reached two weeks later in the Osage River compared to the Gasconade River likely due in part to hydrologic alterations by Bagnell Dam. The temporal mismatch of optimal migration temperatures may be a factor allowing some individuals to migrate in both rivers during a single spring. Previous studies have documented multiple spawning runs within a single tributary (Bruch et al., 2016), residency in multiple rivers in the same year (Ecclestone, Haxton, Pratt, Wilson, & Whillans, 2020), or reproduction in multiple tributaries over unknown time scales (Homola et al., 2012). However, we know of no other published study documenting potential spring reproductive migrations in multiple tributaries in the same spring season. Spawning in multiple places with multiple partners may be a strategy to hedge against unfavorable conditions and increase genetic diversity of offspring (Welsh et al., 2015), and therefore may benefit Lake Sturgeon populations in the Missouri River basin.

Our models identified inconsistent effects of flow, flow change, and temperature change metrics during spring migrations in the Osage and Gasconade rivers. Both G1 and

O2 groups showed a positive association between rkm and warming temperatures or above average flows. Rising water may not only trigger migrations but may be needed in the Osage River to pass the semi permeable barrier of L&D#1. Rising water temperature was also correlated with arrival to spawning sites in the Wolf River, WI (Bruch & Binkowski, 2002) and years of elevated flows have also resulted in increased upstream migration by Lake Sturgeon (Wishingrad et al., 2014). In contrast to O2 or O3 (Osage) migrations, G1 (Gasconade) migrations occurred during stable or receding flows. This suggests that in natural flow regimes, Lake Sturgeon may delay migration until after flood peaks with analogous behaviors documented in the Black River, MI (Forsythe et al., 2012). Rapid ramp down rates at Bagnell Dam make receding hydrographs rare in the Osage River (Figure 2.2A). This could contribute to the longer duration and the greater number of directional changes in Osage River spring migrations. Sturgeon can retain viable eggs if spawning conditions are unfavorable (Dammerman, Webb, & Scribner, 2019; Webb et al., 1999). For example, in the Sturgeon River, MI hydropeaking can prolong spawning site residency 4-6 weeks relative to years with near run-of-river conditions (Auer 1996b). In contrast, when unaffected by hydropeaking, Pallid Sturgeon (*Scaphirhynchus albus*) chose least-cost paths to a single migration apex (no reversals) during spawning in the Missouri River illustrating the benefits of minimizing energetic budgets for migration and maximizing energetic budgets for reproduction (DeLonay et al., 2014; McElroy, DeLonay, & Jacobson, 2012). Although Lake Sturgeon in our study may migrate each year, individuals may wait to spawn until specific flow and water temperature conditions are met.

Our results also suggest other motivations for spring migration besides reproduction. For example, one female had fully developed ova in March 2017 but also migrated upstream in the Osage River in springs of 2018, 2019 and 2020, even though female Lake Sturgeon typically spawn every 4–9 years (Shaw et al., 2013). Roughly 25% of tagged individuals were < 1,000 mm FL at the time of transmitter implantation; therefore, several spring migrants in our study were likely subadults incapable of reproducing (Buszkiewicz et al., 2016). Subadults in the Wolf River, WI that also made spring migrations may visit spawning grounds possibly to feed on eggs (Snobl, Isermann, Koenigs, & Raabe, 2017). Subadults may also follow social cues from adults to learn migratory routes as they approach maturity (Allen, Barth, Peake, Abrahams, & Anderson, 2009; Helfman & Schultz, 1984).

Fall migrations and fall spawning is not known to occur in Lake Sturgeon, but our study showed fall migrations occurred in two of three years in the Osage River, and were much rarer in the Gasconade River, implying differing responses to hydrologic and thermal variables in each river. Osage River fall migrations were associated with temperatures < 18 °C and above average or rising discharges. These conditions may provide a brief window to relocate when movement is physiologically manageable and passage of L&D#1 is possible (Lallaman, 2012). However, our models did not predict a rkm peak at intermediate temperature, and Lake Sturgeon did not synchronously begin retreating downstream at a temperature threshold as they did in spring. Fish relocated from downstream of rkm 19 in the Osage to overwinter primarily between rkm 34 to 37 in 33% of fall Osage migrations (i.e., fall switch from O2 to O3 refugia), and thus began the spring closer to potential spring destinations. Similar “two-step” spawning migrations

have been observed in multiple migratory fishes including Lake Sturgeon (Bemis & Kynard, 1997), Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) (Ingram & Peterson, 2016), and Blue Suckers (*Cycleptus elongatus*) (Tornabene et al., 2020) possibly allowing them to conserve energy for reproduction. Fall migrants that passed L&D#1 but then retreated downstream to overwinter may have been foraging in areas of higher prey densities (Werner & Hayes, 2004) or could be sampling upstream habitats for future use. The strong correlation between fall and subsequent spring migrations that we observed may result from spawning site “scouting” behavior that has also been documented in Coastal Brook Trout (*Salvelinus fontinalis*) (D’Amelio, Mucha, Mackereth, & Wilson, 2008). Spatial memory may enable fish to learn migratory routes and synchronize habitat transitions to environmental conditions (Odling-Smee & Braithwaite, 2003). Weaker relationships with migration and environmental predictors in both fall and spring O3 migrations require further investigation but may be due to smaller sample size or they may be less reliant on environmental conditions to reach upstream destinations with a shorter migration distance and fewer obstacles to cross (e.g., L&D#1).

Although our study identifies spring movements that could be associated with spawning, we did not specifically observe Lake Sturgeon spawning. Lake Sturgeon often spawn at depths up to 12 m in large rivers (Baril et al., 2018) and turbidity in our rivers would have prevented us observing spawning at depths > 1 m. Furthermore, the large study area limited the spatial and temporal resolution of our tracking. Future studies focusing tracking effort on reaches identified as spring movement apexes may be needed to identify spawning site locations and the factors affecting fine scale movements site residency (e.g., Dammerman et al., 2019). The additional receiver stations added after

spring 2018 improved our spatial resolution of passive data. Despite the change we believe the pre-2018 data was important to retain in analyses to describe the variability in migratory patterns across years under different environmental conditions and spring 2018 was a unique low water year compared to 2019 and 2020. We compared versions of GAMMs that excluded 2018 data to our models that included all three years and relationships between upstream movement and environmental predictors were largely consistent.

Our study accentuates the often-overlooked importance of tributary habitats for large-river fishes (Dunn, Brooke, Hrabik, & Paukert, 2018), and how hydrologic regulation may affect their distribution and migration patterns. We highlight river reaches where Lake Sturgeon peaked their spring migrations, and at what flows and temperatures. Biologists could use this information in efforts to validate reproduction with egg mats, larval driftnets, or sonar imaging. Lallaman (2012) concluded that the Osage River may be a population-sink for American Paddlefish due to hydrologic manipulations and it is unclear if this is true for Lake Sturgeon. Consistent reproductive failure may necessitate continued stocking to maintain populations. In addition, consideration of brood stock source may help recovery efforts by identifying sources that have tolerated the selective pressure of the rivers in the southern portion of the Lake Sturgeon range (Berkman, Anderson, Herzog, Moore, & Eggert, 2020). Strategies to protect vulnerable aggregations of Lake Sturgeon in seasonal refugia or at spawning sites may also be considered. Modifications to dam operations such as reducing down-ramping rates to replicate natural gradual discharge declines may reduce direction changes, duration, and energy expenditures during Osage River spring migrations. We recommend that future studies

investigate the physical characteristics associated with the seasonally used habitat patches we identified to help prioritize additional opportunities for population growth in the Lower Missouri River Basin and across the southern portions of its range.

References

- Allen, P. J., Barth, C. C., Peake, S. J., Abrahams, M. V., & Anderson, W. G. (2009). Cohesive social behaviour shortens the stress response: the effects of conspecifics on the stress response in Lake Sturgeon *Acipenser fulvescens*. *Journal of Fish Biology*, 74(1), 90-104. doi:10.1111/j.1095-8649.2008.02112.x
- Auer, N. A. (1996a). Importance of habitat and migration to sturgeons with emphasis on Lake Sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 152-60. doi:10.1139/f95-276
- Auer, N. A. (1996b). Response of spawning Lake Sturgeons to change in hydroelectric facility operation. *Transactions of the American Fisheries Society*, 125, 66-77. doi:10.1577/1548-8659(1996)125<0066:ROSLST>2.3.CO;2
- Baras, E., & Lucas, M. C. (2001). Impacts of man's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. *Ecohydrology and Hydrobiology*, 3, 291-304.
- Baril, A. M., Buszkiewicz, J. T., Biron, P. M., Phelps, Q. E., & Grant, J. W. (2018). Lake Sturgeon (*Acipenser fulvescens*) spawning habitat: a quantitative review. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(6), 925-933. doi:10.1139/cjfas-2017-0100

- Barnickol, P. G., & Starrett, W. C. (1951). Commercial and sport fishes of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. *Illinois Natural History Survey Bulletin*, 25(5), 267–350.
- Bemis, W. E., & Kynard, B. (1997). Sturgeon rivers: an introduction to acipenseriform biogeography and life history. *Environmental Biology of Fishes*, 48(1-4), 167-183. doi:10.1023/A:1007312524792
- Berkman, L. K., Anderson, M. R., Herzog, D. P., Moore, T. L., & Eggert, L. S. (2020). A genetic assessment of Missouri's Lake Sturgeon after 30 years of restoration releases. *North American Journal of Fisheries Management*, 40, 700-712. doi:10.1002/nafm.10430
- Bezold, J., & Peterson D. L. (2008). Assessment of Lake Sturgeon reintroduction in the Coosa River System, Georgia-Alabama. *American Fisheries Society Symposium*, 62, 1-16.
- Boase, J. C., Diana, J. S., Thomas, M. V., & Chiotti, J. A. (2011). Movements and distribution of adult Lake Sturgeon from their spawning site in the St. Clair River, Michigan. *Journal of Applied Ichthyology*, 27, 58-65. doi:10.1111/j.1439-0426.2011.01827.x
- Borkholder, B. D., Morse, S. D., Weaver, H. T., Hugill, R. A., Linder, A. T., Schwarzkopf, L. M., ... & Frank, J. A. (2002). Evidence of a year-round resident population of Lake Sturgeon in the Kettle River, Minnesota, based on radiotelemetry and tagging. *North American Journal of Fisheries Management*, 22(3), 888-894. doi:10.1577/1548-675(2002)022<0888:EOAYRR>2.0.CO;2

- Braaten, P. J., Fuller, D. B., Holte, L. D., Lott, R. D., Viste, W., Brandt, T. F., & Legare, R. G. (2008). Drift dynamics of larval Pallid Sturgeon and Shovelnose Sturgeon in a natural side channel of the upper Missouri River, Montana. *North American Journal of Fisheries Management*, 28(3), 808-826.
- Bridger, C. J., & Booth, R. K. (2003). The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. *Reviews in Fisheries Science*, 11(1), 13-34. doi:10.1080/16226510390856510
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378-400. doi:10.3929/ethz-b-000240890
- Bruch, R. M., & Binkowski, F. P. (2002). Spawning behavior of Lake Sturgeon (*Acipenser fulvescens*). *Journal of Applied Ichthyology*, 18, 570-579.
- Bruch, R. M., Haxton, T. J., Koenigs, R., Welsh, A., & Kerr, S. J. (2016). Status of Lake Sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. *Journal of Applied Ichthyology*, 32, 162–190.
- Bugg, W. S., Yoon, G. R., Schoen, A. N., Laluk, A., Brandt, C., Anderson, W. G., & Jeffries, K. M. (2020). Effects of acclimation temperature on the thermal physiology in two geographically distinct populations of Lake Sturgeon (*Acipenser fulvescens*). *Conservation Physiology*, 8(1), 1-19.
doi:10.1093/conphys/coaa087

- Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30, 492-507.
- Breheny, P., & Burchett, W. (2017). Visualization of Regression Models Using visreg. *The R Journal*, 9(2), 56-71.
- Buszkiewicz, J. T., Phelps, Q. E., Tripp, S. J., Herzog, D. P., & Scheibe, J. S. (2016). Documentation of Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817) recovery and spawning success from a restored population in the Mississippi River, Missouri, USA. *Journal of Applied Ichthyology*, 32, 1-10.
doi:10.1111/jai.13211
- Calenge, C. (2006). The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 1035.
doi:10.1016/j.ecolmodel.2006.03.017
- Carr, M. K., Lacho, C., Pollock, M., Watkinson, D. & Lindenschmidt, K. (2015). Development of geomorphic typologies for identifying Lake Sturgeon (*Acipenser fulvescens*) habitat in the Saskatchewan River system. *River Systems*, 21 (4), 215-227. doi:10.1127/1868-5749/2014/0086
- D'Amelio, S., Mucha, J., Mackereth, R., & Wilson, C. C. (2008). Tracking coaster Brook Trout to their sources: combining telemetry and genetic profiles to determine source populations. *North American Journal of Fisheries Management*, 28(4), 1343-1349. doi:10.1577/M05-193.1
- Dammerman, K. J., Webb, M. A., & Scribner, K. T. (2019). Riverine characteristics and adult demography influence female Lake Sturgeon (*Acipenser fulvescens*)

spawning behavior, reproductive success, and ovarian quality. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(7), 1147-1160. doi:/10.1139/cjfas-2018-0141

- DeInet, S., Scott-Gatty, K., Rotton, H., Twardek, W. M., Marconi, V., McRae, L., Baumgartner, L. J., Brink, K., Claussen, J. E., Cooke, S. J., Darwall, W., Eriksson, B. K., Garcia de Leaniz, C., Hogan, Z., Royte, J., Silva, L., G. M., Thieme, M. L., Tickner, D., Waldman, J., Wannigen, H., Weyl, O. L. F., & Berkhuisen, A. (2020). The Living Planet Index (LPI) for migratory freshwater fish - Technical Report. World Fish Migration Foundation, The Netherlands.
- DeLonay, A. J., Chojnacki, K. A., Jacobson, R. B., Braaten, P. J., Buhl, K. J., Elliott, C. M., & Mestl, G. E. (2014). *Ecological requirements for Pallid Sturgeon reproduction and recruitment in the Missouri River: Annual report 2014*. U.S. Geological Survey Open-File Report 2016–1013. doi:10.3133/ofr20141106.
- Deslauriers, D., Yoon, G. R., Earhart, M. L., Long, C., Klassen, C. N., & Anderson, W. G. (2018). Over-wintering physiology of age-0 Lake Sturgeon (*Acipenser fulvescens*) and its implications for conservation stocking programs. *Environmental Biology of Fishes*, 101(4), 623-637. doi:10.1007/s10641-018-0724-4
- Dunn, C. G., Brooke, B. L., Hrabik, R. A., & Paukert, C. P. (2018). Intensive sampling reveals underreported use of great-river tributaries by large-river fishes in Missouri. *Southeastern Naturalist*, 17(3), 512-520. doi:10.1656/058.017.0316

- Ecclestone, A., Haxton, T. J., Pratt, T. C., Wilson, C. C., & Whillans, T. (2020). Seasonal use of two unregulated Lake Superior tributaries by Lake Sturgeon. *Journal of Great Lakes Research*, 46(5), 1369-1381. doi:10.1016/j.jglr.2020.06.008
- Forsythe, P. S., Scribner, K. T., Crossman, J. A., Ragavendran, A., Baker, E. A., Davis, C., & Smith, K. K. (2012). Environmental and lunar cues are predictive of the timing of river entry and spawning-site arrival in Lake Sturgeon *Acipenser fulvescens*. *Journal of Fish Biology*, 81(1), 35-53. doi:10.1111/j.1095-8649.2012.03308.x
- Fink, M. (2018). Petition to List U.S. Populations of Lake Sturgeon (*Acipenser fulvescens*) as endangered or threatened under the Endangered Species Act. Center for Biological Diversity. Available: <https://www.biologicaldiversity.org/species/fish/pdfs/Lake-Sturgeon-petition-5-14-18.pdf>
- Gerig, B., Moerke, A., Greil, R., & Koproski, S. (2011). Movement patterns and habitat characteristics of Lake Sturgeon (*Acipenser fulvescens*) in the St. Marys River, Michigan, 2007–2008. *Journal of Great Lakes Research*, 37, 54-60. doi:10.1016/j.jglr.2010.09.007
- Glitzen, R. A., & Millsbaugh, J. J. (2003). Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. *Wildlife Society Bulletin*, 31(3), 823-831.
- Graf, W. L. (1999). Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. *Water resources research*, 35(4), 1305-1311. doi:10.1029/1999WR900016

- Harvey-Lavoie, S., Cooke, S. J., Guénard, G., & Boisclair, D. (2016). Differences in movements of Northern Pike inhabiting rivers with contrasting flow regimes. *Ecohydrology*, 9, 1687–1699. doi:10.1002/eco.1758
- Hay-Chmielewski, E. M. (1987). *Habitat preferences and movement patterns of the Lake Sturgeon (Acipenser fulvescens) in Black Lake, Michigan* (p. 51). Ann Arbor: Michigan Department of Natural Resources, Fisheries Division.
- Hayden, T. A., Holbrook, C. M., Fielder, D. G., Vandergoot, C. S., Bergstedt, R. A., Dettmers, J. M., ... & Cooke, S. J. (2014). Acoustic telemetry reveals large-scale migration patterns of Walleye in Lake Huron. *PLoS One*, 9(12), e114833. doi:10.1371/journal.pone.0114833
- Helfman, G. S., & Schultz, E. T. (1984). Social transmission of behavioural traditions in a coral reef fish. *Animal Behaviour*, 32(2), 379-384. doi:10.1016/S0003-3472(84)80272-9
- Holland, K. N., Lowe, C. G., Peterson, J. D., & Gill, A. (1992). Tracking coastal sharks with small boats: Hammerhead Shark pups as a case study. *Australian Journal of Marine and Freshwater Research*, 43(1), 61-66. doi.org/10.1071/MF9920061
- Homola, J. J., Scribner, K. T., Elliott, R. F., Donofrio, M. C., Kanefsky, J., Smith, K. M., & McNair, J. N. (2012). Genetically derived estimates of contemporary natural straying rates and historical gene flow among Lake Michigan Lake Sturgeon populations. *Transactions of the American Fisheries Society*, 141(5), 1374-1388. doi:10.1080/00028487.2012.694829

- Horton, T. B., & Guy C. S. (2004). Influence of time interval on estimations of movement and habitat use. *North American Journal of Fisheries Management*, 24, 690–696. doi:10.1577/M02-069.1
- Hughes, T. C. (2002). *Population characteristics, habitats, and movements of Lake Sturgeon (Acipenser fulvescens) in the lower Niagara River*. [Master's thesis, The College at Brockport State University of New York, Brockport, New York]. Retrieved from https://digitalcommons.brockport.edu/env_theses/78/.
- Ingram, E. C., & Peterson, D. L. (2016). Annual spawning migrations of adult Atlantic Sturgeon in the Altamaha River, Georgia. *Marine and Coastal Fisheries*, 8(1), 595-606.
- Jacobson, R. B., & Galat, D. L. (2008). Design of a naturalized flow regime—an example from the lower Missouri River, USA. *Ecohydrology*, 1(2), 81-104.
- Jacobson, R. B., Johnson, H. E., III, & Dietsch, B. J. (2009). Hydrodynamic simulations of physical aquatic habitat availability for pallid sturgeon in the Lower Missouri River, at Yankton, South Dakota, Kenslers Bend, Nebraska, Little Sioux, Iowa, and Miami, Missouri, 2006-07: U.S. Geological Survey, Scientific Investigations Report 2009-5058, 67 p.
- Jadot, C., Ovidio, M., Voss J. (2002). Diel activity of *Sarpa salpa* (Sparidae) by ultrasonic telemetry in a *Posidonia oceanica* meadow of Corsica (Mediterranean Sea). *Aquatic Living Resources*, 15, 343-350. doi:10.1016/S0990-7440(02)01193-2
- Kessel, S. T., Hondorp, D. W., Holbrook, C. M., Boase, J. C., Chiotti, J. A., Thomas, M. V., ... & Krueger, C. C. (2018). Divergent migration within Lake Sturgeon

(*Acipenser fulvescens*) populations: Multiple distinct patterns exist across an unrestricted migration corridor. *Journal of Animal Ecology*, 87(1), 259-273.
doi:10.1111/1365-2656.12772

Kleinbaum, D. G., Kupper, L. L., Nizam, A., & Rosenberg, E. S. (2013). *Applied regression analysis and other multivariable methods*. Nelson Education.

Knight, R. R., Murphy, J. C., Wolfe, W. J., Saylor, C. F., & Wales, A. K. (2014). Ecological limit functions relating fish community response to hydrologic departures of the ecological flow regime in the Tennessee River basin, United States. *Ecohydrology*, 7(5), 1262-1280. doi:10.1002/eco.1460

Knights, B. C., Vallazza, J. M., Zigler, S. J., & Dewey, M. R. (2002). Habitat and movement of Lake Sturgeon in the upper Mississippi River system, USA. *Transactions of the American Fisheries Society*, 131(3), 507-522.
doi:10.1577/1548-8659(2002)131<0507:HAMOLS>2.0.CO;2

Lallaman, J. J., Damstra, R. A., & Galarowicz, T. L. (2008). Population assessment and movement patterns of Lake Sturgeon (*Acipenser fulvescens*) in the Manistee River, Michigan, USA. *Journal of Applied Ichthyology*, 24(1), 1-6.
doi:10.1111/j.1439-0426.2007.01032.x

Lallaman, J. (2012). *Factors affecting paddlefish reproductive success in the lower Osage River*. [Doctoral dissertation, University of Missouri. Columbia, Missouri].
<https://mospace.umsystem.edu/xmlui/bitstream/handle/10355/33041/research.pdf?sequence=2>

Lennox, R. J., Paukert, C. P., Aarestrup, K., Auger-Méthé, M., Baumgartner, L., Birnie-Gauvin, K., ... & Cooke, S. J. (2019). One hundred pressing questions on the

- future of global fish migration science, conservation, and policy. *Frontiers in Ecology and Evolution*, 7, 286. doi:10.3389/fevo.2019.00286
- Lindén, A. & Mäntyniemi, S. (2011). Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology*, 92(7), 1414-1421. doi:10.1890/10-1831.1
- Liu, X., Qin, J., Xu, Y., Ouyang, S., & Wu, X. (2019). Biodiversity decline of fish assemblages after the impoundment of the Three Gorges Dam in the Yangtze River Basin, China. *Reviews in Fish Biology and Fisheries*, 29(1), 177-195. doi:10.1007/s11160-019-09548-0)
- Lyons, J., & Stewart, J. S. (2014). Predicted effects of future climate warming on thermal habitat suitability for Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in rivers in Wisconsin, USA. *Journal of Applied Ichthyology*, 30, 1508-1513. doi:10.1111/jai.12543
- MacKenzie, C. (2016). *Lake Champlain Lake Sturgeon recovery plan*. Vermont Fish and Wildlife, Montpelier, VT.
- Marra, G., & Wood, S. N. (2011). Practical variable selection for generalized additive models. *Computational Statistics & Data Analysis*, 55(7), 2372-2387. doi:/10.1016/j.csda.2011.02.004
- McManamay, R. A., Bevelhimer, M. S., & Frimpong, E. A. (2015). Associations among hydrologic classifications and fish traits to support environmental flow standards. *Ecohydrology*, 8(3), 460-479. doi:/10.1002/eco.1517

- McDougall, C. A., Blanchfield, P. J. & Anderson, W. G. (2014). Linking movements of Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in a small hydroelectric reservoir to abiotic variables. *Journal of Applied Ichthyology*, 30, 1149-1159. doi:10.1111/jai.12546
- McDougall, C. A., Nelson, P. A., Macdonald, D., Kroeker, D., Kansas, K., Barth, C. C., & MacDonell, D. S. (2017). Habitat quantity required to support self-sustaining Lake Sturgeon populations: an alternative hypothesis. *Transactions of the American Fisheries Society*, 146(6), 1137-1155. doi:10.1080/00028487.2017.1353548
- McElroy, B., DeLonay, A., & Jacobson, R. (2012). Optimum swimming pathways of fish spawning migrations in rivers. *Ecology*, 93(1), 29-34. doi:10.1890/11-1082.1
- McIntyre, P. B., Liermann, C. R., Childress, E., Hamann, E. J., Hogan, J. D., Januchowski-Hartley, S. R., Koning, A. A., Neeson, T. M. Oele, D. L. & Pracheil, B. M. (2016). Conservation of migratory fishes in freshwater ecosystems. In G. P. Closs, M. Krkošek, and J. D. Olden (Eds.). *Conservation of freshwater fishes*. pp. 324-360. Cambridge University Press, Cambridge Massachusetts.
- McKinley, S., Kraak, G., & Power, G. (1998). Seasonal migrations and reproductive patterns in the Lake Sturgeon, *Acipenser fulvescens*, in the vicinity of hydroelectric stations in northern Ontario. *Environmental Biology of Fishes*, 51, 245-256. doi:/10.1023/A:1007493028238
- Moore, T. M. (2021). *A continuing plan for recovery and management of Lake Sturgeon in Missouri*. Missouri Department of Conservation Management Plan Unpublished Draft.

- Moore, M. J., Paukert, C. P., & Moore, T. M. (2020). Effects of latitude, season and temperature on Lake Sturgeon movement. *North American Journal of Fisheries Management*. doi.org/10.1002/nafm.10416
- Mulligan, M., van Soesbergen, A., & Sáenz, L. (2020). GOODD, a global dataset of more than 38,000 georeferenced dams. *Scientific Data*, 7(1), 1-8.
doi:10.6084/m9.figshare.10538486
- Murchie, K. J., Hair, K. P. E., Pullen, C. E., Redpath, T. D., Stephens, H. R., & Cooke, S. J. (2008). Fish response to modified flow regimes in regulated rivers: research methods, effects and opportunities. *River Research and Applications*, 24(2), 197-217. doi:10.1002/rra.1058
- Odling-Smee, L., & Braithwaite, V. A. (2003). The role of learning in fish orientation. *Fish and Fisheries*, 4(3), 235-246. doi:10.1046/j.1467-2979.2003.00127.x
- Olden, J. D., & Naiman, R. J. (2010). Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology*, 55(1), 86-107. doi:10.1111/j.1365-2427.2009.02179.x
- Peterson, D. L., Vecsei, P., & Jennings, C. A. (2007). Ecology and biology of the Lake Sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. *Reviews in Fish Biology and Fisheries*, 17(1), 59-76.
doi:10.1007/s11160-006-9018-6
- Poff, N. L., Richter, B. D., Arthington, A. H., Bunn, S. E., Naiman, R. J., Kendy, E., ... & Henriksen, J. (2010). The ecological limits of hydrologic alteration (ELOHA): a

new framework for developing regional environmental flow standards.

Freshwater Biology, 55(1), 147-170. doi:10.1111/j.1365-2427.2009.02204.x

Rusak, J. A., & Mosindy, T. (1997). Seasonal movements of Lake Sturgeon in Lake of the Woods and the Rainy River, Ontario. *Canadian Journal of Zoology*, 75(3), 383-395. doi:10.1139/z97-048

Schlosser, I. J., & Angermeier, P. L. (1995). Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. In J. L. Nielsen, (Ed.), *Evolution and the aquatic ecosystem: defining unique units in population conservation*. p.p. 392 in 401 American Fisheries Society, Symposium 17, Bethesda, Maryland.

Shao, J., & Zhong, B. (2003). Last observation carry-forward and last observation analysis. *Statistics in Medicine*, 22, 2429-2441. doi:10.1002/sim.1519

Shaw, S., Chipps, S., & Windels, S. (2013). Influence of sex and reproductive status on seasonal movement of Lake Sturgeon in Namakan Reservoir, Minnesota–Ontario. *Transactions of the American Fisheries Society*, 143, 10-20. doi:10.1080/00028487.2012.720625

Smith, A. Smokorowski, K. E., & Power M. (2017). Spawning Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817) and their habitat characteristics in Rainy River, Ontario and Minnesota. *Journal of Applied Ichthyology*, 33, 328-337. doi:10.1111/jai.13372

Snobl, Z. R., Isermann, D. A., Koenigs, R. P., & Raabe, J. K. (2017). Relative sampling efficiency and movements of subadult Lake Sturgeon in the lower Wolf River,

- Wisconsin. *Transactions of the American Fisheries Society*, 146, 1070-1080.
doi:10.1080/00028487.2017.1334703
- Struthers, D. P., Gutowsky, L. F. G., Enders, E. C., Smokorowski, K. E., Watkinson, D. A., Silva, A. T., Cvetkovic, M., Bibeau, E., & Cooke, S.J. (2017). Factors influencing the spatial ecology of Lake Sturgeon and Walleye within an impounded reach of the Winnipeg River. *Environmental Biology of Fishes*, 100, 1085-1103. doi:10.1007/s10641-017-0629-7
- Thayer, D., Ruppert, J. L., Watkinson, D., Clayton, T., & Poesch, M. S. (2017). Identifying correl bottlenecks for the conservation of large-bodied fishes: Lake Sturgeon (*Acipenser fulvescens*) show highly restricted movement and habitat use over-winter. *Global Ecology and Conservation*, 10, 194-205.
doi:10.1016/j.gecco.2017.03.008
- Thiem, J. D., Binder, T. R., Dawson, J. W., Dumont, P., Hatin, D., Katopodis, C., ... & Cooke, S. J. (2011). Behaviour and passage success of upriver-migrating Lake Sturgeon *Acipenser fulvescens* in a vertical slot fishway on the Richelieu River, Quebec, Canada. *Endangered Species Research*, 15(1), 1-11.
doi:10.3354/esr00360
- Tornabene, B. J., Smith, T. W., Tews, A. E., Beattie, R. P., Gardner, W. M., & Eby, L. A. (2020). Trends in River Discharge and Water Temperature Cue Spawning Movements of Blue Sucker, *Cycleptus elongatus*, in an Impounded Great Plains River. *Copeia*, 108(1), 151-162. doi:10.1643/CI-19-256
- Van Etten, J. (2017). R Package gdistance: distances and routes on geographical grids. *Journal of Statistical Software*, 76(13), 1-21.

- Viers, J. H. (2011). Hydropower relicensing and climate change. *Journal of the American Water Resources Association*, 47(4), 655-661. doi:10.1111/j.1752-1688.2011.00531.x
- Vine, J. R., Holbrook, S. C. Post, W. C., & Peoples, B. K. (2019). Identifying environmental cues for Atlantic Sturgeon and Shortnose Sturgeon spawning migrations in the Savannah River. *Transactions of the American Fisheries Society*, 148, 671-681. doi:10.1002/tafs.10163
- Webb, M. A., Van Eenennaam, J. P., Feist, G. W., Linares-Casenave, J., Fitzpatrick, M. S., Schreck, C. B., & Doroshov, S. I. (2001). Effects of thermal regime on ovarian maturation and plasma sex steroids in farmed white sturgeon, *Acipenser transmontanus*. *Aquaculture*, 201(1-2), 137-151. doi:10.1016/S0044-8486(01)00550-6
- Welsh, A. B., Baerwald, M. R., Friday, M., & May, B. (2015). The effect of multiple spawning events on cohort genetic diversity of Lake Sturgeon (*Acipenser fulvescens*) in the Kaministiquia River. *Environmental Biology of Fishes*, 98(3), 755-762. doi:10.1007/s10641-014-0309-9
- Welsh, A. B., & McLeod, D. T. (2010). Detection of natural barriers to movement of Lake Sturgeon (*Acipenser fulvescens*) within the Namakan River, Ontario. *Canadian Journal of Zoology*, 88(4), 390-397. doi:10.1139/Z10-009
- Werner, R. G., & Hayes, J. (2004). Contributing factors in habitat selection by Lake Sturgeon (*Acipenser fulvescens*). State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, <https://ggplot2.tidyverse.org>.
- Wilcove, D. S., & Wikelski, M. (2008). Going, going, gone: Is animal migration disappearing? *PLoS Biology*, 6(7), 1361-1364. doi:10.1371/journal.pbio.0060188
- Wishingrad, V., Carr, M. K., Pollock, M. S., Ferrari, M. C., & Chivers, D. P. (2014). Lake Sturgeon geographic range, distribution, and migration patterns in the Saskatchewan River. *Transactions of the American Fisheries Society*, 143(6), 1555-1561. doi:10.1080/00028487.2014.954052
- Wood, S. N. (2004). Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association*. 99, 673-686. doi:10.1198/016214504000000980
- Zuur, A. F., Saveliev, A. A., & Ieno, E. N. (2012). *Beginner's guide to generalized additive models with R*. United Kingdom: Highland Statistics Limited.

Tables

Table 2.1. Spring and fall GAMM model output predicting relationship between longitudinal position (rkm) and environmental variables. Table includes effective degrees of freedom (K) for each environmental smoother with bold values denoting significance at the 0.05 level. Model output also includes the estimates for R^2 , sample size, and Rho which is the autocorrelation parameter before accounting for AR1 covariance structure.

Parameter	Spring			Fall	
	Gasconade (G1)	Lower Osage (O2)	Upper Osage (O3)	Lower Osage (O2)	Upper Osage (O3)
Group Intercept	3.59 ($<1*10^{-4}$)	-0.16 (0.41)	2.62 ($<1*10^{-4}$)	3.03 ($<1*10^{-4}$)	2.67 ($<1*10^{-4}$)
	Effective Degrees of Freedom			Effective Degrees of Freedom	
Temperature	12.13 ($<1*10^{-4}$)	12.30 ($<1*10^{-4}$)	4.20 ($<1*10^{-4}$)	6.37 ($<1*10^{-4}$)	0.00(0.59)
Discharge	10.06 ($<1*10^{-4}$)	15.62($<1*10^{-4}$)	0.53(0.14)	3.31 ($<1*10^{-4}$)	0.00(0.91)
Δ Discharge	1.43 (0.02)	0.09(0.30)	0.00(1.00)	0.73 (0.04)	0.00(0.76)
Δ Temperature	0.82 (0.01)	0.00(0.53)	0.00(1.00)	3.89 (0.002)	0.00(0.68)
Temp x Discharge	0.64 (0.12)	9.55 ($<1*10^{-4}$)	2.24 (0.01)	6.92 ($<1*10^{-4}$)	0.00(0.77)
Temp x Δ Discharge	3.73 (5*10⁻⁴)	0.00(0.58)	0.00(0.72)	1.87 (0.004)	0.00(0.47)
Temp x Δ Temperature	1.64 (0.01)	1.76 ($5*10^{-4}$)	0.00(0.74)	3.23 (0.05)	0.00(1.00)
Individual Intercept		140.4 ($<1*10^{-4}$)			
R^2	0.58			0.66	
Deviance Explained	58%			66%	
n	25108			3840	
Rho	0.92			0.90	

Figures

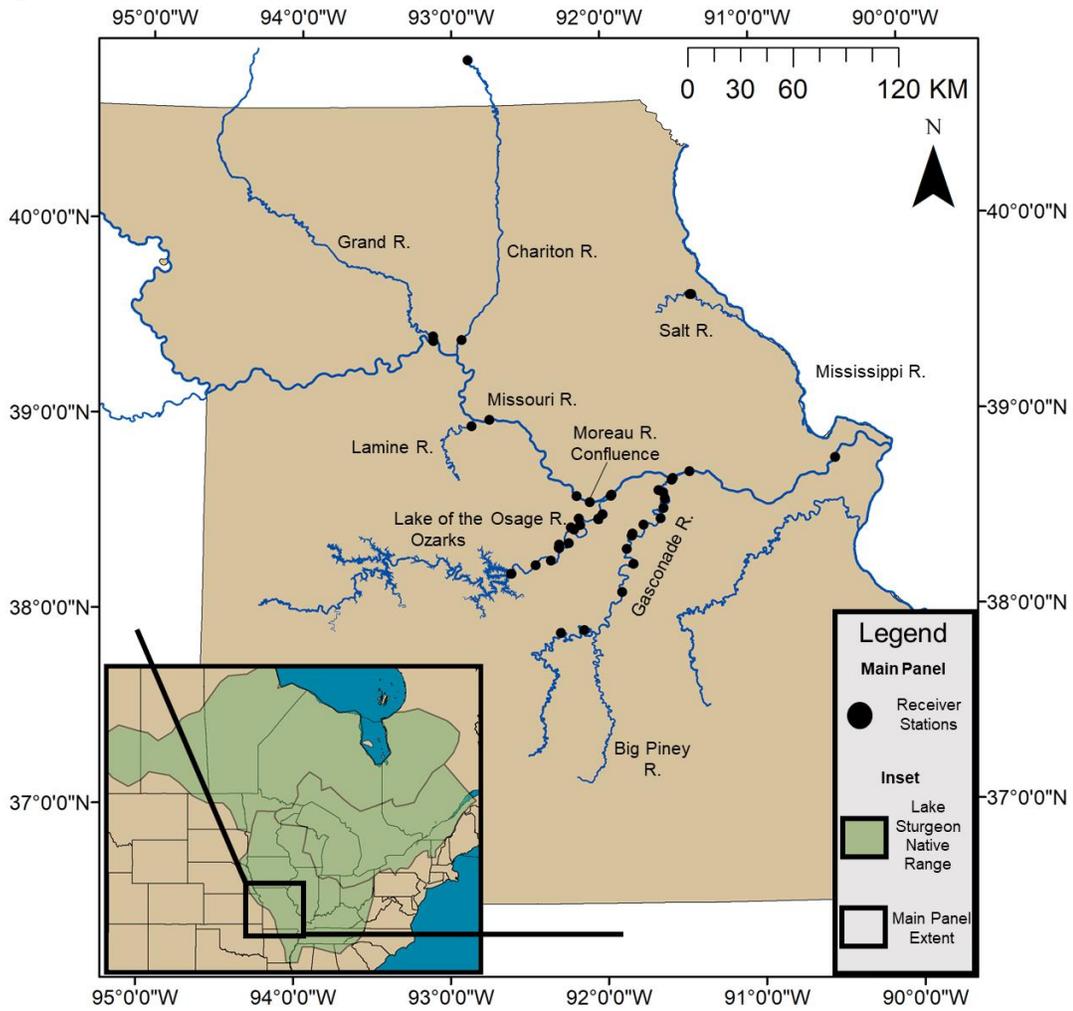
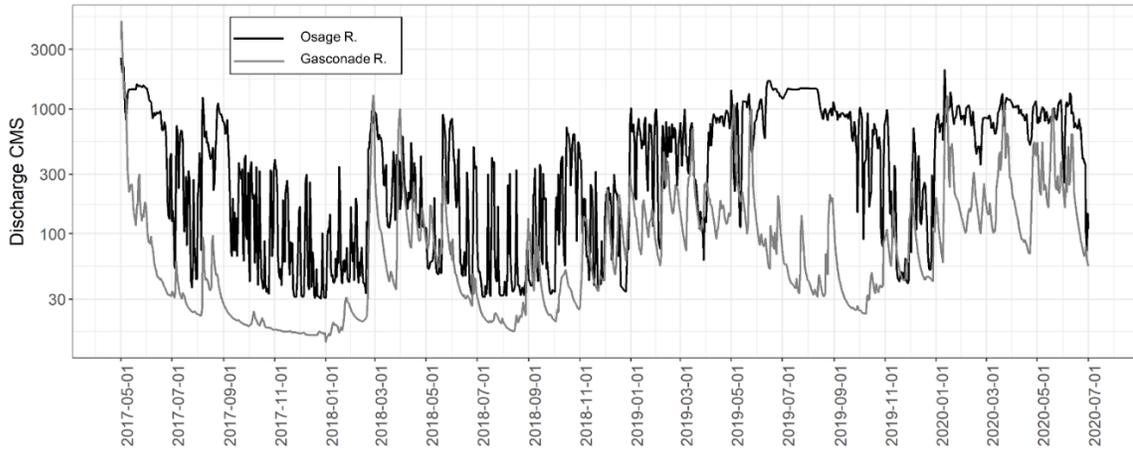
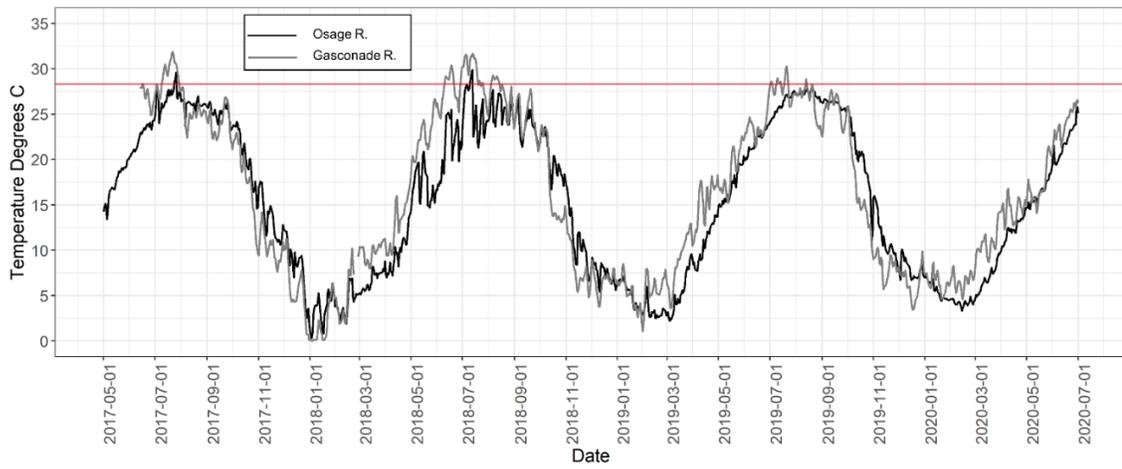


Figure 2.1. Map of study area to determine Lake Sturgeon distribution and movement among Missouri River tributaries from 2018 to 2020. The inset shows the location of the study area in relationship to the Lake Sturgeon's native range. Gray circles indicate Missouri River Basin receiver stations. Additional receivers not pictured exist in the Mississippi River and its tributaries that are maintained by the Missouri Department of Conservation.



A.



B.

Figure 2.2. Average daily discharge in cubic meters per second (cms) (A) and average daily temperature in °C (B) for the Osage River (black line), and Gasconade River (gray line) for the study period from May 2017 to July 2020. The red line plotted at 28 °C indicates one estimated threshold for thermal stress of Lake Sturgeon.

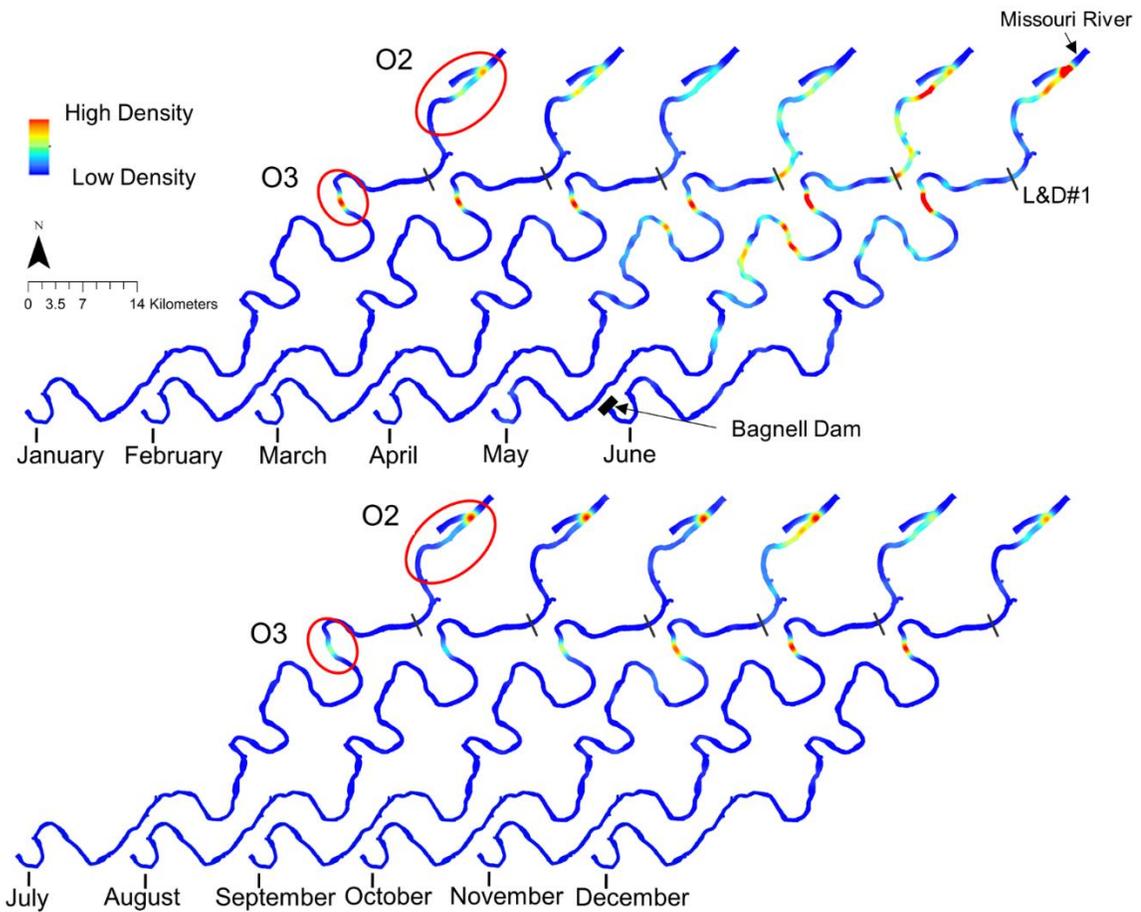


Figure 2.3. Kernel density estimate plots for Osage River manual detections of all Lake Sturgeon from May 2017 to July 2020 illustrating areas of intense use by river month. The primary extent of overwinter and oversummer refugia (O1 and O2) are indicated by the red circles in January and July, respectively. Fish were classified as “migrating” while moving upstream in reaches upstream of these habitats. The dashed line on June’s plot shows the location of Lock and Dam #1 and Bagnell Dam for spatial reference.

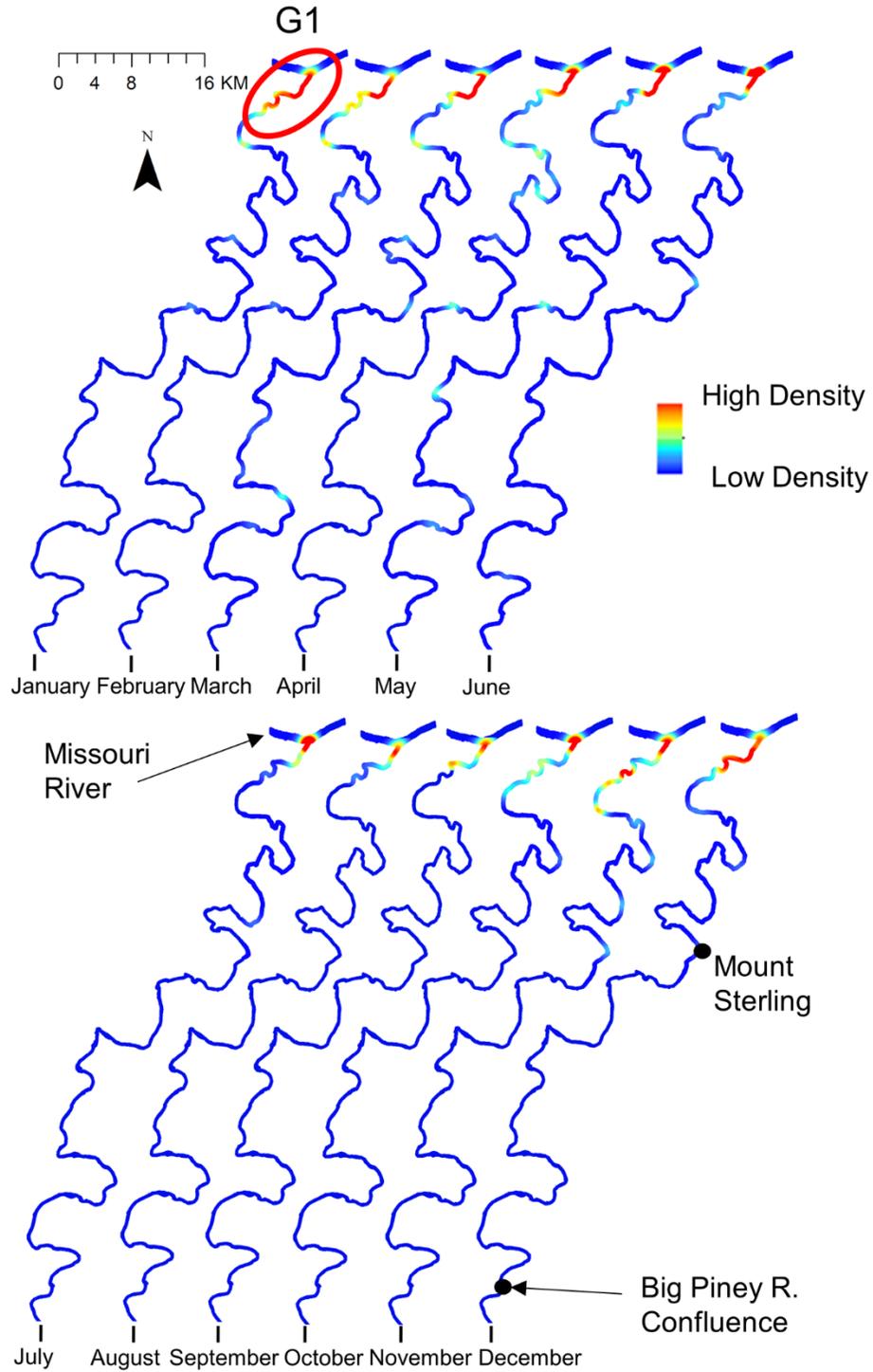


Figure 2.4. Kernel density estimate plots for Gasconade River manual detections of all Lake Sturgeon from May 2017 to July 2020 illustrating areas of intense use by month. The overwinter refugia (G1) is indicated by the red circles in January. Fish were classified as “migrating” while moving upstream in reaches upstream of these habitats. The location of the confluence with the Big Piney River and the town of Mt. Sterling, MO are added for spatial reference.

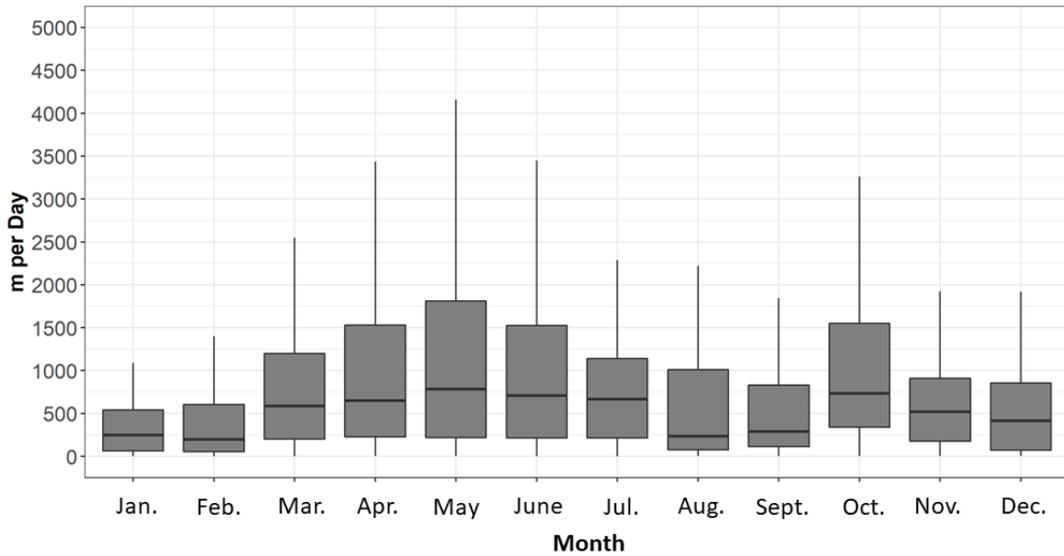


Figure 2.5. Box and whisker plots with box lines representing, the median lower and upper quartiles of monthly movement rates of Lake Sturgeon in the Osage and Gasconade rivers, 2017–2020. The whiskers show data range up to the upper quartile + 1.5 of the interquartile range. Outliers above this threshold are not shown.

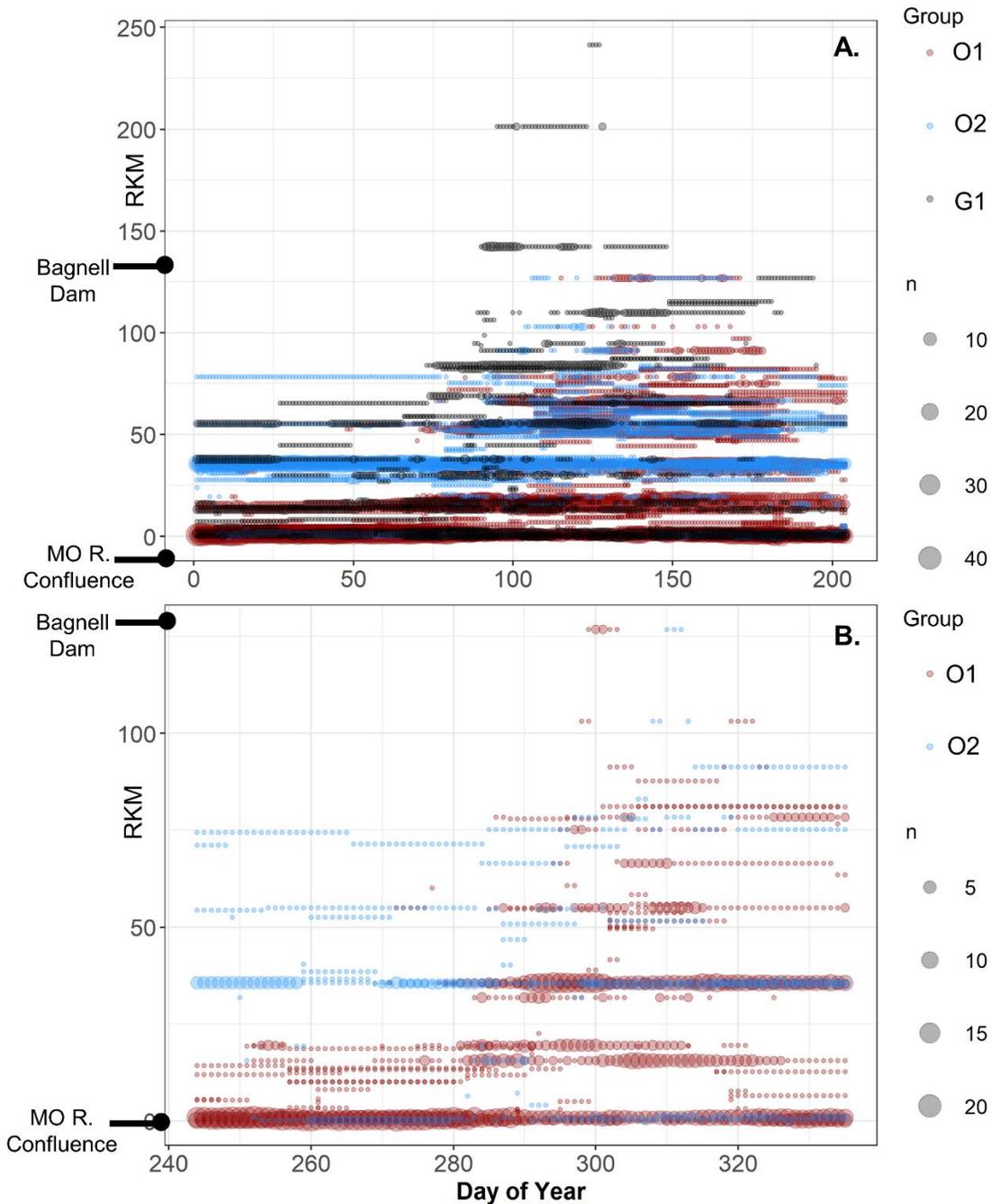


Figure 2.6. Scatterplots of daily longitudinal river km position of Lake Sturgeon within the Osage and Gasconade rivers during the spring (A.) and fall migration periods in Osage R. only (B.). Dot color signifies the group the individual belonged to as well as the river the migration occurred in (red and blue dots are Osage River migrations, black dots are Gasconade River migrations). Dot size indicates the number of fish detected at the same location on a given day. The rkm positions of the Missouri River confluence (rkm 0) and Bagnell Dam (rkm 130) are provided for reference.

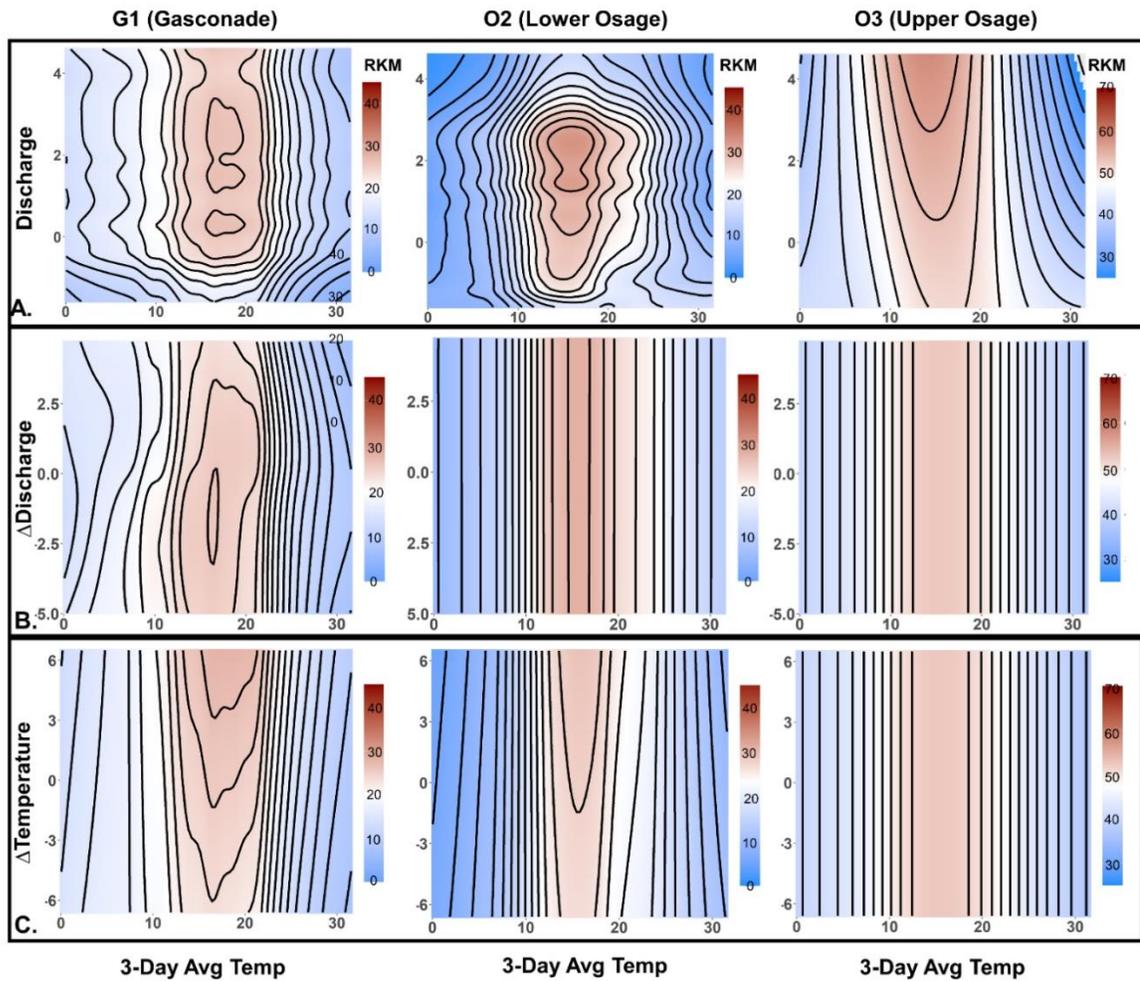


Figure 2.7. Contour plots from spring GAMMs showing the relationships between environmental predictors and predicted rkm position of Lake Sturgeon during spring migrations. The x-axis for all plots is 3-day average temperature. The y-axis is 3-day average standardized discharge (A), 3-day discharge change (B), and 3-day temperature change (C). Each column of the figure represents one of the three migration groups that we assigned based on the start point of spring migration. The z-axis represents longitudinal position in the tributary with deeper red colors indicating further upstream and deeper blue further downstream. For purposes of making comparisons across groups, the range of z-axis scales is the same for all plots. The maximum and minimum values of the z-axis scales are the same for all plots within groups. Fifteen contour lines are placed in each contour to show z-gradients even when variable has small effects on river km (e.g., Group 1 discharge vs. temperature).

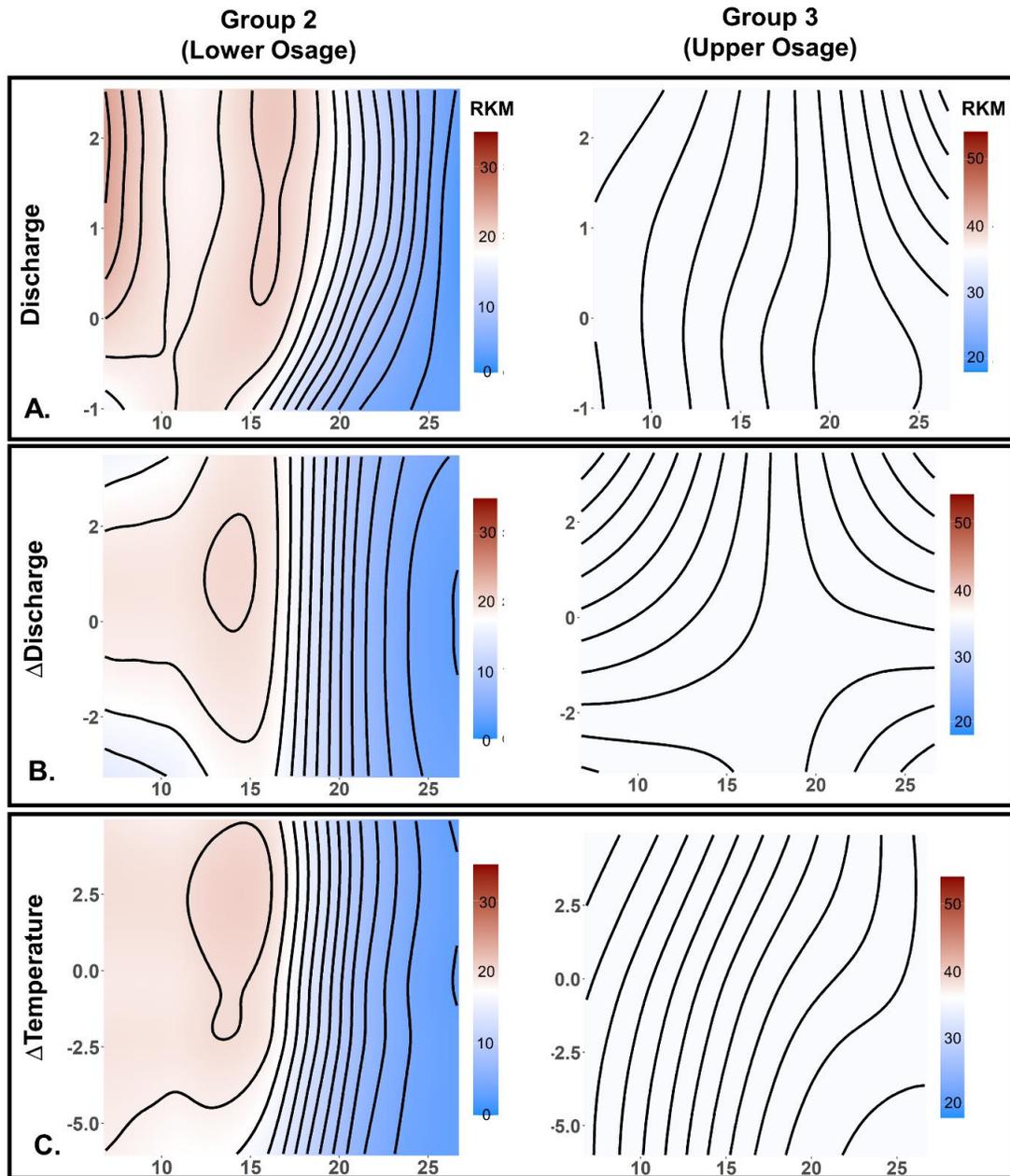


Figure 2.8. Contour plots from fall GAMMs showing the relationships between environmental predictors and predicted rkm position of sturgeon during spring migrations. The x-axis for all plots is 3-day average temperature. The y-axis is 3-day average standardized discharge in panel A, 3-day discharge change in panel B, and 3-day temperature change in panel C. Each column of the figure represents one of the two migration groups that we assigned based on the start point of fall migration. The z-axis represents longitudinal position in the tributary with deeper red colors indicating further upstream and deeper blue further downstream. For purposes of making comparisons across groups, the range of z-axis scales is the same for all plots. The maximum and minimum values of the z-axis scales are the same for all plots within groups. Fifteen contour lines are placed in each contour to show z-gradients even when variable has small effects on river km (e.g., all group 3 plots).

Appendices

Appendix 2.1. Lake Sturgeon sampling summary. Sampling effort is broken down by tributary and month. Effort is reported as the number 4-6 in bar mesh, 100 m gillnet nights or the number of 40 hook setline nights. Setlines were baited with night crawlers. CPUE is calculated by dividing the number of monthly Lake Sturgeon captures or recaptures by sampling effort.

River	Year and Month	Gear	N, Captures or Recaptures	100 m Net Nights	40 Hook Line Night	CPUE/ Line Night	CPUE/ Net Night
Osage	17-Mar	Trotline	22		12.00	1.83	
Osage	17-Apr	Trotline	15		52.68	0.28	
Osage	17-May	Trotline	5		7.10	0.70	
Osage	17-Oct	Trotline	17		12.50	1.36	
Gasconade	17-Mar	Trotline	4		16.98	0.24	
Gasconade	17-Apr	Trotline	0		20.85	0.00	
Gasconade	17-Nov	Trotline	2		16.50	0.12	
Gasconade	17-Nov	Gillnet	9	12			0.75
Gasconade	18-Feb	Gillnet	8	12			0.67
Gasconade	18-Mar	Gillnet	9	21.3			0.42
Gasconade	19-Feb	Gillnet	0	5			0.00
Gasconade	19-Mar	Trotline	3		13.50	0.22	
Gasconade	19-Mar	Gillnet	5	16			0.31

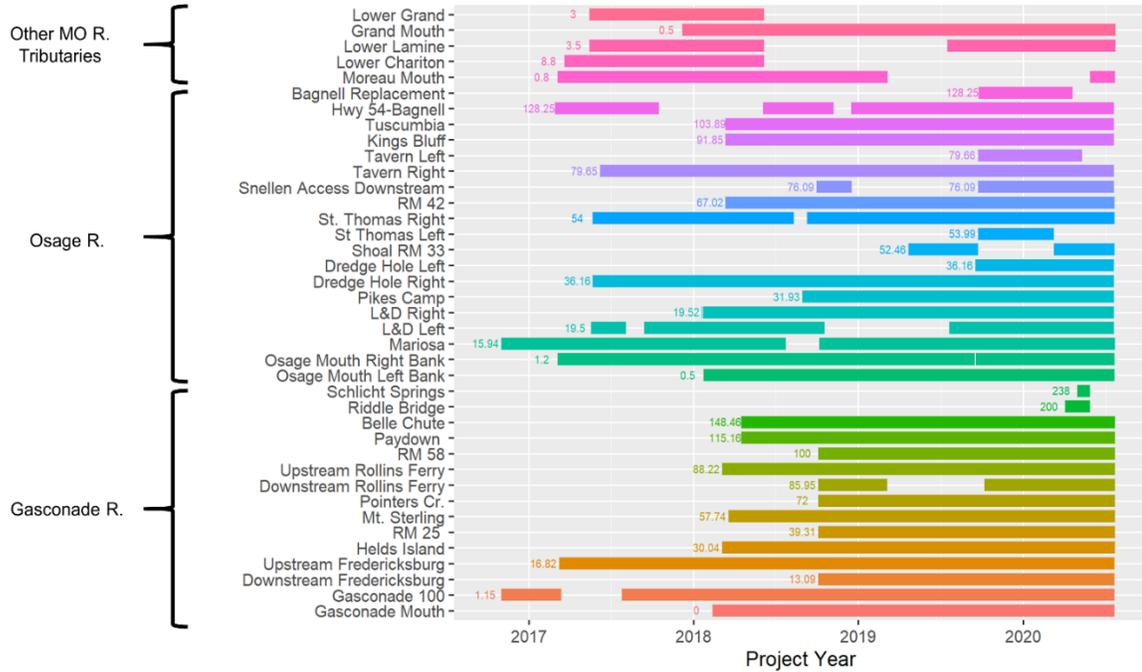
Appendix 2.2. Information for all Lake Sturgeon captured or recaptured during study. Tag code is the V16 transmitter transmission code. CWT column indicates the location of coded wire tag with “D.” an abbreviation for “dorsal scute”. TL stands for total length and fork length, respectively. Other abbreviations include “M” for male, “F” for female, and “UK” for unknown.

Tag Code	PIT New	Floy New	CWT?	TL mm	FL mm	Girth mm	Weight kg	Sex	Tag Date	Tagging Loc.
4140	0A130A1704	54551	UK	UK	1,330	UK	20.5	F	3/18/2015	L. Osage
16182	0A13092463	55066	2nd D.	1,295	1,218	545	15.0	M	3/15/2017	L. Osage
16183	0A13092443	55062	3rd D.	1,144	1,030	408	7.1	UK	3/14/2017	L. Osage
16184	0A13092455	55068	1st D.	1,041	975	403	7.1	UK	3/15/2017	L. Osage
16185	0A13092423	55061	None	1,036	940	374	5.9	F	3/14/2017	L. Osage
16186	0A1309245D	55067	2nd D.	1,181	1,110	443	9.8	M	3/15/2017	L. Osage
16187	4B193A2053	53891	None	1,001	906	329	5	UK	3/23/2017	Gasconade
16188	4311670767	55070	2nd D.	1,241	1,143	448	10.8	M	3/15/2017	L. Osage
16189	0A1309245C	55155	None	1,480	1,370	497	14.8	M	3/23/2017	Gasconade
16190	0A1209246A	55069	2nd D.	1,282	1,197	495	13.6	M	3/15/2017	L. Osage
16191	4AU7333E38	55163	2nd D.	1,031	912	359	5.2	UK	3/28/2017	Gasconade
16192	0A1309246D	55075	2nd D.	1,324	1,237	521	14.4	F	3/15/2017	L. Osage
16193	0A1309244D	55174	1st D.	1,188	1,080	388	8.3	UK	3/29/2017	Gasconade
16194	0A13092454	55073	None	1,180	1,082	439	8.8	M	3/15/2017	L. Osage
16195	0A1309244A	55355	3rd D.	1,402	1,280	604	19.1	F	3/9/2018	Gasconade
16196	471A315744	55074	2nd D.	1,200	1,100	437	9.8	M	3/15/2017	L. Osage
16197	0A1309242A	55353	None	1,576	1,452	554	21.8	M	3/7/2018	Gasconade
16198	0A1309252A	55151	1st D.	1,470	1,358	656	23.6	F	3/16/2017	L. Osage
16200	0A13092415	55051	None	1,331	1,220	490	12.8	M	3/14/2017	L. Osage
16201	0A13092470	55351	2nd D.	1,268	1,154	522	13.8	M	3/6/2018	Gasconade
16202	0A13092429	55055	1st D.	1,250	1,142	452	10.5	M	3/14/2017	L. Osage
16203	0A13092422	55124	None	1,220	1,114	440	9.9	F	3/6/2018	Gasconade
16203		55358	None	1,224	1,120	464	10.5	F	3/25/2019	Gasconade
16204	0A13092474	55052	3rd D.	1,236	1,132	438	9.6	M	3/14/2017	L. Osage
16206	0A1309246E	55054	2nd D.	1,212	1,120	454	10	M	3/14/2017	L. Osage
16208	0A1309246B	55056	2nd D.	1,206	1,100	455	9.0	M	3/14/2017	L. Osage
16210	0A1309242B	55053	Snout	1,285	1,165	430	9.5	M	3/14/2017	L. Osage
16211	0A13092449	55367	1st D.	1,372	1,251	542	17	F	3/28/2019	Gasconade
16212	482114580C	33955	None	1,370	1,240	525	16.2	F	3/14/2017	L. Osage
16214	0A13092436	55060	2nd D.	1,336	1,210	498	12.8	UK	3/14/2017	L. Osage
16215	0A1309242C	55352	None	1,238	1,136	432	10.4	UK	3/7/2018	Gasconade
16216	4704653116	55058	2nd D.	1,202	1,090	436	8.9	F	3/14/2017	L. Osage
16218	0A1309241C	55250	2nd D.	1,080	968	322	5	UK	5/10/2017	Os. Dredge
16220	0A1309244B	55082	None	1,084	975	368	6.2	UK	5/10/2017	Os. Dredge
16221	0A1309243E	36952	3rd D.	1,268	1,150	468	11.7	M	3/9/2018	Gasconade

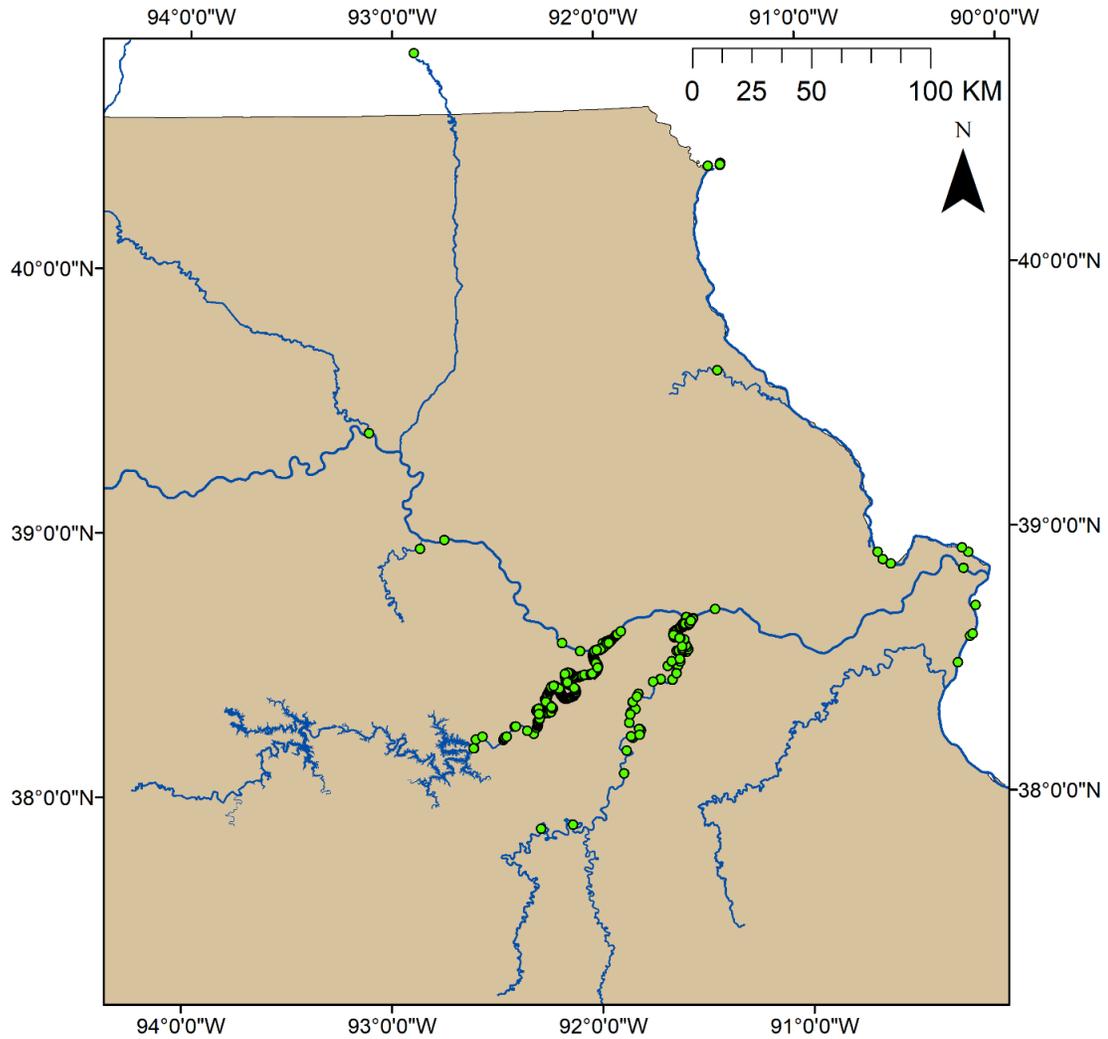
16222	2A13092418	55092	None	1,558	1,470	604	26.3	UK	10/27/2017	Os. Dredge
16223	0A1309241D	55357	2nd D.	1,296	1,166	484	13.5	F	3/9/2018	Gasconade
16224	0A13092434	55090	None	1,184	1,086	450	9.7	UK	10/27/2017	Os. Dredge
16225	43115B4B62	55359	None	1,618	1,510	580	27.1	F	3/25/2019	Gasconade
16226	0A13092438	55091	None	1,262	1,158	592	12.7	UK	10/27/2017	Os. Dredge
16227	0A13092414	55632	2nd D.	1,340	1,222	490	13.7	UK	3/27/2019	Gasconade
16228	4824250523	55093	None	1,292	1,172	420	10.3	UK	10/27/2017	Os. Dredge
16229	0A13092432	55361	None	1,031	937	336	5.4	UK	3/25/2019	Gasconade
16230	0A13092460	55097	None	1,312	1,202	564	15.8	F	10/31/2017	L. Osage
16231	0A1309241E	55112	None	1,080	1,006	368	6.7	UK	11/9/2017	Gasconade
16232	0A13092473	55089	None	1,194	1,020	432	8.9	F	10/27/2017	Os. Dredge
16233	460E58601B	55106	None	1,290	1,164	472	12.0	UK	11/8/2017	Gasconade
16234	0A1309243F	55094	2nd D.	1,194	1,084	438	9.6	UK	10/27/2017	Os. Dredge
16235	0A13092447	55108	None	1,274	1,168	442	11.8	UK	11/8/2017	Gasconade
16236	0A13092442	55098	None	1,298	1,182	490	12	M	10/31/2017	L. Osage
16237	0A13092426	55110	None	1,328	1,206	494	13	F	11/8/2017	Gasconade
16238	0A1309242F	55087	2nd D.	998	911	342	5.15	F	10/27/2017	Os. Dredge
16239	0A13092413	55111	None	1,298	1,208	442	11.9	F	11/9/2017	Gasconade
16240	0A1309245A	55086	Snout	980	874	362	5.15	UK	10/27/2017	Os. Dredge
16241	460D5C0D01	55115	None	1,264	1,174	438	10.7	F	11/10/2017	Gasconade
16242	4868451710	55096	None	1,134	1,022	428	8.6	UK	10/31/2017	L. Osage
16243	0A1309242E	55116	None	1,226	1,102	388	8.8	UK	11/10/2017	Gasconade
16244	0A1309245F	55099	None	1,116	1,022	376	7.3	UK	10/31/2017	L. Osage
16245	0A13092451	55117	None	1,204	1,116	400	8.9	UK	11/10/2017	Gasconade
16246	0A1309243B	55103	2nd D.	1,064	947	340	5.7	UK	10/31/2017	L. Osage
16247	0A1309241A	55118	None	1,192	1,100	418	10.1	UK	2/13/2018	Gasconade
16248	0A13092446	55100	2nd D.	1,138	1,028	416	8.1	UK	10/31/2017	L. Osage
16249	0A13092411	55114	None	1,210	1,114	396	8.9	UK	11/10/2017	Gasconade
16250	0A13092424	55102	None	1,618	1,490	558	23.5	F	10/31/2017	L. Osage
16251	0A1309243A	55119	1st D.	1,408	1,288	520	17.1	M	2/13/2018	Gasconade
16252	0A13092459	55104	3rd D.	1,166	1,066	458	10.4	UK	10/31/2017	L. Osage
16253	0A13092456	55120	None	1,212	1,118	452	10.7	M	2/14/2018	Gasconade
16254	460E477C7D	55218	None	1,131	998	381	7.1	UK	4/4/2017	L. Osage
16256	0A1309243C	55206	3rd D.	908	811	288	3.3	UK	4/6/2017	L. Osage
16258	0A1309250E	55022	3rd D.	1,006	921	355	5.5	M	4/6/2017	L. Osage
16259	0A13092441	55121	None	1,222	1,120	410	9.7	F	2/14/2018	Gasconade
16260	0A13092500	55020	None	1,590	1,405	634	22.8	M	4/6/2017	L. Osage
16262	0A1309247F	55021	1st D.	1,183	1,097	485	10.7	M	4/6/2017	L. Osage
16264	151920245A	54162	None	1,122	1,018	395	7.1	UK	4/6/2017	L. Osage
16265	42330A1B18	55122	None	1,404	1,282	460	13.4	F	2/15/2018	Gasconade
16266	0A1309242D	55202	None	1,311	1,189	421	11.2	M	4/11/2017	L. Osage
16267	0A13092410	55123	2nd D.	1,224	1,102	418	9.5	UK	2/15/2018	Gasconade
16268	0A13092417	55267	1st D.	1,047	954	372	5.5	M	4/11/2017	L. Osage

16269	0A13092469	55354	2nd D.	1186	1,070	410	9.4	UK	3/9/2018	Gasconade
16270	432A2D5153	25490	2nd D.	831	737	261	2.6	UK	4/11/2017	L. Osage
16271	0A13092461	55364	None	1156	1,039	448	8.5	UK	3/28/2019	Gasconade
16272	0A13092460	55268	None	1002	912	354	5.6	M	4/11/2017	L. Osage
16273	0A13092467	55368	None	1172	1,086	430	9.3	UK	3/28/2019	Gasconade
16274	0A13092444	55138	Snout	1328	1,229	484	14	M	4/12/2017	L. Osage
16276	0A13092431	55142	3rd D.	1083	982	364	6.2	M	4/13/2017	L. Osage
16277	0A13092445	55246	2nd D.	1080	965	372	6.3	M	5/10/2017	Os. Dredge
16278	48692C6D37	55147	3rd D.	1130	1,024	430	8.1	M	4/13/2017	L. Osage
16279	0A1309245E	55249	None	956	881	372	5.2	M	5/10/2017	Os. Dredge
16280	0A13092472	55283	2nd D.	1092	979	466	10.3	F	4/13/2017	L. Osage
16281	0A13092416	55247	1st D.	864	780	308	3.1	UK	5/10/2017	Os. Dredge
16282	0A13092412	55226	4th D.	1310	1,178	522	15	F	4/28/2017	L. Osage
16283	0A13092437	55360	1st D.	1114	1,004	400	7.9	UK	3/25/2019	Gasconade
26019	4869224243	6054	UK	UK	1,230	UK	14.6	M	3/30/2016	L. Osage
26020	44240F2851	54725	UK	UK	1,170	UK	11.2	M	3/18/2015	L. Osage
26021	0A1309252F	6069	UK	UK	1,180	UK	12.6	M	3/30/2016	L. Osage
26022	0A130A167F	54566	UK	1210		UK	9.8	M	3/19/2015	L. Osage
26023	0A130A1708	6156	UK	UK	1,348	UK	18.9	F	3/30/2016	L. Osage
26025	0A13092555	55125	Snout	1382	1,266	479	14.4	M	3/6/2018	Gasconade
26025	0A13092555	6068	UK	UK	1,235	UK	14.5	M	3/30/2016	L. Osage
26027	0A13092542	6073	UK	UK	1,190	UK	12.7	M	3/30/2016	L. Osage
26028	0A130A173B	6056	UK	UK	1,345	UK	16.1	F	3/30/2016	L. Osage
26029	0A13092515	6072	UK	UK	1,180	UK	12.7	M	3/30/2016	L. Osage
No Tag	0A1309244C	55088	Snout	733	646	228	1.6	UK	10/27/2017	Os. Dredge
No Tag	0A13092440	55105	Snout	749	660	240	1.9	UK	11/3/2017	Gasconade

Appendix 2.3. Gantt plot depicting 39 Missouri River tributary receiver stations and the date ranges we have detection data for each. The receiver stations are grouped by river and ordered from upstream to downstream within groups. Numbers next to bars are the river km distance from the tributary confluence with the Missouri River.



Appendix 2.4. Map of all active and passive detection locations of Lake Sturgeon in the lower Missouri River and Mississippi River Basins. Another fish that was detected in the Missouri River at Gavin's Point Dam in Yankton, SD is not shown.



**CHAPTER 3- DOES WHERE THEY START AFFECT WHERE
THEY FINISH? A MULTI-METHOD INVESTIGATION OF THE
ROLE OF STOCKING LOCATION ON SURVIVAL AND
DISPERSAL OF HATCHERY-REARED LAKE STURGEON IN
MISSOURI RIVER TRIBUTARIES**

Abstract

Monitoring survival and dispersal of stocked juveniles helps managers understand how reintroduction actions align with recovery objectives such as population growth, spatial distribution, and population structure. Despite ongoing Lake Sturgeon recovery efforts, little is known about the role of introduction location on survival and dispersal to nursery habitats. Through a two-year telemetry study conducted at four stocking sites in two adjacent Missouri River tributaries, we estimated age-0 Lake Sturgeon survival was similar among stocking sites and rivers. Survival estimates from Barker Cormack-Jolly-Seber models that incorporated both receiver detections and auxiliary manual detections were higher than spatial capture-recapture models that only included receiver detections. Barker model overwinter survival averaged 53% and provided information to adjust individual censoring in spatial capture-recapture model dispersal estimates. Within rivers, stocking site had little effect on activity centers with individuals from both sites converging upon similar locations by the end of the study period. However, dispersal distance and direction differed among stocking locations. Our overwinter survival estimates of stocked age-0 Lake Sturgeon in Missouri River tributaries were equal to or higher than other studied populations suggesting stocked juveniles are contributing to the

recovering population here. Tributaries were important overwintering nursery locations with high stream fidelity that may contribute to future homing among adults.

Introduction

Globally, anthropogenic stressors have resulted in an estimated a 91% decline in migratory sturgeon populations over 50 years (DeInet et al., 2020). However, reintroduction is a viable recovery strategy when natural recruitment is insufficient to reestablish populations (Seddon et al., 2007). In the 2000s, reintroduction research expanded to explore social behavior, genetics, and demographic dynamics that influence the fate of reintroduced populations (Seddon et al., 2007). Improvements in telemetry tag technology and spatial analytical approaches have allowed biologists to study survival and dispersal of small-bodied fishes in large river systems to better evaluate reintroduction protocols (Hussey et al., 2015; Whoriskey et al., 2019).

In contrast to other sturgeon species, Lake Sturgeon (*Acipenser fulvescens*) populations are recovering in some portions of their range (Bruch et al., 2016). Progress in North America's Mississippi River basin is due to harvest moratoriums coupled with ongoing stocking in at least five U.S. states. Despite recent successes, threats related to loss of river connectivity, and pollution inhibit natural reproduction in recovering populations (Bruch et al., 2016). Consequently, Lake Sturgeon were recently petitioned for listing under the Endangered Species Act (Fink, 2018). Reliance on reintroduction as a management tool necessitates a more thorough understanding of the influence of spatial allocation of stocking on survival and dispersal across interjurisdictional waterways. No known previously published studies have investigated movement of stocked age-0 Lake Sturgeon near its southwestern range margin, and few studies have addressed the

consequences of stocking location on dispersal or survival of age-0 sturgeon (e.g., Collier et al., 2011; Oldenburg et al., 2011).

Dispersal by age-0 Lake Sturgeon can also have important influences on future population structure, risk exposure, and energetic expenditures. Natal philopatry can occur in Lake Sturgeon and failure of hatchery-reared sturgeon to imprint on receiving streams may lead to straying to non-target populations (DeHaan et al., 2006; Smith et al., 2002). Fin-ray microchemistry suggests that few Lake Sturgeon stocked in the pooled portions of the Mississippi River had spent time lower Mississippi or Missouri rivers (Phelps et al., 2017). However, genetic evidence to support natal philopatry in Great Lakes tributaries is mixed (Homola et al., 2010). Therefore, potential post-stocking dispersal influences on future spatial population structure may require population-specific evaluation (Ward, 2006). Lake Sturgeon population dynamics are highly sensitive to age-0 survival (Schueller & Hayes, 2010). Survival can exhibit spatial variation due to factors such as quality of nursery habitats (Roni et al., 2012) and exposure to predation (Bronte et al., 2007). The proximity of fall stocking locations to overwinter nursery habitats may be important in limiting the energetic costs of long-distance dispersal (Bonte et al., 2012) and spatially explicit survival estimates are key components in age-structured population growth or viability models for sturgeon species (Ganus et al., 2017; Wildhaber et al., 2017).

The Missouri Department of Conservation (MDC) began reintroducing the state endangered Lake Sturgeon in 1984. Recovery efforts have produced mature fish; however, natural reproduction has not yet been verified in the Missouri River Basin. Furthermore, extensive channelization in the mainstem of the lower Missouri River has

reduced shallow, low-velocity habitat by 86%, which may be important nursery habitats for juvenile sturgeons (Jacobson & Galat, 2006). Therefore, by 2009, the MDC switched from stocking the mainstem Missouri and Mississippi rivers to stocking large tributaries. Previous studies have suggested that tributary-stocked Lake Sturgeon emigrate rapidly into the mainstem Mississippi River (Moore, 2021). In contrast, in 2012, 2013, and 2015, fall-stocked age-0 Lake Sturgeon were recaptured in the Gasconade river up to 4 months after stocking, which suggested that stocked sturgeon overwinter in Missouri River tributaries (Pherigo, 2019). Consequently, the extent of tributary use by stocked age-0 Lake Sturgeon remains unresolved and may be site-specific.

Therefore, our objective was to estimate overwinter survival and dispersal of age-0 Lake Sturgeon stocked in two Missouri River tributaries. Specifically, we sought to determine if: 1) apparent survival and tributary retention and 2) spatial distribution (dispersal distance, rates, and direction) differed among four stocking sites. We predicted that stocking site location would be an important consideration to the spatial management of Lake Sturgeon reintroduction through its effects on survival, dispersal, and overwintering location.

Material and methods

Study area

We used multiple tracking methods and capture-recapture models to estimate overwinter survival and dispersal of 187 stocked age-0 Lake Sturgeon in the Osage and Gasconade rivers (Figure 3.1). These rivers are large tributaries to the lower Missouri River located in the Ozark highlands ecoregion (U.S. EPA 2018), yet their differences

permit the comparison age-0 Lake Sturgeon behavior in multiple environments. The 8th Strahler order Osage River with mean width of ~200 m is larger than the 6th order Gasconade River with mean width of ~90 m. The study area encompassed the lower 130 river kilometers (rkm) of the Osage River from Bagnell Dam to its confluence with the Missouri River and the lower 145 rkm of the Gasconade River (Figure 3.2). The hydrology of the Osage River is heavily regulated by Bagnell Dam, a hypolimnetic release, hydropeaking dam responsible for rapid fluctuations in discharge of > 1.0 m in 15 minutes during the study period. In contrast, the Gasconade River watershed contains no major impoundments, retains a more natural hydrologic and thermal regime, and has fewer dispersal barriers. The Gasconade River cooled faster during the fall and warmed faster during the spring. Average winter temperatures were 5.4 °C in the Osage River and 6.1 °C in the Gasconade River. The Osage River also contains a non-operational navigation lock and dam (L&D#1) 19 rkm from the Osage-Missouri River confluence that can impede fish passage at low flows. These tributaries contain populations of adult Lake Sturgeon and have been stocked with age-0 Lake Sturgeon since 2009. Furthermore, both contain coarse substrates that may provide suitable habitat for natural reproduction. We selected two stocking locations at roughly equivalent longitudinal positions in each tributary: the Mari-Osa Access at rkm 16 (hereafter Osage-16), a private access at rkm 76 (Osage-76), the Fredericksburg Ferry Access at rkm 13 (Gasconade-13) and the Rollins Ferry Access at rkm 87 (Gasconade-87).

Hatchery Protocols and Transmitter Implantation

The MDC Lost Valley Hatchery obtained Lake Sturgeon embryos from the upper Mississippi River basin in the late spring of 2018 and 2019. We implanted 100 age-0 sturgeon in each study year (September or October of 2018 and 2019) with Vemco V8-4L acoustic transmitters with 60 second transmission delays and 141-day battery life. Surgical procedures generally followed established protocols (e.g., Snobl et al., 2015). Surgeons inserted transmitters into the body cavity through an abdominal incision and sealed incisions with non-absorbable monofilament nylon sutures using a curved needle.

For the 2018-2019 field season, we implanted 100 transmitters on September 25th and batteries expired on February 13th, 2019. The mean size of Lake Sturgeon tagged in 2018 was 46 g, 203 mm FL. Transmitters averaged 4.4% of body weight and for 87% of individuals transmitter weight was $\leq 5\%$ of body weight, a size shown not to affect growth, survival, or swimming performance, in Lake Sturgeon (McCabe et al., 2019; Snobl et al., 2015). Using a Welch Test to compare the means of two samples with unequal variance we determined that mass of tagged fish did not differ significantly by stocking site ($F(3, 51.69) = 2.16, p = 0.10$). A total of 95 age-0 Lake Sturgeon survived with transmitters intact to stocking on October 8th, 2018 with 23 being released at Osage-16, 23 at Osage-76, 24 at Gasconade-13, and 25 at Gasconade-87.

For the 2019-2020 season, we implanted transmitters on September 26, and October 21, 2019. The 76 fish implanted on September 26, 2019 ($\bar{x} = 26$ g, 176 mm FL) were smaller in mass than the 100 fish implanted on September 25, 2018 ($T(168) = 32.76, p < 0.01$). For fish implanted on September 26, 2019 transmitter weights were $> 5\%$ of body weight for all fish and $> 7\%$ of body weight for 74% of fish tagged. Mortality from this tagging event (36%) during recovery was greater than in 2018. The 49 fish that

survived were retained longer to ensure recovery prior to release and were stocked in the Gasconade River (24 at Gasconade-13, and 25 at Gasconade-87) on October 17, and monitored until batteries expired on February 14, 2020. We waited three weeks before attempting additional transmitter implantations for the Osage River sites to provide additional time for growth. By the second tagging date on October 21, 2019, the mean size of implanted sturgeon increased to 35 g and 194 mm FL. Transmitter weights were < 5% of body weight for 12% of the fish and < 7% for all of the fish. Only two of 51 fish tagged during the second round died following transmitter implantation. These 49 fish were stocked on October 28, with 25 released at Osage-16, and 24 at Osage-76. Transmitter batteries expired on March 10, 2020.

Data Collection and Preparation

We monitored Lake Sturgeon dispersal using passive detections from a network of 26 Vemco VR2Tx or VR2W acoustic receivers during the fall and winter of 2018–2019 and 2019–2020. We positioned receivers ~ 10–15 km apart in each river with additional receivers deployed immediately upstream and downstream of each stocking site, and two receivers near their confluence with the Missouri River to detect emigration out of the study area. Receivers were deployed between rkm 0.5 and 128.3 in the Osage River and between rkm 0 and 148.5 in the Gasconade River (Figure 3.2). We performed a receiver range test in June 2018 in a glide in the Osage River. We anchored a single V8-4L test tag and deployed 5 VR2Tx receivers at distances ranging from < 100 m to ~ 400 m for a total of 18 hours. We obtained 80% detection efficiency at 85 m and 50% at 250 m. The Osage River channel width ranges from approximately 150 to 330 m. We

increased channel coverage at some stations by cabling receiver anchors to trees near both banks or deployed a single receiver anchored mid-channel with a float. During cold weather, we moved mid-channel receiver anchors to near-bank positions to limit the risk of float loss during icefloes.

We also relocated individuals using manual boat tracking with a Vemco VR-100 receiver and omnidirectional and directional hydrophones. We limited manual tracking to a single river in each year of the study (Osage River 2018-2019 and Gasconade River 2019-2020) to ensure the implementation of thorough systematic tracking protocols across all occupied reaches within tracking periods. Position accuracy was estimated to be < 30 m based on a companion study where we located hidden V16 transmitters (M. Moore, University of Missouri, unpublished data, November 2, 2020). V8 transmitters were likely more accurate (< 10 m) due to reduced transmission power. We tracked all portions of the study area known to have tagged individuals four times (i.e., monthly) which provided auxiliary data to evaluate survival estimates from models that incorporated only data from stationary receivers (e.g., Hightower et al., 2001).

Data Analysis

Acoustic telemetry solves the issue of low recapture probability encountered in physical mark-recapture studies (Lees et al., 2021) making these data well-suited for multiple varieties of Cormack-Jolly-Seber (CJS) mark-recapture models. Linear spatial capture-recapture (SCR) models are an emerging method to estimate individual dispersal while accounting for survival (Raabe et al., 2014) and are 1-dimensional versions of SCR models developed for terrestrial camera trapping grids (Gardner et al., 2010). Despite

these benefits, linear SCR models rely solely on data from stationary receivers and their ability to estimate survival during periods of restricted movement has not been evaluated (Whoriskey et al., 2019). Therefore, we also incorporated manual and receiver detections to estimate survival using non-spatial Barker joint live-recapture/live resight/tag-recovery models (Barker, 1997). With higher-resolution tracking data, Barker models provided the “gold-standard” survival estimates for our populations. However, these auxiliary manual detections were only available for two of the four river-year combinations we refer to as “cohorts” and do not consider the spatial location of individuals needed to evaluate dispersal. Therefore, we exploited the advantages of each through a multi-method approach that uses Barker survival estimates to adjust censoring in SCR models to improve dispersal estimates for all four cohorts during periods when movement was low (Figure 3.1). Both models adhered to open capture-recapture assumptions that the tagging process does not influence survival, that recapture probability is comparable across individuals, and overcome the assumption of instantaneous, discrete sampling that is violated by continuously monitoring receiver arrays (Barbour et al., 2013; Pollock et al., 1990).

Spatial Capture Recapture Models

We developed separate models for $n = 4$ cohorts. SCR input consisted of detections of tagged individual Lake Sturgeon at $j = 13$ receiver stations per river. We condensed detection counts to one per receiver per hour over $t = 9$ biweekly sampling periods. We removed four fish from the analysis in 2018-2019 and two in 2019-2020 that

were not detected on receiver stations and thus may have perished immediately after stocking.

The SCR model was comprised of an observational model based on the detections that is conditional on the combination of a state model of the survival of individuals and a spatial model describing their movements. In the observational model, $y(i, j, t)$ are the biweekly hourly transmitter detection counts of observations for each individual ($i = 1, 2, \dots, n$), near each receiver ($j = 1, 2, \dots, J$), during each sampling period ($t = 1, 2, \dots, T$) and were modeled using a negative binomial distribution (Lindén & Mäntyniemi, 2011):

$$y(i, j, t) | z(i, t) \sim \text{Negative Binomial} \left(\frac{r}{r + (\lambda * z(i, t) * g(i, j, t))}, r \right),$$

where r is a dispersion parameter and λ is the theoretical baseline number of detections for fish with activity centers near receiver station j . We conditioned the $y(i, j, t)$ counts on the latent state, $z(i, t)$, based on the probability that an individual (i) is both alive and still within the study area (apparent survival) during the time period (t), given it was alive in the previous period ($t-1$):

$$z(i, t) \sim \text{Bernoulli}(\varphi z(i, t - 1)),$$

where φ , is the constant biweekly apparent survival rate. We set the state of each fish in the first time period, $z(i, 1)$, to alive given stocking.

Detection probabilities are conditioned on individual activity centers and estimated range during a study period. Receivers could detect fish within an estimable range or conversely, fish movements/activity could bring them within range of receivers at variable frequencies. Therefore, we used the approach by Raabe et al., (2014) that includes a spatial process to model activity using a Gaussian kernel, defined as:

$$g(i, j, t) \equiv e^{\left[-d(i, j, t)^2 / 2\sigma^2 \right]},$$

where

$$d(i, j, t) = \|s(i, t) - x(j)\|$$

is the distance between an estimated individual activity center $s(i, t)$ and each sampling location (i.e., receiver station) $x(j)$ in time period t . The scale parameter, σ , determines how quickly detection counts decrease as an activity center moves away from a receiver station and is considered representative of an individual's movement range (Raabe et al., 2014; Royle & Young, 2008). We estimated latent activity centers, $s(i, t)$, based on spatial location of detections as a Markovian process that assumed correlation (τ) between $s(i, t)$ and $s(i, t - 1)$. We set initial s for each individual at their stocking location.

All stocked individuals entered the model during the first period. We fixed z at 0 following an individual's "last" period alive within the state space that was inferred when: 1) a tag remained immobile at a receiver station with constant detections for ≥ 1 month, or 2) a fish was detected on the downstream most receiver indicating emigration to the Missouri River. Fish were not censored when continuously detected at the receiver in a gravel dredging pool at rkm 36 in the Osage River, which was one of three overwinter refugia that were collectively occupied by over 95% of adult and subadult Lake Sturgeon in the Osage and Gasconade rivers (M. Moore, University of Missouri, unpublished data, February 19, 2021).

We fit Bayesian models using Markov Chain Monte Carlo estimation in the `jagsUI` package in R (Kellner, 2019) by running three chains over 80,000 total iterations with an adaptive phase of 20,000 iterations, and a thinning rate of 10. Uninformative prior distributions were provided for parameters (i.e., ϕ , uniform (0,1), r uniform (0.1,

50), τ uniform (0, 30)). We assessed model convergence by calculating the Gelman-Rubin statistic for each estimated parameter (Gelman, Carlin, Stern, & Rubin, 2004).

Mean and standard errors for $s(i, t)$ and $z(i, t)$ were calculated from posterior distributions. We compared estimates of ϕ extrapolated over the study period to identify differences in overwinter survival between the four cohorts. Each model iteration estimates the latent state of each individual in each period as alive and within study area: $z=1$, or dead or outside study area $z=0$. We calculated a mean of individual z estimates (1's and 0's) from the posterior distribution in the final period (Raabe et al., 2014). Individuals were initially considered alive where mean posterior estimates of $z(i, t) > 0.5$. To examine site-specific survival differences, we compared the proportion of fish from each site estimated alive in the final period.

Barker Joint Recapture and Resight Cormack Jolly Seber Models

For the Osage River 2018-2019 and Gasconade River 2019-2020 data, we evaluated apparent survival estimates from the SCR models against those generated by a non-spatial Barker models (Barker, 1997). We set the physical recapture probability and emigration rate to 0 since we did not conduct discrete physical recapture sampling and instead combined passive receiver and manual tracking detections under the continuous resight portion of the observational model (Conner et al., 2015). We classified emigrating individuals or individuals that did not move between manual tracking events as dead resights (Barbour et al., 2013; Conner et al., 2015). we evaluated models with and without a grouping covariate for ϕ , to identify site differences in survival apparent

monthly survival. We fit models in the RMark package (Laake, 2013). We corrected for overdispersion ($\hat{c} > 1$) in model selection by using $QAICc$ (Anderson et al., 1994).

SCR Model Correction for Dispersal Estimates

We determined that $z \geq 0.5$ threshold was underestimating survival for individuals overwintering between receivers. Therefore, we established lower corrected z thresholds for each cohort's SCR output that produced the same overwinter survival as the average from Barker models. We used corrected SCR output to calculate mean and 95% intervals confidence limits for individual activity centers, $s(i,t)$, for each period within each cohort from posterior distributions. We also assessed correlation between σ , a proxy for period-specific movement, and water temperature and discharge (Osage USGS, gage, St. Thomas MO: 06926510, rkm 54; Gasconade, USGS gage, Rich Fountain, MO: 06934000, rkm 80) metrics that might explain temporal changes in dispersal behaviors. Final dispersal distances were compared among stocking sites as the rkm difference between stocking location and an individual's final detection. Movements outside of stocking tributaries were not considered in dispersal analyses. All plots were constructed in R package ggplot2 (Wickham, 2016).

Results

Telemetry performance

Receiver stations performed well detecting 305 passage events in the Osage River in 2018-2019 and 211 in the Gasconade River in 2019-2020. This was 92% and 88% of known station passages, respectively. The hourly-thinned receiver detection database

used in SCR analysis consisted of 29,107 detections of 91 individuals in 2018-2019 and 19,797 of 96 individuals in 2019-2020. Overall, the median number of hourly-thinned receiver detections per individual was 46 in 2018-2019 and 59.5 in 2019-2020.

Individuals were detected at a minimum of 1 and a maximum of 11 receivers in 2018-2019 and from 1 to 12 receivers in 2019-2020. We also collected 214 manual locations of 47 individuals in the Osage River during 2018-2019 and 143 locations of 45 individuals in the Gasconade River in 2019-2020.

Survival and Tributary Retention

SCR-estimated monthly survival rates from three of four river-year cohorts were similar, ranging from 0.60 to 0.74 (95% CI 0.48–0.82) (Table 3.1), which resulted in overwinter survival estimates ranging from 0.10 to 0.26 (95% CIs from 0.04–0.42). Survival estimates were higher for the 2018-2019 Osage River cohort with a mean monthly survival rate of 0.86 (95% CI 0.78–0.92) (Table 3.1) and an overwinter survival rate of 0.54 (95% CI 0.33–0.68). The differences in estimated overwinter survival between downstream and upstream stocking sites within a river were small, ranging from -0.17 to 0.04 in the Osage River, and -0.16 to 0.02 in the Gasconade River (Table 3.2).

Survival estimates from Barker models were similar to SCR estimates in the Osage 2018-2019 cohort (overwinter Barker mean only 0.05 < than SCR mean). However, in the Gasconade 2019-2020 cohort overwinter Barker survival mean estimates were three times as high as SCR means due to lower dispersal and less frequent receiver detections compared to the Osage 2018-2019 cohort. In contrast to SCR results, Barker models suggested no significant difference in overwinter survival between Osage River

2018-2019 (mean 0.47, 0.32–0.63 95% CL) and Gasconade 2018-2019 (mean 0.58, 95% CL 0.22–0.83) cohorts. Most dead tag resights incorporated into Barker models occurred during the first month post-stocking (Figure 3.3). Similar to SCR models, Barker AIC model rankings suggested no difference in survival between stocking sites between the 2018-2019 Osage and 2019-2020 Gasconade cohorts (Table 3.3).

Emigration into the mainstem Missouri River was rare. In 2018-2019 only 6% ($n = 6$) of stocked fish emigrated out of either tributary; including two from Osage River sites and four from Gasconade River sites. In 2019-2020, 18% ($n = 17$) emigrated; including 12 fish from Osage River sites and five from Gasconade River sites. Nearly five times as many fish emigrated to the Missouri River from the downstream than upstream stocking sites. Emigration events were most common at warmer temperatures and high discharges in the Osage River with 93% of emigration events in the Osage River occurring at discharges $> 500 \text{ m}^3/\text{sec}$ (Figure 3.4).

Spatial Distribution and Dispersal Rates and Directions

During both years at least one fish emigrated and traveled 40 km through the mainstem Missouri River to the other tributary. In 2018-2019, one fish stocked at Gasconade-13 dispersed to the Osage River, and in 2019-2020 two fish from Osage-16 dispersed to the Gasconade River. We also documented long-distance dispersal events within tributaries. In the Osage River 2018-2019 cohort, two sturgeon stocked at Osage-16 migrated to the uppermost receiver station near Bagnell Dam $> 112 \text{ km}$ upstream with one individual traveling $> 167 \text{ km}$ over the 4-month study.

Dispersal rates were highest in the first period in both years. Maximum σ_t averaged across both rivers was $\sigma_1 = 8.7$ in 2018-2019 and $\sigma_1 = 12.5$ in 2019-2020. Lowest dispersal rates occurred in later study periods with minimum σ_t averaged across rivers of $\sigma_8 = 1.4$ in 2018-2019 and 1.6 in 2019-2020. Biweekly average water temperature was strongly positively correlated with σ estimates when combined across all four cohorts (Pearson's partial correlation, $r = 0.79$) and weakly correlated with river flow (m^3/sec) ($r = 0.38$) (Figure 3.5).

Survival was likely underestimated by SCR models in three of four cohorts and was adjusted to match Barker models. Barker suggested adjusting SCR z survival probability thresholds to < 0.03 to improve dispersal inferences. With or without the Barker survival correction in place, average rkm of activity centers of apparent alive fish from each stocking site converged over time. By period nine, individuals from both stocking sites in tributaries mixed with 95% confidence intervals of average activity centers from upstream and downstream sites overlapping in 2 of 4 cohorts (Figure 3.6).

Dispersal directions and distances differed among sites. All fish stocked at Gasconade-87 immediately dispersed downstream (mean final rkm dispersal distance both years = -40.75 km). In contrast, at least initially, fish dispersed in both directions from the three other stocking sites (Figure 3.6). Fish stocked at Osage-76 gradually dispersed downstream over time (mean final dispersal both years combined = -33.06 km). In 2018-2019, fish stocked at Osage-16 initially migrated rapidly upstream before returning downstream (mean final dispersal = +31.84 km). Initial upstream dispersal from Osage-16 in 2019-2020 was much lower (mean final dispersal = -3.56 km) with many individuals remaining near the stocking site or emigrating into the Missouri River. In

cohorts where manual tracking occurred, absolute dispersal distance between stocking sites in the Osage River in 2018-2019 were similar. However, absolute dispersal distance was greater from stocking site Gasconade-87 than Gasconade-13 in the Gasconade 2019-2020 cohort (Figure 3.7). L&D#1 on the Osage did not appear to block Lake Sturgeon dispersal during our study. Among fish stocked at Gasconade-13, 37 of 48 or 77% were detected passing the next receiver that was 1.9 km upstream whereas a similar percentage of fish stocked at Osage-16, 38 of 48 or 79% were detected dispersing at least 3.2 km upstream and passing L&D#1.

Discussion

Stocking location had minimal effects on overwinter survival and location, but greater effects on dispersal distance and direction of stocked age-0 Lake Sturgeon in Missouri River tributaries. Survival estimates were similar across three of four cohorts analyzed with SCR models and between both cohorts analyzed with Barker models. Manual detections in the Barker models greatly improved the accuracy and precision of survival estimates when dispersal rates were low and allowed us to correct individual censoring in our SCR analysis of spatial distribution. Upstream-stocked fish largely dispersed downstream to occupy similar locations as downstream stocked fish by winter's end. High fidelity to stocking tributaries and convergence of individual activity centers within the tributaries indicate that nursery habitats in the lower portions of Missouri River tributaries may be selected by individuals regardless of release site.

Our age-0 survival estimates were the first we are aware of for Lake Sturgeon in the Missouri or Lower Mississippi River basins. Barker model estimates of 47% and 58%

were comparable to the > 40% overwinter age-0 survival estimates in Black Lake Michigan (Crossman et al., 2009), and much higher than those from northern Manitoba rivers that experience extreme cold (McDougall et al., 2014). Substantial mortality occurred in our study within the first month when tagged fish encountered a novel environment. Our expectation that survival would differ among cohorts and by stocking site was not definitively supported, suggesting that age-0 survival may be more spatially and temporally consistent in Missouri River tributaries. In contrast, other studies have documented high interannual variability in natural Lake Sturgeon recruitment (Caroffino et al., 2009; Nilo et al., 2011). Hatchery rearing may allow Lake Sturgeon to bypass environmental sources of mortality at early life stages, thereby reducing interannual recruitment variability and increasing uniformity in the age structure of the adult population.

The movement distances we observed of up to 167 km (mean dispersal from stocking site 3–41 km) in 4 months were among the greatest documented for age-0 Lake Sturgeon and were similar to annual movements of two-year old hatchery-reared juveniles (mean 22–34 km; Ganus et al., 2017). In other systems, age-0 Lake Sturgeon were sedentary, occupying core areas < 2 to 9 km (Barth et al., 2011; Benson et al., 2005; Caroffino et al., 2009). Although less than our study, maximum dispersal of stocked age-0 Lake Sturgeon in the French Broad River, Tennessee was 69.6 km (Huddleston, 2006) suggesting that overwinter movement may be greater in warmer southern rivers than in previously studied northern populations. Future confirmation of natural reproduction would allow biologists to study dispersal differences between wild and hatchery origin fish (Homola et al., 2010; Jordan et al., 2006). However, previous studies found similar

dispersal rates in wild and streamside-reared fish, suggesting that the movement patterns we observed may also apply to future wild cohorts (Mann et al., 2011).

Our results supported our expectation that dispersal distances would vary among stocking sites. The greatest dispersal from the Osage-16 site was in 2018-2019. Although age-0 Lake Sturgeon avoid swimming through areas of swift turbulent water (Barth et al., 2011; Peake et al., 1997), our results suggest that L&D#1 is not an impassible barrier for stocked Lake Sturgeon with passage being contingent on upstream Osage and downstream Missouri River discharges (Lallaman, 2012). Both study years were high water level years and thus our study may not represent typical fall passage conditions. Missouri River discharge (USGS gage, Booneville, MO: 06926510) exceeded the 75th percentile on every day during of the study. Osage River discharge exceeded the 75th percentile on 43% and 64% of days in 2018-2019 and 2019-2020 study periods, respectively. Large upstream dispersal distances in the 2018-2019 Osage River cohort overall resulted in more receiver detections and higher SCR survival estimates for this cohort. Greater movement in this cohort may be related to the correlation between movement rates and water temperatures as age-0 Lake Sturgeon reduce winter metabolic activity to conserve energy at low temperatures (Deslauriers et al., 2018). The 2018 cohort was stocked earlier when average temperatures in the Osage River were 6 °C warmer than in 2019.

Regardless of stocking site within rivers, age-0 sturgeon selected similar overwinter locations, especially from rkm 30 to 50 in the Osage and the lower 30 km of the Gasconade River. Dispersal distance was similarly associated with stocking site in age-0 Pallid Sturgeon (*Scaphirhynchus albus*) in the Upper Missouri River, which

exhibited greater downstream dispersal from the upstream site, but with fish from both sites mixing in river reaches near Fort Peck Reservoir (Oldenburg et al., 2011).

Overwintering locations in our study were centered near moderately deep pools or glides immediately upstream of areas impacted by Missouri River backwater. These low-velocity areas also contained more sand or fine gravel substrate conducive for juvenile sturgeon foraging (Benson et al., 2005; Peake, 1999), as opposed to areas near our upstream stocking sites that are dominated by coarse gravel and cobble and more flow variability. Previous research also found Lake Sturgeon dispersed downstream to deep, low-velocity overwintering locations in larger rivers or lakes as age-0 juveniles in the fall or as larvae during the spring/summer (Auer & Baker, 2002; Benson et al., 2005; Holtgren & Auer, 2004).

Additional gaps remain in our understanding of the mechanisms such as predation, energetic costs of movement, and habitat suitability that drive age-0 Lake Sturgeon vital rates. Piscivorous fish native to these rivers such as Channel Catfish (*Ictalurus punctatus*), Walleye (*Sander vitreus*), and black bass (*Micropterus spp.*) have consumed small juvenile sturgeon (usually < 160 mm TL) in lab trials (Baird et al., 2019; Gadowski & Parsley, 2005). However, benthic behavior, sharp scutes, and large size likely limited the predation risk in our study (Caroffino et al., 2010). Telemetry tags equipped with predation sensors may provide insurance against “predation bias” in survival estimates and confirm the assumption that small telemetry tags are not retained in digestive tracts of predators (Daniels et al., 2019). The effects of differential dispersal rates on growth or other fitness-related attributes remain unclear and could be investigated through longer duration telemetry studies. The proclivity of fish in our study

to disperse to distinct overwintering nursery habitats regardless of stocking sites underscores the importance of selecting stocking sites with proximal nursery habitats. Similarly, site habitat condition was a better predictor of reintroduction outcome than stocking variables (i.e., quantity, frequency, or individual size) (Cochran-Biederman, Wyman, French, & Loppnow, 2014). Future work should seek to identify habitat preferences for juvenile sturgeon in these rivers.

In conclusion, we estimate that ~53% of stocked age-0 Lake Sturgeon may survive their first winter and contribute to ongoing recovery of Lake Sturgeon in the Missouri River basin. Previous versions of Missouri's recovery plan recommended a cumulative stocking goal of 12.5 fish per acre, but this target was deemed unrealistic given Missouri's numerous large rivers and hatchery production rates (Moore, 2021). The combination of survival and dispersal estimates could produce juvenile density estimates in nursery habitats to establish more attainable stocking goals in Missouri and other southern states. High overwinter fidelity could promote natal philopatry in these streams and stocking efforts in other tributaries with adequate habitat may be important to restoring the species throughout the basin (DeHaan et al., 2006). Stocking at upstream sites during periods of lower flow may reduce emigration rates. Alternatively, Lake Sturgeon appear to seek out lower reaches of tributaries, thus, natural resource entities may consider stocking these environments. Agencies may also consider stocking upstream of semi-permeable barriers (e.g., L&D#1) during low water levels that would prevent access to upstream suitable nursery habitats.

References

- Anderson, D. R., Burnham, K. P., & White, G. C. (1994). AIC model selection in overdispersed capture-recapture data. *Ecology*, *75*, 1780-1793.
- Auer, N. A., & Baker, E. A. (2002). Duration and drift of larval Lake Sturgeon in the Sturgeon River, Michigan. *Journal of Applied Ichthyology*, *18*, 557-564. doi:10.1046/j.1439-0426.2002.00393.x
- Baird, S. E., Steel, A. E., Choquerell, D. E., Poletto, J. B., Follenfant, R., & Fangue, N. A. (2019). Experimental assessment of predation risk for juvenile Green Sturgeon, *Acipenser medirostris*, by two predatory fishes. *Journal of Applied Ichthyology*, *36*, 14-24. doi:10.1111/jai.13990
- Barbour, A. B., Ponciano, J. M., & Lorenzen, K. (2013). Apparent survival estimation from continuous mark-recapture/resighting data. *Methods in Ecology and Evolution*, *4*(9), 846-853. doi:10.1111/2041-210X.12059
- Barker, R. J. (1997). Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics*, *53*(2), 666-677.
- Barth, C. C., Anderson, G. W., Henderson, L. M., & Peake, S. J. (2011). Home range size & seasonal movement of juvenile Lake Sturgeon in a large river in the Hudson Bay Drainage Basin. *Transactions of the American Fisheries Society*, *140*, 1629-1641. doi:10.1080/00028487.2011.641881
- Benson, A. C., Sutton, T. M., Elliot, R. F., & Meronek, T. G. (2005). Seasonal movement patterns and habitat preferences of Age-0 Lake Sturgeon in the Lower Peshtigo River, Wisconsin. *Transactions of the American Fisheries Society*, *134*(5), 1400-1409. doi:10.1577/T04-179.1

- Bezold, J., & Peterson, D. L. (2008). Assessment of Lake Sturgeon reintroduction in the Coosa River System, Georgia-Alabama. *American Fisheries Society Symposium*, 62, 1-16.
- Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M. Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoetihne, S., Bagueette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier, C. M., Palmer, S. C. F., Turlure, C., & Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, 87, 290-312. doi:10.1111/j.1469-185X.2011.00201.x
- Bronte, C. R., Holey, M. E., Madenjian, C. P., Jonas, J. L., Claramunt, R. M., McKee, P. C., Toneys, M. L., Ebener, M. P., Breidert, B., Fleischer, G. W., Hess, R., Martell, A. W., & Olsen, E. J. (2007). Relative abundance, site fidelity, and survival of adult Lake Trout in Lake Michigan from 1999 to 2001: implications for future restoration strategies. *North American Journal of Fisheries Management*, 27(1), 137-155. doi:10.1577/M05-214.2
- Bruch, R. M., Haxton, T. J., Koenigs, R. Welsh, A., & Kerr, S. J. (2016). Status of Lake Sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. *Journal of Applied Ichthyology*, 32, 162-190. doi:10.1111/jai.13240
- Caroffino, D. C., Sutton, T. M., & Lindberg, M. S. (2009). Abundance and movement patterns of age-0 juvenile Lake Sturgeon in the Peshtigo River, Wisconsin. *Environmental Biology of Fishes*, 86, 411-422. doi:10.1007/s10641-009-9540-1

- Caroffino, D. C., Sutton, T. M., Elliott, R. F., & Donofrio, M. C. (2010). Predation on early life stages of Lake Sturgeon in the Peshtigo River, Wisconsin. *Transactions of the American Fisheries Society*, *139*, 1846-1856. doi:10.1577/T09-227.1
- Cochran-Biederman, J. L., Wyman, K. E., French, W. E., & Loppnow, G. L. (2015). Identifying correlates of success and failure of native freshwater fish reintroductions. *Conservation Biology*, *29*(1), 175-186. doi.org/10.1111/cobi.12374
- Collier, W. R., Bettoli, P. W., & Scholten, G. D. (2011). Dispersal and dam passage of sonic-tagged juvenile Lake Sturgeon in the Upper Tennessee River. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, *65*, 143-147.
- Conner, M. M., Bennett, S. N., Saunders, W. C., & Bouwes, N. (2015). Comparison of tributary survival estimates of Steelhead using Cormack-Jolly-Seber and Barker Models; Implications for sampling efforts and designs. *Transactions of the American Fisheries Society*, *144*(1), 34-47. doi:10.1080/00028487.2014.963254
- Crossman, J. A., Forsythe, P. S., Baker, E. A., & Scribner, K. T. (2009). Overwinter survival of stocked age-0 Lake Sturgeon. *Journal of Applied Ichthyology*, *25*, 516-521. doi:10.1111/j.1439-0426.2009.01310.x
- Daniels, J., Sutton, S., Webber, D., & Carr, J. (2019). Extent of predation bias present in migration survival and timing of Atlantic Salmon smolt (*Salmo salar*) as suggested by a novel acoustic tag. *Animal Biotelemetry*, *7*(16), 1-11. doi:/10.1186/s40317-019-0178-2

- DeHaan, P. W., Libants, S. V., Elliott, R. F., & Scribner, K. T. (2006). Genetic population structure of remnant Lake Sturgeon populations in the upper Great Lakes basin. *Transactions of the American Fisheries Society*, 135(6), 1478-1492. doi: 10.1577/T05-213.1
- DeInet, S., Scott-Gatty, K., Rotton, H., Twardek, W. M., Marconi, V., McRae, L., Baumgartner, L. J., Brink, K., Claussen, J. E., Cooke, S. J., Darwall, W., Eriksson, B. K., Garcia de Leaniz, C., Hogan, Z., Royte, J., Silva, L., G. M., Thieme, M. L., Tickner, D., Waldman, J., Wanningsen, H., Weyl, O. L. F., & Berkhuisen, A. (2020). The Living Planet Index (LPI) for migratory freshwater fish - Technical Report. World Fish Migration Foundation, The Netherlands.
- Deslauriers, D., Yoon, G. R., Earhart, M. L., Long, C., Klassen, C. N., & Anderson, W. G. (2018). Over-wintering physiology of age-0 Lake Sturgeon (*Acipenser fulvescens*) and its implications for conservation stocking programs. *Environmental Biology of Fishes*, 101, 623-637. doi:10.1007/s10641-018-0724-4
- Fink, M. (2018). Petition to List U.S. Populations of Lake Sturgeon (*Acipenser fulvescens*) as endangered or threatened under the Endangered Species Act. Center for Biological Diversity. Available: <https://www.biologicaldiversity.org/species/fish/pdfs/Lake-Sturgeon-petition-5-14-18.pdf>
- Gadomski, D. M., & Parsley, M. J. (2005). Laboratory studies on the vulnerability of young White Sturgeon to predation. *North American Journal of Fisheries Management*, 25, 667-674. doi:/10.1577/M03-220.1

- Ganus, J. E., Mullen, D. M., Miller, B. T., & Cobb, V. A. (2017). Quantification of emigration and habitat use inform stocking rates of Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in the Cumberland River, Tennessee, USA. *Journal of Applied Ichthyology*, *34*, 331-340. doi:10.1111/jai.13568
- Gardner, B., Reppucci, J., Lucherini, M., & Royle, J. A. (2010). Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology*, *90*(4), 1106-1115. doi:10.1890/09-0804.1
- Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2004). Bayesian data analysis, second edition. CRC/Chapman and Hall, Boca Raton, Florida, USA.
- Hightower, J. E., Jackson, J. R., & Pollock, K. H. (2001). Use of telemetry methods to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society*, *130*(4), 557-567. doi:10.1577/1548-8659(2001)130<0557:UOTMTE>2.0.CO;2
- Holtgren, J. M., & Auer, N. A. (2004). Movement and habitat of juvenile Lake Sturgeon (*Acipenser fulvescens*) in the Sturgeon River/ Portage Lake System, Michigan. *Journal of Freshwater Ecology*, *19*(3), 419-432. doi:10.1080/02705060.2004.9664915
- Homola, J. J., Scribner, K. T., Baker, E. A., & Auer, N. A. (2010). Genetic assessment of straying rates of wild and hatchery reared Lake Sturgeon (*Acipenser fulvescens*) in Lake Superior tributaries. *Journal of Great Lakes Research*, *36*(4), 798-802. doi:10.1016/j.jglr.2010.08.011
- Huddleston, M. D. (2006). *Dispersal, persistence, and areas of core use of reintroduced juvenile Lake Sturgeon in the Upper Tennessee River System*. [Master's thesis,

University of Tennessee, Knoxville]. Retrieved from
https://trace.tennessee.edu/utk_gradthes/3604

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T.,
Harcourt, R. G., Holland K. N., Iverson, S. J., Kocik, J. F., Mills Flemming, J. E.,
& Whoriskey, F. G. (2015). Aquatic animal telemetry: a panoramic window into
the underwater world. *Science*, *348*(6240). doi:1255642-1–1255642-10.

10.1126/science.1255642

Jacobson, R. B., & Galat, D. L. (2006). Flow and form in rehabilitation of large-river
ecosystems: An example from the Lower Missouri River. *Geomorphology*, *77*,
249-269. doi:10.1016/j.geomorph.2006.01.014

Jordan, G. R., Klumb, R. A., Wanner, G. A., & Stancill, W. J. (2006). Poststocking
movements and habitat use of hatchery-reared juvenile Pallid Sturgeon in the
Missouri River below Fort Randall Dam, South Dakota and Nebraska.

Transactions of the American Fisheries Society, *135*(6), 1499-1511.

doi:10.1577/T05-201.1

Kellner, K. (2015). jagsUI: a wrapper around rjags to streamline JAGS analyses. *R
package version, 1*(1).

Laake, J. L. (2013). RMark: An R Interface for analysis of capture-recapture data with
MARK.

Lallaman, J. (2012). *Factors affecting paddlefish reproductive success in the lower
Osage River* [Doctoral dissertation, University of Missouri, Columbia]. Retrieved
from

<https://mospace.umsystem.edu/xmlui/bitstream/handle/10355/33041/research.pdf?sequence=2>

- Lees, K. J., MacNeil, M. A., Hedges, K. J. & Hussey, N. E. (2021). Estimating demographic parameters for fisheries management using acoustic telemetry. *Reviews in Fish Biology and Fisheries*, 31, 25-51. doi:10.1007/s11160-020-09626-8
- Lindén, A. & Mäntyniemi, S. (2011). Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology*, 92(7), 1414-1421. doi:10.1890/10-1831.1
- Mann, K. A., Holtgren, J. M., Auer, N. A., & Ogren, S. A. (2011). Comparing size, movement and habitat selection of wild and streamside-reared Lake Sturgeon. *North American Journal of Fisheries Management*, 31(2), 305-314. doi:10.1080/02755947.2011.576199
- McCabe, M. M., Chiotti, J. A., Boase, J. C., Fisk, A. T., & Pitcher, T. E. (2019). Assessing acoustic tagging effects on survival, growth and swimming ability of juvenile Lake Sturgeon. *North American Journal of Fisheries Management*, 39, 574-581. doi: 10.1002/nafm.10294
- McDougall, C. A., Pisak, D. J., Barth, C. C., Blanchard, M. A., MacDonell, D. S., & Macdonald, D. (2014). Relative recruitment success of stocked age-1 vs. age-0 Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in the Nelson River, northern Canada. *Journal of Applied Ichthyology*, 30, 1451-1460. doi:10.1111/jai.12555

- Moore, T. M. (2021). *A continuing plan for recovery and management of Lake Sturgeon in Missouri*. Missouri Department of Conservation Management Plan Unpublished Draft.
- Nilo, P., Dumont, P., & Fortin, R. (1997). Climatic and hydrological determinants of year- class strength of St. Lawrence River Lake Sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 774-780.
- Oldenburg, E. W., Guy, C. S., Cureton, E. S., Webb, M. A. H., & Gardner, W. M. (2011). Effects of acclimation on poststocking dispersal and physiological condition of age-1 Pallid Sturgeon. *Journal of Applied Ichthyology*, *27*, 436-443.
- Peake, S., Beamish, F. W. H., McKinley, R. S., Scruton, D. A., & Katopodis, C. (1997). Relating swimming performance of Lake Sturgeon, *Acipenser fulvescens*, to fishway design. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 1361-1366.
- Peake, S. (1999). Substrate preferences of juvenile hatchery-reared Lake Sturgeon, *Acipenser fulvescens*. *Environmental Biology of Fishes*, *56*, 367-374.
- Phelps, Q. E., Hupfeld, R. N., & Whitley, G. N. (2017). Lake Sturgeon (*Acipenser fulvescens*) and Shovelnose Sturgeon (*Scaphirhynchus platorynchus*) environmental life history revealed using pectoral fin-ray microchemistry: implications for interjurisdictional conservation through fishery closure zones. *Journal of Fish Biology*, *90*, 626-639. doi:10.1111/jfb.13242
- Pherigo, E. K. (2019). *Seasonal fish community and reproductive biology of fishes in two tributaries of the lower Missouri River, USA*. [Master's thesis, University of

- Missouri, Columbia]. Retrieved from
<https://mospace.umsystem.edu/xmlui/handle/10355/70159>.
- Pollock, K. H., Nichols, J. D., Brownie, C., & Hines, J. E. (1990). Statistical inference for capture–recapture experiments. *Wildlife Monographs*, *107*, 1-97.
- Raabe, J. K., Gardner, B., & Hightower, J. E. (2014). A spatial capture-recapture model to estimate fish survival and location from linear continuous monitoring arrays. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 120-130.
doi:10.1139/cjfas-2013-0198
- Roni, P., Bennett, T., Holland, R., Pess, G., Hanson, K., Moses, R., ... & Walter, J. (2012). Factors affecting migration timing, growth, and survival of juvenile Coho Salmon in two coastal Washington watersheds. *Transactions of the American Fisheries Society*, *141*(4), 890-906. doi: 10.1080/00028487.2012.675895
- Royle, J. A., & Young, K. V. (2008). A hierarchical model for spatial capture–recapture data. *Ecology*, *89*(8), 2281-2289. doi:10.1890/07-0601.1. PMID: 18724738
- Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation biology*, *21*(2), 303-312.
- Schueller, A. M., & Hayes, D. B. (2010). Sensitivity of Lake Sturgeon population dynamics to demographic parameters. *Transactions of the American Fisheries Society*, *139*, 521-534. doi:10.1577/T09-035.1
- Smith, T. I. J., McCord, J. W., Collins, M. R., & Post, W. C. (2002). Occurrence of stocked Shortnose Sturgeon *Acipenser brevirostrum* in non-target rivers. *Journal of Applied Ichthyology*, *18*, 470-474.

- Snobl, Z. R., Koenigs, R. P., Bruch, R. M., & Binkowski, F. P. (2015). Do tags exceeding 2% of total body weight impair Lake Sturgeon Movement? *North American Journal of Fisheries Management*, 35(5), 880-884.
doi:10.1080/02755947.2015.1069425
- U.S. Environmental Protection Agency. (2018). *Level III Ecoregions of the Continental United States* (Corvallis, Oregon: U.S. EPA—National Health and Environmental Effects Research Laboratory). <https://epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states>.
- Ward, R. D. (2006). The importance of identifying spatial population structure in restocking and stock enhancement programs. *Fisheries Research*, 80(1), 9-18.
doi:10.1577/T07-013.1
- Whoriskey, K., Martins, E. G., Auger-Méthé M., Gutkowsky, L. F., Lennox, R. J., Cooke, S. J., Power, M., & Flemming, J. M. (2019). Current and emerging statistical techniques for aquatic telemetry data: A guide to analyzing spatially discrete animal detections. *Methods in Ecology and Evolution*, 10, 935-948.
doi:10.1111/2041-210X.13188
- Wildhaber, M. L., Albers, J. L., Green, N. S., & Moran, E. H. (2017). A fully-stochasticized, age-structured population model for population viability analysis of fish: Lower Missouri River endangered Pallid Sturgeon example. *Ecological Modelling*, 359, 434-448. doi:10.1016/j.ecolmodel.2015.07.019
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Tables

Table 3.1. Parameter estimates from Spatial Capture Recapture (SCR) models fit using only receiver detections in all four river-year cohorts and from top Barker resight models that also incorporate manual detection data for 2018-2019 Osage River and 2019-2020 Gasconade River cohorts. Estimates of survival parameter, ϕ , are scaled to the monthly time period. τ is a correlation parameter linking activity center estimates within individuals across periods, r is the probability that an individual that dies between periods is found dead, R is the probability that an individual that survives between periods is found alive.

River	Model	Parameter	2018-2019			2019-2020		
			Mean	2.5%	97.5%	Mean	2.5%	97.5%
Gasconade R.	SCR	ϕ (monthly)	0.60	0.48	0.73	0.69	0.59	0.79
		τ	14.57	12.27	17.36	20.00	17.12	23.34
	Barker	ϕ (monthly)				0.89	0.71	0.96
		r				0.83	0.11	0.99
		R				0.96	0.76	0.99
	Osage R.	SCR	ϕ (monthly)	0.86	0.78	0.92	0.74	0.65
τ			17.88	15.06	19.37	14.14	12.39	15.92
Barker		ϕ (monthly)	0.84	0.68	0.92			
		r	0.62	0.23	0.90			
		R	0.91	0.75	0.97			

Table 3.2. Stocking site-specific survival (18-week) estimates for age-0 Lake Sturgeon in the Osage and Gasconade rivers based only on spatial capture recapture (SCR) models. Overwinter survival was calculated as the number of stocked individuals divided by the number of individuals with final period average z parameter estimates > 0.5 . The downstream sites were Gasconade-13 and Osage-16. The upstream sites were Gasconade-87 and Osage-76.

River/Year	Downstream Site	Upstream Site
Gasconade 2018-2019	0.12	0.10
Gasconade 2019-2020	0.09	0.25
Osage 2018-2019	0.52	0.48
Osage 2019-2020	0.08	0.25

Table 3.3 Barker model ranking for age-0 Lake Sturgeon survival in the Osage 2018-2019 and Gasconade 2019-2020 cohorts. Models included detections from passive receivers and monthly manual tracking combined into binary resight bins. We ranked a null survival model against models allowing ϕ to vary by stocking location (Phi(group)), or four approximately 1-month study periods (Phi(time)), or both (Phi(group+time)). K = number of model parameters, $QAIC_C$ = AIC corrected for overdispersion and small sample size, weight = AIC-derived model support.

Model	K	QAICc	$\Delta QAICc$	Weight
Osage River 2018-2019				
Phi(.)	4	73.72	0	0.70
Phi(group)	5	75.93	2.20	0.23
Phi(time)	7	78.96	5.23	0.05
Phi(group+time)	8	81.31	7.58	0.02
Gasconade River 2019-2020				
Phi(.)	4	46.99	0	0.53
Phi(group)	5	48.37	1.38	0.31
Phi(time)	7	49.79	2.80	0.11
Phi(group+time)	8	51.14	4.14	0.06

Figures

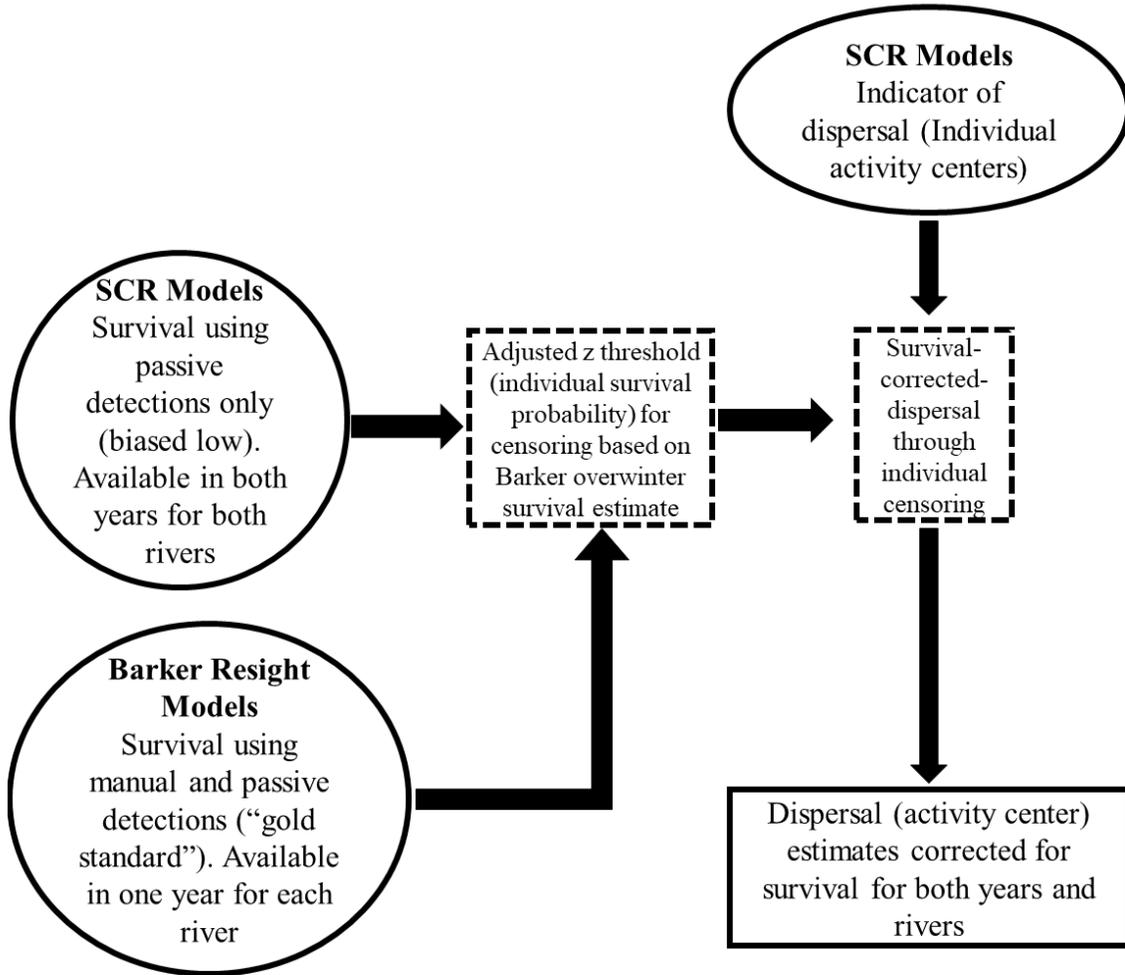


Figure 3.1. Conceptual diagram of analysis multi-method workflow that illustrates how Barker models were used to inform individual censoring for SCR dispersal analysis.

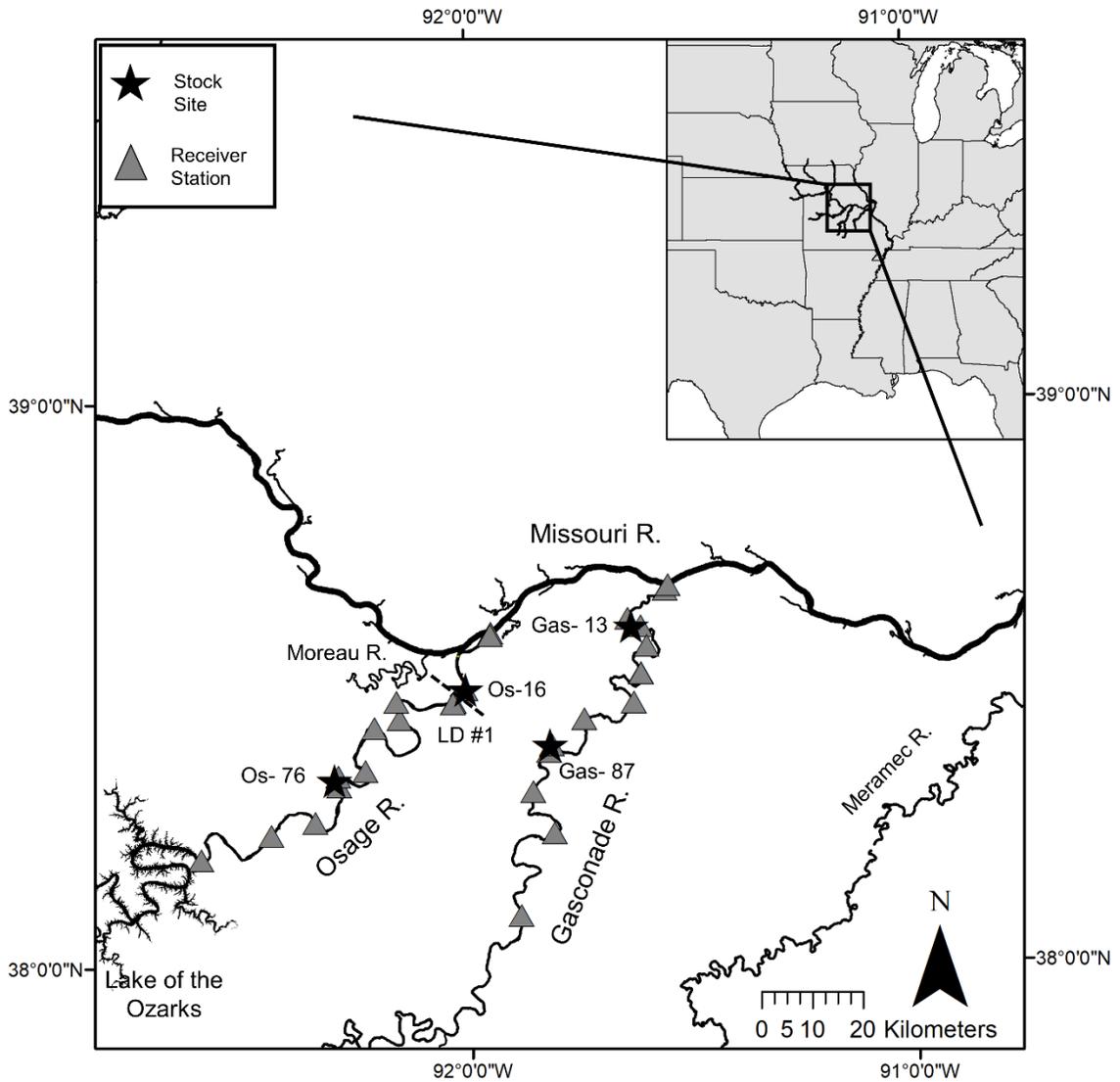


Figure 3.2. Map of our study area. Acoustic receiver stations are represented by gray triangles while stocking sites are represented by black stars and labeled with site names used in text. Lock and Dam #1 (L&D#1), is marked on the Osage River with a dashed line. Manual tracking occurred in occupied areas from uppermost receiver to confluence with Missouri River in Osage River October 2018–February 2019, and the Gasconade River October 2019–February 2020.

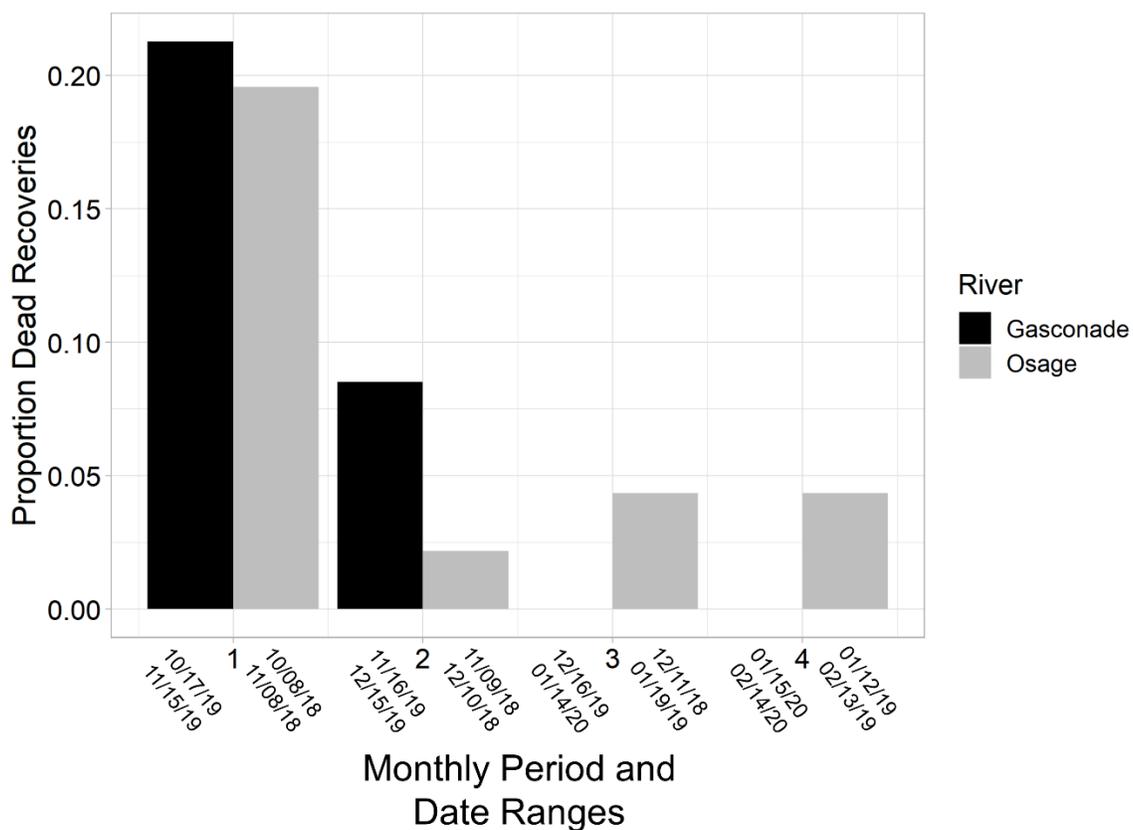


Figure 3.3 Histogram of dead tag recoveries of Lake Sturgeon for the Gasconade 2019-2020 and Osage 2018-2019 datasets inferred from receiver and manual detections. Time periods are approximately one month long (differ based on stocking date) and were defined based by dividing the period during which the transmitters were active into four equal intervals.

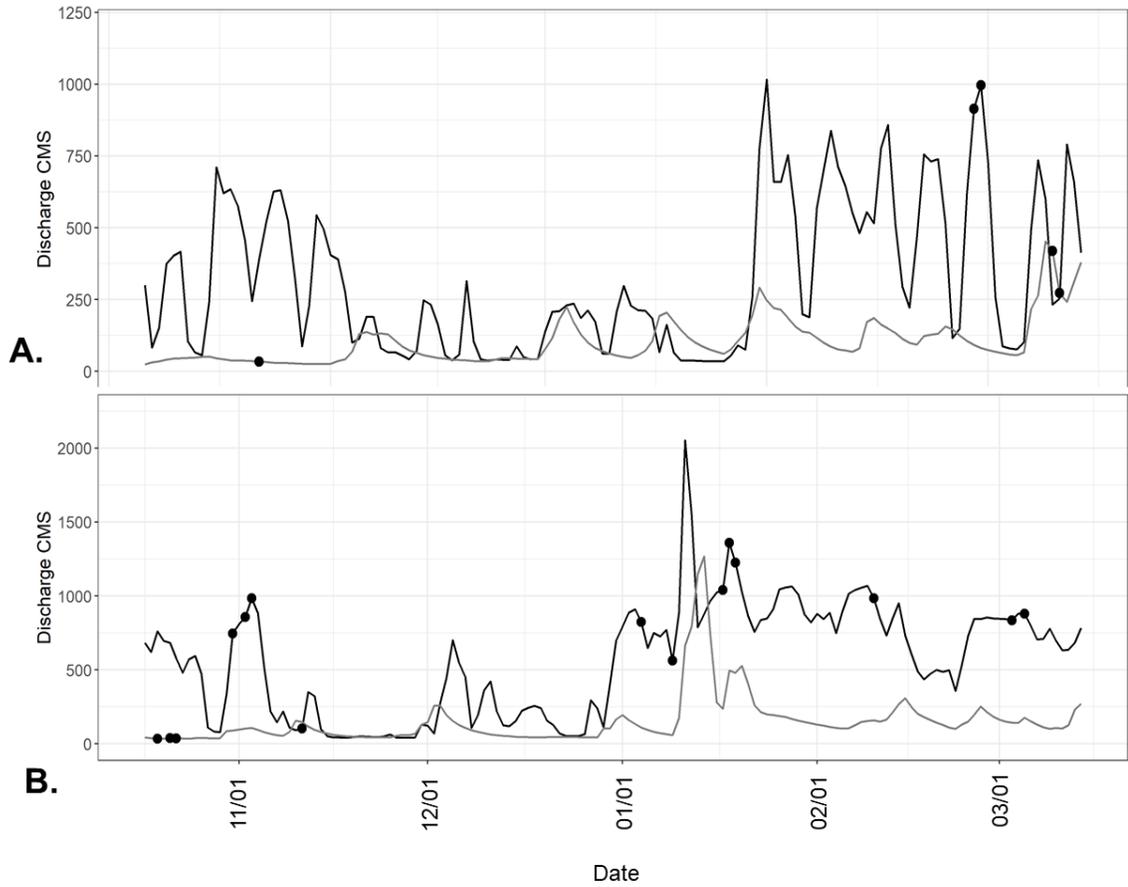


Figure 3.4. Discharge conditions (CMS= m³/second) during the 2018-2019 in panel A and 2019-2020 in panel B. Osage River discharge is plotted with a black line and Gasconade with gray line. Dates of emigration events are marked with points along each river's discharge line.

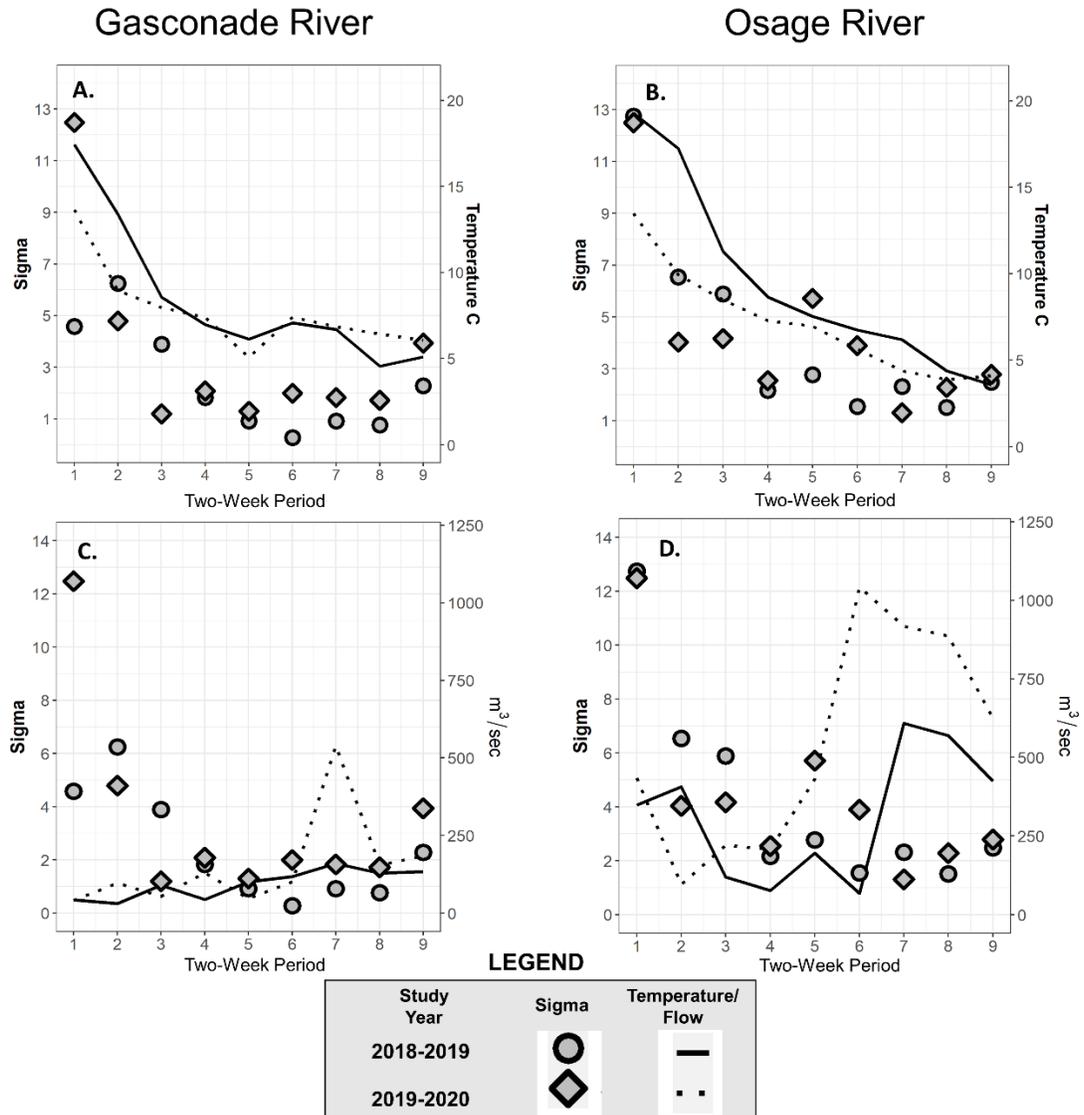


Figure 3.5. Plot of Lake Sturgeon cohort-specific σ (sigma), indicative of individual movement around activity centers during each two-week period. River-year cohorts are designated by point style and correspond to sigma values on the primary (left) y-axis. The secondary y-axis (right) illustrates the average flow or temperature values for each two-week period of the study. Panel A illustrates the relationship between σ , temperature, and period in the Gasconade River in both study years. Panel B illustrates the relationship between σ , temperature, and period in the Osage River in both study years. Panel C illustrates the relationship between σ , discharge, and period in the Gasconade River in both study years. Panel D illustrates the relationship between σ , discharge, and period in the Osage River in both study years. Study date ranges in the 2018-2019 study year were 10/08/18 to 02/10/19 in both rivers. Study date ranges in the 2019-2020 study year were 10/17/19 to 02/20/20 in the Gasconade River and 10/28/19 to 03/02/20 in the Osage River. Period 9 for Gasconade River in 2019-2020 was only 8 days long due to battery expiration as a result of longer time retained in hatchery post-surgery.

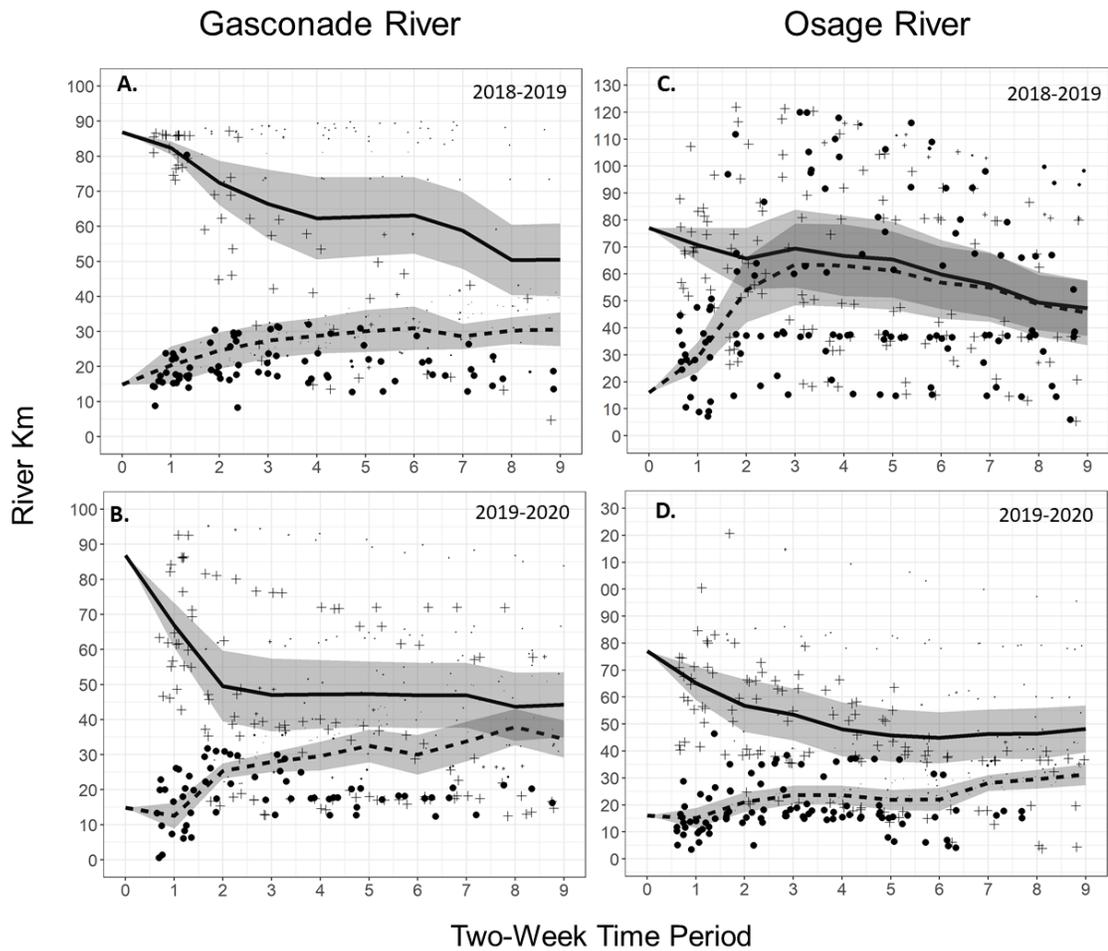


Figure 3.6. Estimates of age-0 Lake Sturgeon activity centers for 9, two-week periods in each study year of the Gasconade and Osage rivers. Jittered points display individual S (activity center) estimates from SCR models within each period for fish estimated alive at each cohort's Barker model corrected z threshold. Individuals from downstream stocking sites appear as circles and upstream stocking sites as plus signs. Point size is proportional to z probability. Panel A depicts 2018-2019 Gasconade River data, panel B the 2019-2020 Gasconade River data, panel C the 2018-2019 Osage River data, and panel D the 2019-2020 Osage River data. Solid lines are the average of individual S estimates for the upstream stocking site and dashed lines the mean individual S estimate for downstream stocking site. Associated 95% confidence intervals from Z-distribution are shaded in gray. Study date ranges in the 2018-2019 study year were 10/08/18 to 02/10/19 in both rivers. Study date ranges in the 2019-2020 study year were 10/17/19 to 02/20/20 in the Gasconade River and 10/28/19 to 03/02/20 in the Osage River. Note that period nine for Gasconade River 2019-2020 was only eight days long due to battery expiration as a result of longer recovery time in hatchery post-surgery.

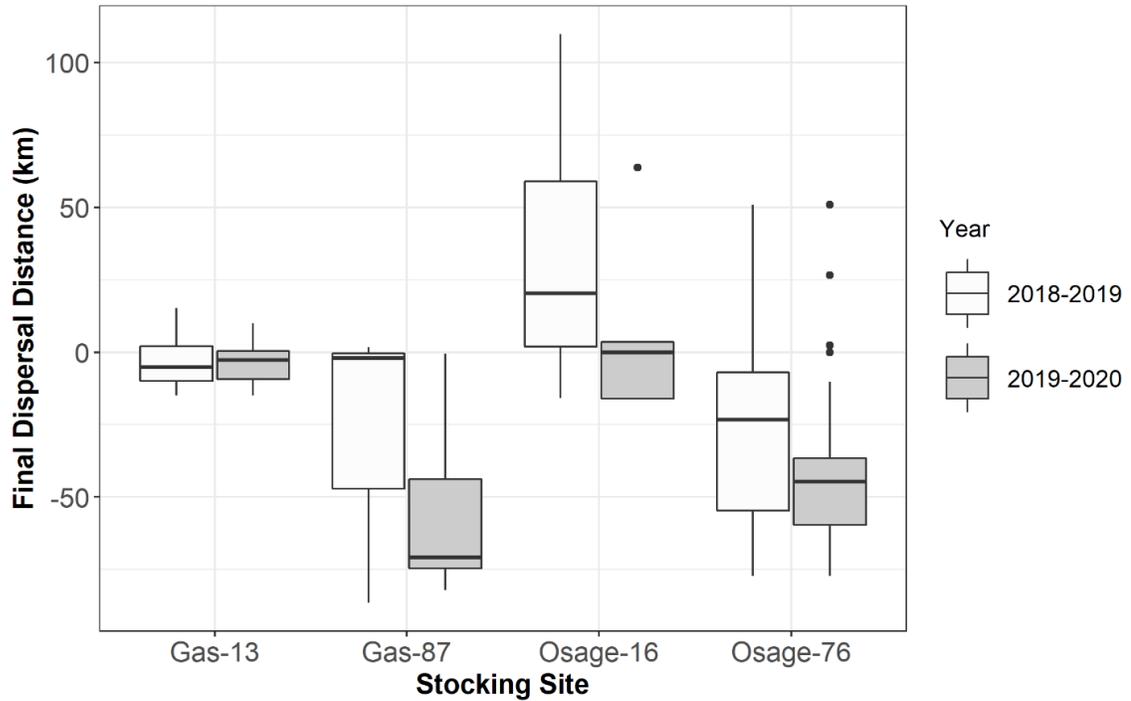
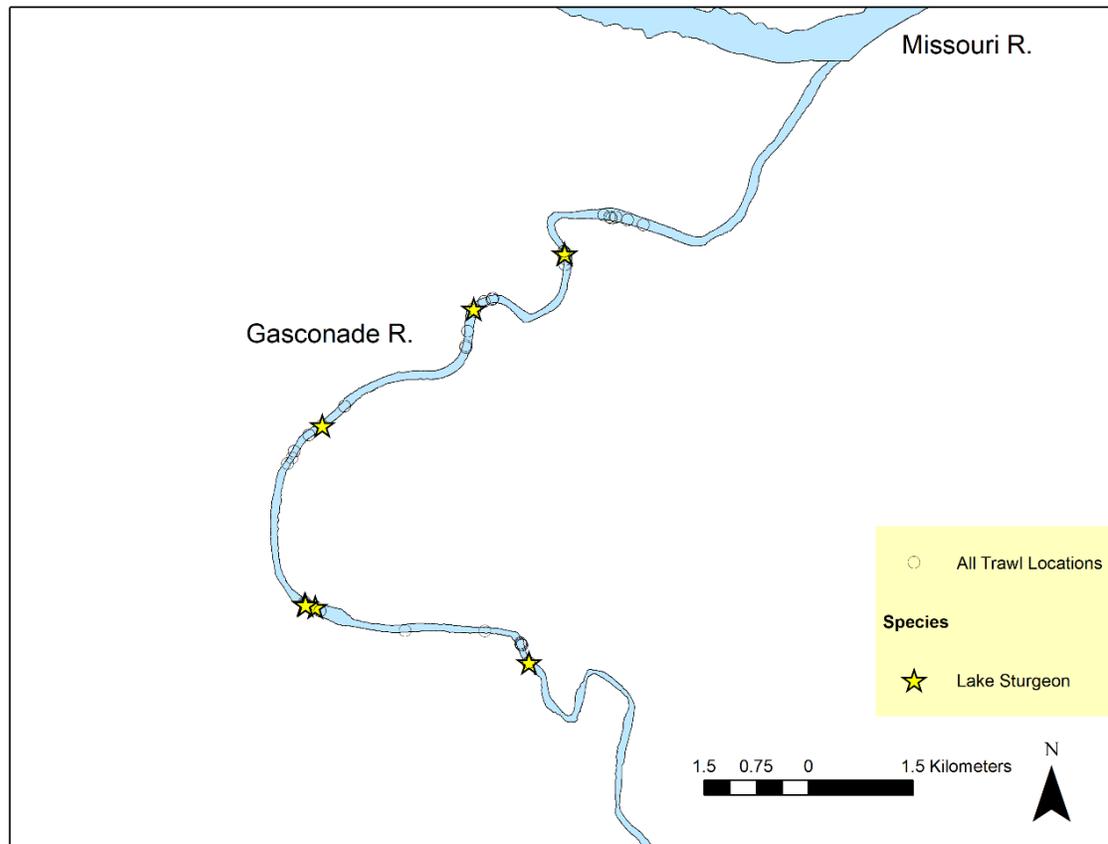


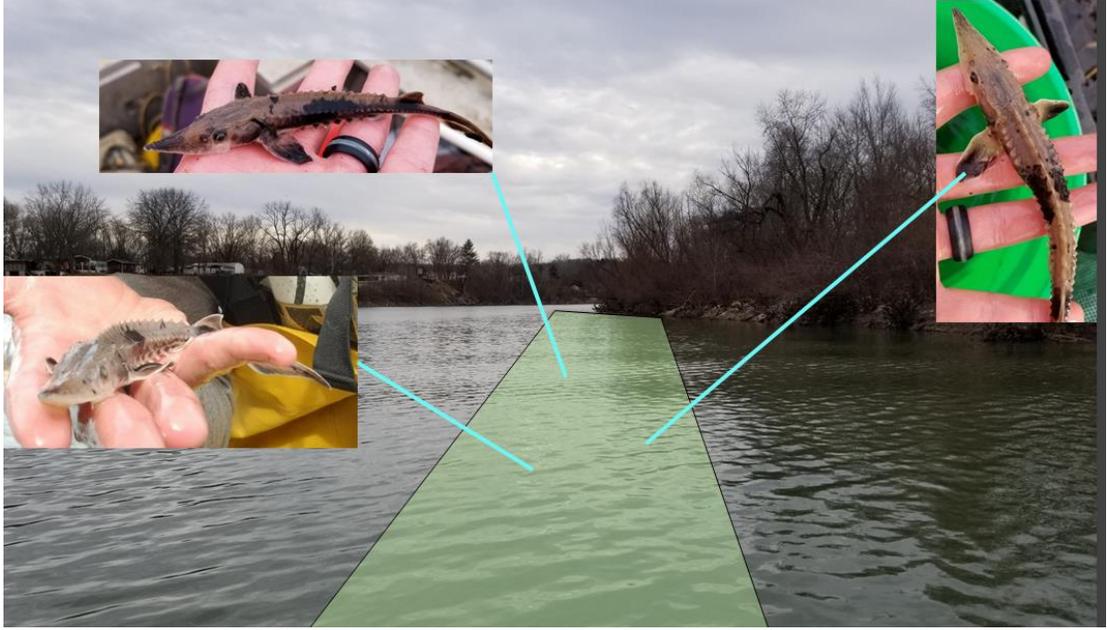
Figure 3.7. Box and whisker plots of Lake Sturgeon final dispersal distances for the Gasconade (GAS) and Osage river-year cohort defined as the distance from the stocking site to the final detection of tagged individuals. Boxes display the lower quartile, median, and upper quartile for each group. The end of the whiskers are quartiles ± 1.5 times the interquartile range, with dots being outliers. Positive values represent upstream dispersal and negative values downstream dispersal.

Appendices

Appendix 3.1. Map of benthic trawling locations in the lower Gasconade River in February 2019. Stars indicate locations where stocked age-0 or age-1 juvenile Lake Sturgeon were captured.



Appendix 3.2. Photograph of age-0 Lake Sturgeon habitat along an inside bend current seam where three juvenile Lake Sturgeon were captured in a benthic trawl in the Gasconade River in 2019.



CHAPTER 4- HABITAT SELECTION IN A SOUTHERN LAKE STURGEON POPULATION: IMPLICATIONS OF TEMPORAL, SPATIAL, AND ONTOGENETIC VARIATION FOR RESTORATION

Abstract

Successful species reintroduction requires restoration of receiving habitats to support growth, survival, and reproduction to reverse initial causes of decline. Relatively little is known about whether present habitat conditions can support all life stages of reintroduced southern Lake Sturgeon populations that were extirpated by the mid-1900s due to overharvest and habitat degradation. Therefore, we designed a study to assess annual adult and subadult and overwinter age-0 Lake Sturgeon habitat selection and suitability to identify potential population restoration bottlenecks in two Missouri River tributaries. Spring habitat selection models were unable to define spawning habitat characteristics, but application of criteria from other studies suggest that substrate and depths for spawning are suitable in both rivers. In other seasons adult and subadult Lake Sturgeon exhibited strong selection for pools greater than 8 m deep which comprised less than 5% of our study streams. Habitat selection in age-0 Lake Sturgeon differed from adults with cross-river model validation showing that some general habitat patterns persisted regardless of habitat availability in each river, suggesting specialized habitat requirements in southern Lake Sturgeon that differ from previous studies further north. These results may be used to direct sampling for validation of reproduction and

restoration of not only spawning habitats, but age-0 and summer and winter refugia important to southern populations.

Implications for Practice

- We provide some of the first habitat selection data for Lake Sturgeon in southern rivers. We demonstrate a method for developing standardized HSMs to predict preferred habitats. This technique could be used to identify habitat limitations along the Lake Sturgeon's southern range boundary.
- Models identified ontogenetic and seasonal habitat selection differences and greater summer/winter specificity than in mid-latitude populations. This highlights the importance of maintaining habitat diversity and connectivity for southern Lake Sturgeon conservation.
- Tributary confluences provide diverse and productive habitats for age-0 and ASA refugia, although in the spring Lake Sturgeon likely relocate to upstream reaches with swifter flows and coarse spawning substrates.
- Hydrodynamic models of habitat conditions would improve our understanding of Lake Sturgeon response to flow regulation.

Introduction

Reintroductions of native fish species have increased in recent years, yet they may fail if the variability in the species' geographic (Huang & Frimpong 2016), seasonal (Edge et al. 2020), and ontogenetic (Miyazono et al. 2020) habitat requirements are not considered (Cochran-Biederman et al. 2014). Habitat specialization is particularly

important at species' range margins where environmental factors can approach niche limits (Holt 2003). Lake Sturgeon have a broad native range in the Mississippi River, Laurentian Great Lakes, and Hudson Bay watersheds. Overharvest and habitat degradation depleted populations during the early 1900s and pollution, dams, and habitat degradation remain persistent threats to recovery (Bruch et al. 2016). Yet our understanding of the geographic, temporal, and ontogenetic variability in Lake Sturgeon habitat requirements is incomplete, hindering population recoveries along the species' southern range boundary (Bezold & Peterson 2008; Walker & Alford 2016; Moore 2021).

Most information on Lake Sturgeon habitat use comes from mid-latitude populations (Moore et al. 2020). Lake Sturgeon require rocky lotic habitats for reproduction in the spring (Baril et al. 2018). In some mid-latitude studies adult and juvenile Lake Sturgeon were habitat generalists during non-spawning periods (Nilo et al. 2006; Bruch et al. 2016) foraging in areas of abundant benthic prey across a range of depths and substrate types (Hay-Chmielewski 1987; Rusak & Mosindy 1997). Therefore, reproductive habitats were identified as limiting in mid-latitude populations and habitat restoration was implemented to address these deficiencies (Daugherty et al. 2009).

Environmental conditions at the Lake Sturgeon's southern range margin likely approach its niche limit, posing additional challenges to conservation in other seasons. Lake Sturgeon were extirpated from large portions of the Mississippi River basin (Barnickol & Starrett 1951; Bezold & Peterson 2008). In response U.S. states such as Missouri, Tennessee, Georgia, and Kentucky have reintroduced hatchery-reared juveniles sourced from remnant mid-latitude populations (Peterson et al. 2007; Herrala 2015). The

low abundance of adult Lake Sturgeon in most southern populations that can take 20 years to reach maturity has been an obstacle to studying habitat selection (e.g., Huddleston 2006). Spatial transferability of generalist habitat associations is often poor (Huang & Frimpong 2016); therefore, available Lake Sturgeon habitat associations in the literature may not apply range-wide. For example, recent research near the northern range margin has identified potential winter habitat bottlenecks for juvenile and adult Lake Sturgeon that may not exist in mid-latitude populations (Thayer et al. 2017). Conversely, southern Lake Sturgeon may experience thermal stress at temperatures greater than 28°C, a threat expected to increase due to climate change (Lyons & Stewart 2014). Lake Sturgeon experience water temperatures in excess of 35°C in Georgia, and high temperatures correlate with reduced summer movements and low fall body condition (Bezold & Peterson 2008; Moore et al. 2020). Southern rivers are also heavily fragmented by hydropeaking dams, which impose additional habitat limitations (Bednarek & Hart 2005).

Missouri was the first “southern” state to initiate Lake Sturgeon recovery in 1984. The Missouri Department of Conservation (MDC) has stocked greater than 400,000 juveniles producing a population of adult Lake Sturgeon. Natural reproduction has not yet been documented in the Missouri River basin and hydrologic regulation, channelization, and warm temperatures are persistent threats. Adult and subadult Lake Sturgeon spend over 70% of the time primarily in short reaches of two Missouri River tributaries (Chapter 1) and most juveniles exhibit overwinter fidelity to stocking tributaries (Chapter 2). However, the habitat factors explaining these movement patterns have not been explored. Habitat limitations during key life history events such as

spawning, juvenile overwintering, foraging, or resting, may be conservation bottlenecks hindering recovery progress. As a result, Missouri's Lake Sturgeon Recovery Plan identified understanding Lake Sturgeon habitat requirements as a research priority (Moore 2021). This information can guide habitat restoration efforts such as hydrologic management (Bednarek & Hart 2005), barrier passage facilitation (McDougall et al. 2013), spawning site construction (Roseman et al. 2011) and ensure that stocking is conducted near suitable habitats.

Therefore, we established three research questions: 1) Do adult and subadult (hereafter ASA) Lake Sturgeon exhibit seasonal habitat selection that are spatially transferrable between rivers with differing habitat characteristics? 2) Does habitat selection differ between stocked age-0 and ASA Lake Sturgeon during the combined fall and winter period? 3) Does the availability of age-0 or ASA habitat differ in tributaries (Fig. 4.1)? We hypothesized ASA Lake Sturgeon would select swift flowing near-shore habitats with coarse substrates during the spring and deep low-velocity habitats during the rest of the year. Habitat data were only available for age-0 juveniles in the late fall/winter, but we expected them to select shallower depths, slower velocities, and finer substrates relative to ASAs. Finally, outside of the spring spawning season, we expected that unlike some mid-latitude populations, ASA Lake Sturgeon would exhibit similar habitat selection in both tributaries related to resting refugia at times of potential thermal stress (Heggenes et al. 2002; Thayer et al., 2017). We expected Lake Sturgeon to exhibit range-edge habitat specialization and therefore expected differences in preferred habitat availability in each river caused by size and degree of human alteration.

Methods

Study Area Description

The study area encompassed the lower Osage and Gasconade rivers which are two major tributaries to the Missouri River in the Ozark Physiographic Province in central Missouri (Fig. 4.2). Mature Lake Sturgeon have been documented in both tributaries but spawning has not. Substrate in each is gravel with a mixture of cobble and boulder along bluffs and silt and sand in depositional areas. The Osage River is an eighth-order stream with ~200 m average channel widths and the Gasconade River is a sixth-order stream with average channel widths of ~90 m. Water level fluctuations are greater in the Osage River due to hydropeaking at the upstream Bagnell Dam whereas Gasconade River has a relatively natural hydrologic and thermal regime. Water temperatures at U.S. Geological Survey gage stations ranged from 0.3 to 32.0°C in the Osage River and 0 to 33.2°C in the Gasconade River.

Telemetry Data Collection

We implanted Vemco V16-4H (Halifax, Nova Scotia, Canada) acoustic transmitters (1540-day battery life) in 97 adult and subadult Lake Sturgeon (mean 1,119 mm Fork Length [FL], range 737–1,510 mm FL), 63 in the Osage and 34 in the Gasconade river, during March 2015, March 2016, March–April of 2017, October–November 2017, February–March 2018, and March 2019 (Chapter 1). Sex or maturity was unavailable for 40% of individuals so they were combined under the ASA category in analyses. We also stocked 46 hatchery-reared age-0 Lake Sturgeon (at release mean 194 mm Total Length [TL], range 157–224 mm TL) with Vemco V8-4L acoustic

transmitters (141-day battery life) in the Osage River in October 2018 and 47 age-0 individuals in the Gasconade River in October 2019. Age-0s were divided evenly between two stocking sites in each river (Fig. 4.2). We attempted to manually locate all ASA or age-0 juvenile individuals occupying a tributary once a month using directional hydrophones and the ground-zero method from May 2017–May 2020 (Holland et al., 1992). We determined positional accuracy of V-16 transmitters was less than 30 m with high precision based on pre-study relocations of hidden tags and successive relocations of shed tags and locations were likely even more accurate for the lower-power V-8 transmitters. Tracking for age-0 habitat selection focused on the Osage River from October 2018–February 2019, and the Gasconade River from October 2019–February 2020.

Habitat Measurements

We measured habitat at used and three “available” points within 1 hour to form “choice sets” for discrete choice analysis (Cooper & Millspaugh 2001). Available ranges were the estimated seasonally variable area ASA individuals sample during a day (Harris et al. 2018). We calculated range-wide estimates of Lake Sturgeon average daily movement rates of 750 m March–May, 1000 m June–August, 500 m September–November, and 250 m December–February (Hay-Chmielewski 1987; Rusak & Mosindy 1997; Knights et al. 2002; Adams 2005; Snellen 2008; Shaw et al. 2013; Buszkiewicz et al. 2016; Thayer 2016). We calculated monthly average daily movement rates for our population to use in choice set selection after May 2018, although these values were similar to those from the literature review (Table 4.1). We randomly selected available

points within the bank-full channel because Lake Sturgeon seldomly used floodplain habitats.

We measured depth (m), average water column velocity (velocity m/s), distance to bank (m), presence of woody debris (LWD), substrate (presence or absence of sand/silt or cobble/boulder), and whether the point occurred in a secondary-channel unit (backwater or side channel). Depth (m) and velocity (m/s) were measured with an acoustic Doppler current profiler. Distance to bank (m) was the distance to the nearest dry land measured using an optical range finder. We used a Lowrance HDS side-scan sonar unit and a steel sounding weight to determine the dominant substrate class and presence of LWD (wood >1 m in length and >10 cm in diameter) within the 30 m surrounding a point. Substrate class approximations were based on Wentworth particle diameters: silt/sand (<0.06–2 mm), gravel (2 mm–64 mm), and cobble+ (>64 mm). Gravel comprised greater than 70% of the study area and therefore was less useful in differentiating selected and available habitats. Dissolved oxygen and temperature data were omitted due to low variability within choice sets.

For objective 3, we assembled continuous raster layers of depth, substrate, and macrohabitat unit types for areas of the tributaries used by Lake Sturgeon, including 131 km of the Osage and 36 km Gasconade River in ArcMap 10.6 (Environmental Systems Research Institute [ESRI], Redlands, CA, U.S.A.) (Fig. 4.2). We collected ~60 m wide Lowrance side-scan sonar images along parallel transects for the entire river channels at a frequency of 455 kHz during bank-full flows (GPS accuracy <3 m). Images were georectified using the SonarTrx software (Leraand Engineering; Honolulu, Hawaii). Patches of the three substrate classes were visually delineated and reviewed by a second

experienced reviewer. We validated substrate classifications in the field using a sounding weight at random points in both rivers (Appendix 4.1). Points that were within 1 boat length (5 m) of the correct substrate polygon were considered a correct classification that may be due boat positioning (Kaesler & Litts 2010). Depth measurements were recorded every two seconds along sonar tracks and high-bank lines from aerial imagery were set to 0 m depth. Sonar tracks collected on different days overlapped, allowing us to standardize depths to a single day when conditions were closest to the historical median daily flow. We used ordinary kriging methods with an exponential variogram model to interpolate bathymetry throughout the river channel that assumed stationarity across modeled space (Wu et al. 2019). Finally, the coverage of seven main-channel and four secondary-channel unit types were obtained for the Osage River only from a previous study (Lobb & Lueckenhoff 2013; Appendix 4.2). Although macrohabitat units became more homogenous at higher flows the general defining characteristics were preserved (i.e., riffles and runs swift and shallow, pools slow and deep).

Habitat Selection Analysis

We used multinomial logistic discrete choice modeling to investigate Lake Sturgeon habitat selection (e.g. Cooper & Millspaugh 1999). Discrete choice is uniquely suited for temporally dynamic habitats in regulated rivers because they allow for comparison of used and available habitat characteristics at the time an individual is located (Edge et al. 2020). We fit models using Markov Chain Monte Carlo estimation and a Bayesian approach in the jagsUI package in R (Kellner 2019) by running three chains over 40,000 total iterations with an adaptive phase of 10,000 iterations, and a

thinning rate of 10. We used vague priors with a normal distribution for μ (mean = 0; variance = 100) and uniform prior distribution for σ (min = 0; max = 10). The utility, U , a habitat provides to individual, i , at point, j , is determined by the following equation where β 's are the coefficients for the habitat variables, x . We incorporated a random intercept term to account for repeated observations on individuals and a random slope for seasonal differences in habitat selection. Seasons were defined based on migratory and sedentary periods observed in Missouri River tributaries (Chapter 1) spring, April–June; summer, July–September; fall, October–November; and winter, December–March.

$$U_{ij} = \alpha_i + \beta_1 x_{1j} + \beta_2 x_{2j} \dots \beta_m x_{mj} + e_{ij}$$

With the assumption that errors are independent and normally distributed. Then the relative probability (P) of an individual choosing a specific habitat type (A) instead of any of the other available habitat types (i) during a choice event is (Cooper & Millspaugh 1999):

$$P_j(A|i) = \frac{\exp(U_{aj})}{\sum_{Atoi} \exp(U_{ij})}$$

Continuous variables were standardized by mean and standard deviation. Quadratic terms were added for continuous variables to allow selection probability to peak at intermediate values. Mean and 95% credible limits for beta values were calculated from posterior distributions. Presence or absence of binary substrate and macrohabitat unit types were considered significant if the 95% credible intervals of beta estimates did not overlap 0. However, selection for continuous habitat variables across

seasons and life stages were primarily compared by visually inspecting the shape of the mean and 95% credible interval relative probability selection curves.

To answer our first question, we developed separate a global ASA seasonal habitat selection models for each tributary that included all variables. We omitted side channel presence/absence in the Gasconade River analyses because they were rarely accessible. We validated the model's predictive ability using k-fold cross validation (Boyce et al. 2002). We subsampled a dataset 10 times with 80% used for model training and 20% for validation. We calculated mean estimates for each parameter from 1000 bootstrap iterations of the training model posterior distributions. Training models were used to rank predicted relative probability of each point being used in the testing data sets. We calculated the proportion of choice sets where training models correctly classified used points (used with greatest relative probability), or nearly classified the used point (used with second greatest relative probability). We would expect used points to be correctly classified greater than 25% (random chance) of the time with declining probabilities of being ranked 2, 3, or 4. Next, we tested whether influential habitat selection criteria were consistent in two rivers with different levels of habitat alteration by comparing selected habitats in the Osage and Gasconade rivers and applying the global models to predict used or available points in the other river's choice sets.

Similarly, for question two, we developed models that compared age-0 and ASA (October–February; hereafter “overwinter”) habitat selection in the Osage and Gasconade rivers, separately. We used ASA monthly available habitat distances to form age-0 choice sets, which were generally low for winter months. Random slope for life stage (age-0 vs. ASA) replaced the seasonal slope in our ASA models. Age-0s were not observed in

secondary-channel habitats and thus macrohabitat unit variables were omitted from these models. We applied the same within and across validation steps.

Habitat Suitability analysis

We estimated habitat availability for 131 km of the lower Osage river and 39 km of the lower Gasconade River for three life history events that may be limiting factors for Lake Sturgeon recovery: lotic spawning, age-0 first winter, and ASA summer/winter refugia because discrete choice models indicated ASA selection for deep pools was similar in both seasons. Habitat suitability models (HSMs) are based on habitat suitability indices (HSIs) that reclassify mapped variable values to a 0-1 scale. Scoring criteria was primarily informed by selection data (type III HSI), which provide the most reliable predictions of suitability across a species range (Moir et al. 2005) and thus may be more useful than other HSIs developed for Lake Sturgeon in mid latitudes (e.g., Threader et al., 1998; Daugherty et al., 2009; Baril et al., 2018).

We used results from the discrete choice models to develop type III HSIs separately for each tributary and when necessary incorporated type II data (i.e., habitat utilization) from our study and literature reviews. For the age-0 and ASA summer/winter periods we assigned depth suitability scores based on threshold areas under the relative probability curves. We joined depths from Lake Sturgeon locations to modeled depths in bathymetry rasters to develop a linear equation to transform selection curve depths to better approximate bank-full depths represented in bathymetry layers. r^2 values and slopes near 1 suggested good correlation between measured and modeled depths and, as expected, intercepts indicated that measured depths collected during summer, fall or

winter were shallower than modeled depths (Appendix 4.3). Next, we assigned substrate scores based on examination of seasonal selection for substrate classes (e.g., Appendix 4.4, Appendix 4.5, or Fig. 4.3). Velocity data was unavailable, but previous habitat suitability models have used stream gradient as a proxy for velocity (Hay-Chmielewski and Whelan 1997; Daugherty et al. 2008). Our study rivers had little discernable longitudinal variation in stream gradient. Instead, we decided to use macrohabitat units to as a coarse proxy for velocity. In the Osage River, we spatially joined all ASA summer/winter refugia and age-0 fall/winter locations to a macrohabitat layer. Relative macrohabitat unit frequencies were standardized to a 0–1 scale and rounded to develop suitability scores (Baril et al., 2018). We did not observe spawning and therefore lacked data to develop population-specific habitat criteria. Instead, we used HSIs from a range-wide type II spawning HSM for Lake Sturgeon spawning sites and assigned higher scores to riffles and runs and lower scores to pools or back channels based on the Lake Sturgeon’s preference for spawning habitats with velocities exceeding 0.5 m/s (Table 4.2).

Composite suitability layers in each period were developed as the geometric mean of overlapping 5 m resolution raster grids for individual variables (Threader et al. 1998; Daugherty et al., 2009). Habitats from 1.0–0.75 were defined as preferred, 0.749–0.50 suitable, 0.499–0.25 marginal, and less than 0.25 unsuitable. We used sturgeon locations that were not used in fitting models to independently validate our ASA summer/winter and age-0 overwinter HSMs for each river using odds ratios and chi-square tests to evaluate the null hypothesis that there is no association between habitat suitability classification (preferred or not preferred) and whether a point was used or random.

Finally, we divided the Osage into 12, 10.7-km reaches and the Gasconade into 4, 9.0-km reaches to identify spatial limitations in preferred habitat.

Results

Telemetry Locations

In the Osage River we recorded habitat at 777 observations (279 in spring, 211 in summer, 119 in fall, and 168 in winter) of 72 individual ASA Lake Sturgeon. During the fall and winter of 2018-2019 we collected 39 observations of 28 individual age-0 Lake Sturgeon in the Osage River. In the Gasconade River we collected habitat data for 224 observations (100 in spring, 44 in summer, 34 in fall and 47 in winter) of 37 individual ASA Lake Sturgeon. During the fall and winter of 2019-2020 we collected habitat data for 60 observations of 24 individual age-0s in the Gasconade River.

Adult/Subadult Seasonal Selection

Mean used depths were greater than the mean available depths in all seasons (Appendix 4.4). The top one-third of posterior relative probability distributions from discrete choice models suggested that when available, ASA Lake Sturgeon preferred habitats greater than 7.6 m deep in all seasons in both rivers. ASA Lake Sturgeon preferred the deepest habitats during winter in the Osage River (top one-third = 11.1–14.0 m), and during the summer in the Gasconade River (top one-third = 13.2–14.4 m). They preferred the shallowest habitats during the fall in the Osage River (top third = 7.6–10.3 m) and during the winter in the Gasconade River (top one-third = 7.9–9.3 m) (Fig. 4.3).

Selection for current velocity varied seasonally and between tributaries. Broad relative probability curves and insignificant betas indicated weak selection for velocity in the Osage River during the spring and summer (Fig. 4.3; Appendix 4.6). In contrast, ASA Lake Sturgeon selected slow current velocities in the Osage River during the fall and winter and in the spring, summer, and fall in the Gasconade River (Fig. 4.3; Appendix 4.6). Lake Sturgeon selected high flow velocities greater than 1.5 m/s in the winter in the Gasconade River, however, velocities this high are rare during in the winter and eliminating the quadratic term produces a negative beta for velocity with credible intervals overlapping zero indicative of non-significant selection for lower winter velocities.

ASA Lake Sturgeon preferred offshore main-channel habitats and preferred habitats slightly closer to the shore in spring and winter and further from shore in the summer and fall (Fig. 4.3). These results align with their avoidance of shallow habitats and lack of selection for LWD, both of which are more common in littoral environments. ASA Lake Sturgeon selected for silt substrate in all seasons in the Osage River and during the fall in the Gasconade River.

Although ASA Lake Sturgeon primarily occupied main-channel macrohabitat units such as pools and glides, secondary channel habitats appear to be seasonally important in the Gasconade River. Lake Sturgeon significantly preferred backwaters when available in the winter, and we recorded 10 observations of 6 individuals using backwaters during the spring. In contrast, in the Osage River we never observed a Lake Sturgeon in a backwater and recorded only five observations of three individuals using side channels.

ASA discrete choice models correctly classified used points in 41% and 50% of choice sets and used points ranked first or second in 72% and 76% of choice sets for the Osage and Gasconade rivers, respectively (Fig. 4.4). These values are well above the predictive accuracies expected from a null model and indicate predictable seasonal habitat selection.

The ranges of values containing the top one-third of posterior relative probability distributions overlapped in each river for 15 variable x season combinations and did not overlap in 13 variable x season combinations (Appendix 4.4). Both models also exhibited predictive power when applied to the other river's data, suggesting that some selection patterns were spatially transferrable between rivers. The Osage River model correctly identified used points in 42% of Gasconade ASA choice sets and the Gasconade River model correctly predicted 36% of Osage River used points (Fig. 4.4).

Ontogenetic Differences in Overwinter Habitat Selection

Age-0 Lake Sturgeon preferred shallower habitats closer to shore than ASAs in the fall/winter. Age-0s preferred low velocity habitats similar to ASAs in the Osage River (<0.39 m/s) but selected swifter currents than those selected by ASAs in the Gasconade River (top one-third = 0.37–0.52 m/s) (Fig. 4.5). Significant substrate selection differed in both rivers, however, age-0s either selected the finest (sand/silt in the Gasconade River) or avoided the coarsest (cobble+ in the Osage River) substrates (Fig. 4.5, Appendix 4.7). Classification accuracy of overwinter locations by age-0 and ASA Lake Sturgeon was 43% in the Osage River and 45% in the Gasconade River. Used points ranked within the top two in predicted probability for 75% of Osage River and 83% of

Gasconade River choice sets. Both the Osage River (38%) and Gasconade River (49%) age-0 models predicted age-0 habitat use in the other stream better than random.

Comparison of Habitat Suitability in two Missouri River Tributaries

Bank-full average depths from our bathymetry model were greater in the mapped portions of the Osage River at 6.3 m than in the smaller Gasconade River at 5.3 m. Field validation confirmed sonar substrate classifications at 85% of Osage River points and 74% of Gasconade River points (Appendix 4.1). Used locations validated selection for habitats classified as “preferred” by habitat suitability models. Osage River ASA Lake Sturgeon locations were 31.1 times ($X^2, p < 0.001$) and Gasconade River locations 12.1 times ($X^2, p < 0.001$) more likely to be in preferred habitats than random points. Similarly, Osage age-0 fall/winter Lake Sturgeon locations were 2.0 times ($X^2, p = 0.004$) and Gasconade River locations 2.4 times ($X^2, p < 0.001$) more likely to be classified as preferred than random points (Table 4.3).

Preferred depth, substrate, and macrohabitat units for Lake Sturgeon spawning were widespread including 32% of the Osage mapped area and 78% of the Gasconade mapped area (Fig. 4.6). Preferred spawning habitat was lowest in the furthest downstream reach of both tributaries that contained greater proportions of fine sediments and was relatively similar in other reaches (Fig. 4.7).

Preferred ASA summer/winter refugia was rare in the mapped portions of the Osage River (3%) and the Gasconade River (2%) (Fig. 4.6). The majority of preferred habitat occurred in deep pools with fine sediments in both rivers near their confluence with the Missouri River (Fig. 4.7). Small proportions of preferred habitat existed in all

reaches of the Osage River including in a deep gravel dredging pool in reach #4 at river km (rkm) 35 in the Osage River however, no preferred habitat existed in the shallower Gasconade River upstream of rkm 7 (Fig. 4.7).

More specific depth preferences by age-0 Lake Sturgeon in the Gasconade River resulted in less preferred age-0 overwinter habitat in the Gasconade (11%) than the Osage river (36%). The greatest proportions of preferred age-0 habitat occurred in the reach #1 in the Osage River and in reach #2 of the Gasconade River and preferred nursery habitat declined further upstream in both tributaries. (Fig. 4.7).

Discussion

Our results contribute to closing knowledge gaps in the spatial, temporal, and ontogenetic variation in habitat requirements of Lake Sturgeon and identify potential habitat limitations. Habitat selection criteria during the spring season that includes the spawning period was not well-defined by our study, but summer and winter ASA tributary habitat selection was driven by a strong preference for deep, low-velocity pools in both rivers. Habitat selection between age-0 and ASA Lake Sturgeon differed, with age-0s being more selective for shallower depths in both rivers and slightly faster current velocities in the Gasconade River. Although verification of natural reproduction should remain a primary objective, HSMs suggest that maintaining habitat diversity for other life stages should also be considered in future conservation actions and research for southern Lake Sturgeon.

Other than weak selection for faster current velocities in the spring in the Osage River, our prediction that Lake Sturgeon would select shallow, swift-flowing, near-shore

habitats with the largest substrate for spawning in the spring was not supported. The monthly tracking frequency in our study was not well-suited to observe spawning site residency, which can average 2.9 to 3.5 days in some populations (Dammerman et al. 2018). Therefore, spring selection curves likely include spawning site use, use of deep staging areas near spawning habitats, and resting or foraging habitats by non-reproductive individuals. The inability to disentangle various mechanisms for spring habitat use required us to apply a range-wide review of spawning habitat selection to develop HSM models discussed below (Baril et al. 2018).

Selection models affirmed our hypothesis that Lake Sturgeon would occupy deep pools in the summer and winter. In the Great Lakes, Lake Sturgeon are considered a “shallow-water fish” (Holtgren & Auer 2004), which may contribute to an underemphasis on the critical role of deep-water refugia at range margins (Thayer et al. 2017). Depth appears to be the dominant factor dictating suitability of summer and winter refugia in Missouri River tributaries. We hypothesize that deep main-channel pools may offer cooler summer temperatures near areas of groundwater input or thermal stratification (Nielsen et al. 1994; Hitt et al. 2017). Furthermore, as resting and maximum metabolic rates converge near species’ thermal limits, aerobic scope becomes limited for other functions (Whitney et al. 2016), and sturgeon species can adjust movement behaviors to reduce energetic demands along migratory pathways (McElroy et al. 2012), or in deep low-velocity pools during peak summer temperatures (Heise et al. 2005). Modeled selection for silt/sand substrates in the Osage River during all seasons and in the fall in the Gasconade River may simply be correlated with fine sediments naturally accumulating in preferred pools. However, Lake Sturgeon prefer foraging in fine

sediments (Threader et al. 1998). Shallower off-channel habitats with seemingly suitable low current velocities and fine substrates were rarely used in the Osage or Mississippi rivers, MO (Snellen 2008). Conversely, Lake Sturgeon did use off-channel habitats in winter and spring in the Gasconade River similar to studies of Lake Sturgeon in the Wisconsin River, WI (Knights et al. 2002). Selection of off-channel habitats may depend on the availability of suitable main-stem pools and off-channel water quality.

Our hypothesis that age-0 Lake Sturgeon would select different habitats than ASAs was also supported. Habitats preferred by age-0 Lake Sturgeon in the Gasconade River contained 3.0–3.9 m depths, current velocities from 0.37–0.52 m/s and sand, gravel, or pebble substrate, which was similar to northern populations in Laurentian Great Lakes basin rivers (Benson et al. 2005; Mann et al. 2011). Juvenile Lake Sturgeon are poor swimmers that are unable to sustain swimming speeds of more than 0.7 m/s for longer than 1 minute (Peake et al. 1997). However, moderate currents may help mobilize macroinvertebrate prey for age-0 Lake Sturgeon drift feeding (Nilo et al. 2006). Age-0 Lake Sturgeon in the regulated Osage River selected slightly deeper habitats with slower current velocities, but in both rivers age-0 Lake Sturgeon selected shallower depths than ASAs. In the regulated Tennessee River, juveniles were observed in deeper habitats in response to rising river discharge (Huddleston 2006). Deeper habitats over 13.7 m were also used by juvenile Lake Sturgeon (<530 mm FL) in the Winnipeg River, MB in all seasons (Barth et al. 2009); indicating that the transition to deeper habitats may occur after the first year of life or greater depths may be preferred in rivers with greater ice accumulation. Similar to our study, Lake Sturgeon selected finer substrates where it may be easier to forage or maintain position (Peake 1999) potentially to maximize energetic

stores that are critical for overwinter survival (Deslauriers et al. 2018). Differences in age-0 selection curves may indicate more generalized habitat associations, different selective pressures in either river, or be a result of the single year of data available for each river failing to fully represent variation in habitat selection at this life stage.

With minor differences in ASA and age-0 discrete choice selection curves between rivers, our prediction that seasonal habitat selection patterns would be spatially transferrable to different habitat contexts was partially supported. Performance of spatially extrapolated suitability models for Lake Sturgeon are mixed (Haxton et al. 2008; Krieger et al. 2018). Persistent habitat selection in different environments may indicate rigid habitat requirements (Heggenes et al. 2002). Validation indicated greater predictive performance for models within the river they were developed except the Osage ASA and Gasconade age-0 models which predicted the used points better in the other river. Overall, the results suggest that although spatial variation in habitat selection can be important, especially at large spatial scales, some habitat associations such as use of deep water refugia during summer and winter are likely spatially transferrable across Missouri River Basin tributaries and may even apply to other rivers along Lake Sturgeon's southern range boundary.

Our spawning HSM likely overestimated the availability of preferred Lake Sturgeon spawning habitat as it was greater than 10 times more prevalent than high quality spawning habitat in Lake Michigan tributaries (Daugherty et al. 2008). Water velocities from 0.5–1.4 m/s and coarse substrates are often the physical habitat factors deemed the most critical to Lake Sturgeon reproduction (Baril et al. 2018). In contrast, spawning can occur at depths from 0–25 m in large rivers across its range (Baril et al.,

2018). In the St. Clair-Detroit River, where flows are not regulated and hydraulic conditions are stable, coarse substrate availability was identified as the limiting factor and was addressed through the construction of spawning reefs (Roseman et al. 2011). However, greater than 78% of our study area contained gravel or larger substrates suitable for spawning. Therefore, especially in the regulated Osage River, current velocity changes and dewatering of spawning sites may be of greater importance. Unfortunately, we lacked data to describe current velocity in the Gasconade River and used macrohabitat units in the Osage River as a proxy for current velocity. An appropriate application of these spawning HSMs may be to couple them with Lake Sturgeon locations at water temperatures from 12–18°C to target potential spawning sites for future study. For example, Lake Sturgeon aggregations occur in the spring near rip-rap training structures from rkm 50 to 80 in the Osage River (Chapter 1), which were predicted to contain preferred spawning habitat. However, in the Gasconade River, Lake Sturgeon spring migrations can extend 238 km upstream; indicating spawning is more likely to occur upstream of our mapped reaches (Chapter 1). With an abundance of preferred habitats predicted to occur in the lower reaches of both rivers, the reason for energetically expensive long-distance migrations is unknown, but may have to do with providing larvae space to drift into suitable nursery habitats (Braaten et al., 2008).

In contrast to many Lake Sturgeon populations where tributaries are used primarily for spring reproduction (Peterson et al. 2007), Missouri River tributaries contain vital Lake Sturgeon habitat for ASA Lake Sturgeon throughout the year. An average of 74% of tagged ASA Lake Sturgeon occupied the Osage or Gasconade rivers during summer or winter, however movement data (Chapter 1) and model validation

accuracy (Table 4.4) indicated that use is restricted to deep pools classified as preferred habitats constituting less than 5% of their area. Although the overall proportions of preferred refuge habitat were similar, HSMs indicated the larger Osage River likely contains more preferred refuge habitat since it was present in all reaches of the Osage River but was confined to the lower 7 rkm of the Gasconade River. This pattern was supported by summer movement data that showed declines in the percentage of tagged Lake Sturgeon occupying the warmer Gasconade River from 22–10% from April–July contrasted with increases from 59–75% in the Osage River (Chapter 1). Lower availability of thermal refugia may be limiting Lake Sturgeon summer use of the Gasconade River and points to these being rare habitats to conserve in the Lower Missouri River basin.

HSMs suggested that preferred age-0 habitat was similarly distributed in both rivers with the greatest concentration occurring in lower reaches near the Missouri River confluences. This aligns with the greater downstream dispersal observed from upstream stocking sites into lower river reaches of Missouri River tributaries (Chapter 2), which is similar to a northern population in Wisconsin (Benson et al. 2005). One advantage of these reaches is that current velocities are lower and depositional substrates greater due to backwater effects of the mainstem Missouri River. Furthermore, convergent flows at major tributary junctions can concentrate nutrients, sediment, and LWD forming complex and biologically productive habitats (Benda et al. 2004). Similarly, there was greater macroinvertebrate production and Lake Sturgeon use of major tributary confluences in the Mississippi River and Hudson Bay drainages (Chiasson et al. 1997; Knights et al. 2002). Although they were not selected for in our rivers, LWD provided current breaks

used by age-0 Lake Sturgeon in the Sturgeon River, MI (Holtgren & Auer 2004). Finally, we also observed age-0 Lake Sturgeon in preferred moderate current velocities and finer substrates in inside riverbend habitats similar to areas where juvenile Lake Sturgeon were observed in the Big South Fork, KY. (Herrala 2015). Although we did not track the 6–18% of age-0s that exited tributaries during the fall to winter study period. (Chapter 2), the channelized mainstem Missouri River contains current velocities exceeding 1 m/s and may not provide slow velocity nursery habitat for juvenile sturgeon (Jacobson & Galat 2006). Selection of reach #2 over the deeper reach #1 in the Gasconade River that was preferred by ASAs during the same period may be a strategy to reduce predator exposure, although sharp scutes afford juvenile Lake Sturgeon protection from predation (Crossman et al. 2018). It remains unknown whether overwinter nursery habitat is limiting survival of wild or hatchery stocked juveniles. Survival of stocked fingerlings in these two tributaries was estimated to be ~50% (Chapter 2), which is substantially higher than some northern populations and implies that sufficient suitable nursery habitat may exist. The spatial concentration of both summer winter refuge and age-0 habitats near the confluences reinforces the importance of tributaries for the maintenance of large river biodiversity (Pracheil et al. 2013).

There are many opportunities to build off these results to provide higher spatial and temporal resolution to habitat selection predictions in southern Lake Sturgeon rivers. Static hydraulic models have been used to guide spawning reef construction and developing larval HSMs in the St. Clair-Detroit River Systems (Krieger & Diana 2017; Fischer et al. 2020). However, the static nature of our HSMs limited our ability characterize habitat suitability changes due to depth and velocity resulting from

hydrologic regulation. A future approach could be to pair two-dimensional hydrodynamic models currently being constructed in ten 2-km reaches of the Osage River (N. Farless, 2021, personal communication) with substrate maps and continuous positioning data from VEMCO Positioning System (VPS) receiver arrays near putative spawning sites to direct reproduction monitoring as has been used for Green Sturgeon (*Acipenser medirostris*) in the Sacramento River, CA (Wyman et al. 2018). Hydrodynamic models and VPS arrays would also help biologists understand the role of temporal habitat stability in Lake Sturgeon summer/winter refugia. Greater discharge variability closer to Bagnell Dam may limit the utility of upstream deep pools that our model identified as preferred summer or winter refugia, but which were not used by tagged Lake Sturgeon. Sonar technology is rapidly advancing and may present future opportunities to map additional substrate classes (e.g., sand vs. silt) and increase classification accuracy, although our accuracy was in line with 77% observed in previous studies (Kaeser & Litts 2010). Many misclassified points were within 10 m of banks which are often near the edge of sonar images and where substrate aggradation and degradation may occur depending on flow velocities. We also lack information on sediment stability, and shifting sediments may alter suitability of Lake Sturgeon habitats over time (Fischer et al. 2020). Finally, additional work is needed to validate the habitat associations we observed in Missouri River tributaries in the Dissected Till Plains with bedloads dominated by finer sediments (e.g., Grand, Chariton) and in other southern states.

There are numerous applications of suitability models to habitat restoration and population recovery. Physical habitat remediation is costly in a river the size of the Osage and our HSMs suggest that suitable spawning habitat may be available in both tributaries.

If future investigations deem spawning shoals to be limiting, reconstruction of swift flowing riffle habitats may be more feasible in divided channels around islands (Lobb & Luekenhoff (2013). Backwater habitats appear to be important in the Gasconade River during spring and winter and these areas should be protected against channelization and floodplain development. Restoration of connectivity and water quality of off-channel habitats where dissolved oxygen is lower during hydropeaking (Farless et al. 2018) than in the main channel could increase the amount of low velocity habitat available to Lake Sturgeon. Oxy-thermal stress may be compounded as a result of discharge of anoxic water from the hypolimnetic releases at Bagnell Dam. In August, 27% of dissolved oxygen readings at rkm 122 fell below the state standard of 5.0 mg/L compared to only 3% of the readings at rkm 53 (Farless & Landwer 2020). Using dredging to create additional cool deepwater may not be feasible since it would likely have ancillary undesirable effects to geomorphology and biotic communities (Brown et al. 1998). Instead, efforts to conserve refugia by increasing dissolved oxygen through aeration of dam discharges or protection of shading riparian buffers may help mitigate the effects of climate change. Additional study of Lake Sturgeon habitat use in the mainstem Missouri River may highlight opportunities to increase seasonal ASA refugia and age-0 low velocity nursery habitats through modification of wing dikes and other channel control structures. A non-functioning lock and dam structure exists at rkm 19 in the Osage River. Removal of this structure would allow juvenile and adult Lake Sturgeon to access suitable habitats upstream during periods of low water levels.

Literature Cited

- Baril AM, Buszkiewicz JT, Biron PM, Phelps QE, Grant JWA (2018) Lake Sturgeon (*Acipenser fulvescens*) spawning habitat: a quantitative review. Canadian Journal of Fisheries and Aquatic Sciences 75:925-933
- Barnickol PG, Starrett WC (1951) Commercial and sport fishes of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. Illinois Natural History Survey Bulletin 25:267–350
- Barth CC, Peake SJ, Allen PJ, Anderson WG (2009) Habitat utilization of juvenile Lake Sturgeon, *Acipenser fulvescens*, in a large Canadian river. Journal of Applied Ichthyology 25:18-26
- Bednarek AT, Hart DD (2005). Modifying dam operations to restore rivers: ecological responses to Tennessee River dam mitigation. Ecological Applications 15:997-1008.
- Benda LEE, Andras K, Miller D, Bigelow P (2004) Confluence effects in rivers: Interactions of basin scale, network geometry, and disturbance regimes. Water Resources Research 40:1-15
- Benson AC, Sutton TM, Elliott RF, & Meronek TG (2005) Seasonal movement patterns and habitat preferences of age-0 Lake Sturgeon in the lower Peshtigo River, Wisconsin. Transactions of the American Fisheries Society 134:1400-1409
- Bezold J, Peterson DL (2008) Assessment of Lake Sturgeon reintroduction in the Coosa River System, Georgia-Alabama. American Fisheries Society Symposium 62:1-16

- Braaten PJ, Fuller DB, Holte LD, Lott RD, Viste W, Brandt TF, Legare RG (2008) Drift dynamics of larval Pallid Sturgeon and Shovelnose Sturgeon in a natural side channel of the upper Missouri River, Montana. *North American Journal of Fisheries Management* 28:808-826
- Brown AV, Lyttle MM, Brown KB (1998) Impacts of gravel mining on gravel bed streams. *Transactions of the American Fisheries Society* 127:979-994
- Bruch RM, Haxton TJ, Koenigs R, Welsh A, Kerr SJ (2016) Status of Lake Sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. *Journal of Applied Ichthyology* 32:162-190
- Chiasson WB, Noakes DLG, Beamish FWH (1997) Habitat, benthic prey, and distribution of juvenile Lake Sturgeon (*Acipenser fulvescens*) in northern Ontario rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2866-2871
- Cochran-Biederman JL, Wyman KE, French WE, Loppnow GL (2015) Identifying correlates of success and failure of native freshwater fish reintroductions. *Conservation Biology* 29:175-186
- Cooper AB, Millspaugh JJ (1999) The application of discrete choice models to wildlife resource selection studies. *Ecology* 80:566-575
- Crossman JA, Scribner KT, Forsythe PS, Baker EA (2018) Lethal and non-lethal effects of predation by native fish and an invasive crayfish on hatchery-reared age-0 Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817). *Journal of Applied Ichthyology* 34:322-330
- Dammerman KJ, Webb MA, Scribner KT (2019) Riverine characteristics and adult demography influence female lake sturgeon (*Acipenser fulvescens*) spawning

- behavior, reproductive success, and ovarian quality. *Canadian Journal of Fisheries and Aquatic Sciences* 76:1147-1160
- Daugherty DJ, Sutton TM, Elliott RF (2009) Suitability modeling of Lake Sturgeon habitat in five northern Lake Michigan tributaries: implications for population rehabilitation. *Restoration Ecology* 17:245-257
- Edge EN, Paukert CP, Lobb MD, Landwer BH, Bonnot TW (2020) Seasonal selection of habitat by Spotted Bass and Shorthead Redhorse in a regulated river in the Midwest, USA. *River Research and Applications* 36:1087-1096
- Farless N, Baebler E, Landwer B, Lobb D (2018) Evaluation of habitat for mussels and their fish hosts in the lower Osage River. U.S. Fish and Wildlife Service Task Order No. F11AC01144
- Farless N, Landwer B (2020) Lower Osage River habitat and fish community evaluation. U.S. Fish and Wildlife Service Task Order No. F11AF00170
- Fischer JL, Roseman EF, Mayer C, Wills T (2020) If you build it and they come, will they stay? Maturation of constructed fish spawning reefs in the St. Clair-Detroit River System. *Ecological Engineering* 150, 105837
- Harris JM, Paukert CP, Bush SC, Allen MJ, Siepker MJ (2018) Diel habitat selection of Largemouth Bass following woody structure installation in Table Rock Lake, Missouri. *Fisheries Management and Ecology* 25:107-115
- Haxton TJ, Findlay CS, Threder RW (2008) Predictive value of a Lake Sturgeon habitat suitability model. *North American Journal of Fisheries Management* 28:1373-1383

- Hay-Chmielewski E (1987) Habitat preferences and movement patterns of the Lake Sturgeon (*Acipenser fulvescens*) in Black Lake, Michigan. Master's Thesis, University of Michigan, Ann Arbor.
- Heise RJ, Slack WT, Ross ST, & Dugo, MA (2005) Gulf Sturgeon summer habitat use and fall migration in the Pascagoula River, Mississippi, USA. *Journal of Applied Ichthyology* 21:461-468
- Heggenes J (2002) Flexible summer habitat selection by wild, allopatric Brown Trout in lotic environments. *Transactions of the American Fisheries Society* 131:287-298
- Herrala JR (2015) Movement of reintroduced Lake Sturgeon in Lake Cumberland. *Fisheries Bulletin*, Kentucky Department of Fish and Wildlife Resources 116.
- Hitt NP, Snook EL, Massie DL (2017) Brook Trout use of thermal refugia and foraging habitat influenced by Brown Trout. *Canadian Journal of Fisheries and Aquatic Sciences* 74:406-418
- Holt RD (2003) On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* 5:159-178.
- Holtgren J, Auer N (2004) Movement and habitat of juvenile Lake Sturgeon (*Acipenser fulvescens*) in the Sturgeon River/ Portage Lake System, Michigan. *Journal of Freshwater Ecology* 19:419-432
- Huang J, Frimpong EA, Orth DJ (2016) Temporal transferability of stream fish distribution models: can uncalibrated SDMs predict distribution shifts over time? *Diversity and Distributions* 22:651-662

- Huddleston M (2006) Dispersal, persistence, and areas of core use of re-introduced juvenile Lake Sturgeon in the upper Tennessee River system. Master's Thesis, University of Tennessee, Knoxville.
- Jacobson RB, Galat DL (2006) Flow and form in rehabilitation of large-river ecosystems: an example from the Lower Missouri River. *Geomorphology* 77:249-269
- Kaesler AJ, Litts TL (2010) A novel technique for mapping habitat in navigable streams using low-cost side scan sonar. *Fisheries* 35:163-174
- Kellner K (2015) jagsUI: a wrapper around rjags to streamline JAGS analyses. R package version 1(1)
- Knights B, Vallazza J, Zigler S (2002) Habitat and movement of Lake Sturgeon in the upper Mississippi River system, USA. *Transactions of the American Fisheries Society* 131:507-522
- Koch B, Brooks RC, Oliver A, Herzog D, Garvey JE, Hrabik R, Colombo R, Phelps Q, Spier T (2012) Habitat selection and movement of naturally occurring Pallid Sturgeon in the Mississippi River. *Transactions of the American Fisheries Society* 141:112-120
- Krieger JR, Diana JS (2017) Development and evaluation of a habitat suitability model for young lake sturgeon (*Acipenser fulvescens*) in the North Channel of the St. Clair River, Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 74:1000-1008
- Lobb D, Lueckenhoff R (2013) Reconnaissance mapping of habitat features in the lower Osage River and testing of methods to evaluate hydraulic and water quality

effects of training structures. U.S. Fish and Wildlife Service Final Report Task Order No. F10AC00277

Mann KA, Holtgren JM, Auer NA, Ogren SA (2011) Comparing size, movement, and habitat selection of wild and streamside-reared Lake Sturgeon. *North American Journal of Fisheries Management* 31:305-314

McDougall CA, Hrenchuk CL, Anderson WG, Peake SJ (2013) The rapid upstream migration of pre-spawn Lake Sturgeon following trap-and-transport over a hydroelectric generating station. *North American Journal of Fisheries Management* 33:1236-1242

McDougall CA, Pisiak DJ, Barth CC, Blanchard MA, MacDonell DS, Macdonald D (2014) Relative recruitment success of stocked age-1 vs age-0 Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in the Nelson River, northern Canada. *Journal of Applied Ichthyology* 30:1451-1460

McElroy B, DeLonay A, Jacobson R (2012) Optimum swimming pathways of fish spawning migrations in rivers. *Ecology* 93:29-34

Miyazono S, Pease AA, Fritts S, Grabowski TB (2020) Ontogenetic shifts in mesohabitat use of young-of-year Rio Grande Blue Sucker in the big bend region of the Rio Grande. *Environmental Biology of Fishes* 103:1471-1480

Moir HJ, Gibbins CN, Soulsby C, Youngson AF (2005) PHABSIM modelling of Atlantic Salmon spawning habitat in an upland stream: testing the influence of habitat suitability indices on model output. *River Research and Applications* 21:1021-1034

- Moore MJ, Paukert CP, Moore TL (2020) Effects of latitude, season, and temperature on Lake Sturgeon movement. *North American Journal of Fisheries Management*.
- Moore TM (2021) A continuing plan for recovery and management of Lake Sturgeon in Missouri. Missouri Department of Conservation Management Plan Unpublished Draft
- Nielsen JL, Lisle TE, Ozaki V (1994) Thermally stratified pools and their use by Steelhead in northern California streams. *Transactions of the American Fisheries Society* 123:613-626
- Nilo P, Tremblay S, Bolon A, Dodson J, Dumont P, Fortin R (2006) Feeding ecology of juvenile Lake Sturgeon in the St. Lawrence River system. *Transactions of the American Fisheries Society* 135:1044-1055
- Peake S, Beamish FW, McKinley RS, Scruton DA, Katopodis C (1997) Relating swimming performance of Lake Sturgeon, *Acipenser fulvescens*, to fishway design. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1361-1366
- Peake S (1999) Substrate preferences of juvenile hatchery-reared Lake Sturgeon, *Acipenser fulvescens*. *Environmental Biology of Fishes* 56:367-374
- Peterson DL, Vecsei P, Jennings CA (2007) Ecology and biology of the Lake Sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. *Reviews in Fish Biology and Fisheries* 17:59-76
- Pracheil BM, McIntyre PB, Lyons JD (2013) Enhancing conservation of large-river biodiversity by accounting for tributaries. *Frontiers in Ecology and the Environment* 11:124-128

- Roseman EF, Manny B, Boase J, Child M, Kennedy G, Craig J, Soper K, Drouin R. (2011) Lake Sturgeon response to a spawning reef constructed in the Detroit River. *Journal of Applied Ichthyology* 27:66-76
- Rusak JA, Mosindy T (1997) Seasonal movements of Lake Sturgeon in Lake of the Woods and the Rainy River, Ontario. *Canadian Journal of Zoology* 74:383-395
- Shaw SL (2010). Lake Sturgeon (*Acipenser fulvescens*) population attributes, reproductive structure, and distribution in Namakan Reservoir, Minnesota and Ontario. Master's Thesis, South Dakota State University, Brookings.
- Snellen G (2008). Habitat use of adult Lake Sturgeon (*Acipenser fulvescens*) in Pool 24 of the Mississippi River. Master's Thesis, Western Illinois University, Macomb.
- Thayer D, Ruppert JLW, Watkinson D, Clayton T, Poesch MS (2017) Identifying temporal bottlenecks for the conservation of large-bodied fishes: Lake Sturgeon (*Acipenser fulvescens*) show highly restricted movement and habitat use over-winter. *Global Ecology and Conservation* 10:194-205
- Threader RW, Pope RJ, Shaap PRH (1998) Development of a habitat suitability index model for Lake Sturgeon (*Acipenser fulvescens*). Ontario Ministry of Natural Resources, Report H-07015.01-0012
- Walker DJ, Alford JB (2016) Mapping Lake Sturgeon spawning habitat in the Upper Tennessee River using side-scan sonar, *North American Journal of Fisheries Management* 36:1097-1105
- Whitney JE, Al-Chokhachy R, Bunnell DB, Caldwell CA, Cooke SJ, Eliason EJ, Rogers M, Lynch AJ, Paukert CP (2016) Physiological basis of climate change impacts on North American inland fishes. *Fisheries* 41:332-345

Wu C, Mossa J, Mao L, Almulla M (2019) Comparison of different spatial interpolation methods for historical hydrographic data of the lowermost Mississippi River.

Annals of GIS 25:133-151.

Wyman MT, Thomas MJ, McDonald RR, Hearn AR, Battleson RD, Chapman ED,

Kinzel P, Minear JT, Mora EA, Nelson JM, Pagel MD, Klimley AP (2018) Fine-scale habitat selection of Green Sturgeon (*Acipenser medirostris*) within three spawning locations in the Sacramento River, California. Canadian Journal of Fisheries and Aquatic Sciences 75:779-791

Tables

Table 4.1. Average daily movement rate estimates used to establish search radii for available habitat points in discrete choice models. During first year of study, we used data from the literature from across the Lake Sturgeon's range. From year 2 on, we calculated average daily movement distances by month from a companion movement study.

Month	Average daily movement distance from literature review (m)	Average daily movement distance from 1 st year of Data (m)
December		96
January	250	90
February		243
March		577
April	750	1194
May		1144
June		901
July	1000	351
August		237
September		212
October	500	346
November		270

Table 4.2. Habitat suitability model criteria used to identify preferred, suitable, marginal, and unsuitable habitats in the mapped portions of the study area. SI columns contain the suitability index scores for each variable.

<i>Life Stage</i>	<i>Habitat Variable</i>	<i>Levels Osage</i>	<i>SI Osage</i>	<i>Levels Gasconade</i>	<i>SI Gasconade</i>	<i>Source</i>	
Spawning Adult	Substrate						
		Silt/Sand	0.1	Silt/Sand	0.1	Baril et al. 2017	
		Gravel	0.75	Gravel	0.75	Baril et al. 2017	
		Cobble+	1	Cobble+	1	Baril et al. 2017	
	Water depth (m)						
		<1	0.5	<1	0.5	Baril et al. 2017	
		1-4	0.75	1-4	0.75	Baril et al. 2017	
		4-11	1	4-11	1	Baril et al. 2017	
		>11	0.75	>11	0.75	Baril et al. 2017	
	Macrohabitat						
		Backwater	0	NA		Baril et al. 2017	
		Pool	0.5	NA		Baril et al. 2017	
		Side Channel	1	NA		Baril et al. 2017	
		Dam					
		Tailwater	1	NA		Baril et al. 2017	
		Run/Glide	1	NA		Baril et al. 2017	
		Riffle	1	NA		Baril et al. 2017	
		Tributary	0	NA		Baril et al. 2017	
	ASA Winter/ Summer	Substrate					
			Silt/Sand	1	Silt/Sand	1	Substrate selection analysis
		Gravel	1	Gravel	1	Substrate selection analysis	
		Cobble+	0.25	Cobble+	0.25	Substrate selection analysis	
Water depth (m)							
		<4	0	<5.5	0	no selection probability	
		4-7	0.25	5.5-6.5	0.25	lower tail	
		7-8	0.5	6.5-7	0.5	widest 5/6 selection curve area	
		8-9.5	0.75	7-7.5	0.75	widest 2/3 selection curve area	
		9.5-11.5	1	7.5-8	1	widest 1/3 selection curve area	
		11.5-13	0.75	8-8.5	0.75	widest 2/3 selection curve area	

13-14	0.5	8.5-9	0.5	widest 5/6 selection curve area
14-16	0.25	9-10.5	0.25	upper tail
>16	0	>10.5	0	no selection probability

Macrohabitat

Backwater	0.05	NA		Type II macrohabitat unit use
Pool	1	NA		Type II macrohabitat unit use
Side				
Channel	0	NA		Type II macrohabitat unit use
Dam				
Tailwater	0	NA		Type II macrohabitat unit use
Run/Glide	0.01	NA		Type II macrohabitat unit use
Riffle	0.05	NA		Type II macrohabitat unit use
Tributary	0	NA		Type II macrohabitat unit use

Age-0
Overwinter

Substrate

Silt/Sand	1	Silt/Sand	1	Substrate selection analysis
Gravel	0.8	Gravel	0.8	Substrate selection analysis
Cobble+	0.7	Cobble+	0.7	Substrate selection analysis

Water depth (m)

<6	0	<6	0	no selection probability
6-11	0.25	6-12	0.25	lower tail
11-12	0.5	12-13	0.5	widest 5/6 selection curve area
12-13.5	0.75	13-14	0.75	widest 2/3 selection curve area
13.5-18	1	>14	1	widest 1/3 selection curve area
18-19	0.75			widest 2/3 selection curve area
19-20	0.5			widest 5/6 selection curve area

Macrohabitat unit

Backwater	0	NA		Type II macrohabitat unit use
Pool	1	NA		Type II macrohabitat unit use
Side				
Channel	0	NA		Type II macrohabitat unit use
Dam				
Tailwater	0	NA		Type II macrohabitat unit use
Run/Glide	0.05	NA		Type II macrohabitat unit use
Riffle	0.05	NA		Type II macrohabitat unit use
Tributary	0	NA		Type II macrohabitat unit use

Table 4.3. Validation results using the Lake Sturgeon locations that were not used to fit selection models. Odds ratios and chi-square results show that used habitats were significantly more likely to be classified as preferred than an equivalent number of randomly generated points.

Validation Map	Used Pts Preferred	Random Pts Preferred	Odds Ratio	X^2 p-value
Osage Nursery	0.53	0.36	2.04	0.004
Osage ASA Summer/Winter	0.57	0.03	31.13	<0.001
Gasconade Nursery	0.23	0.11	2.45	<0.001
Gasconade ASA Summer/Winter	0.18	0.02	12.13	<0.001

Figures

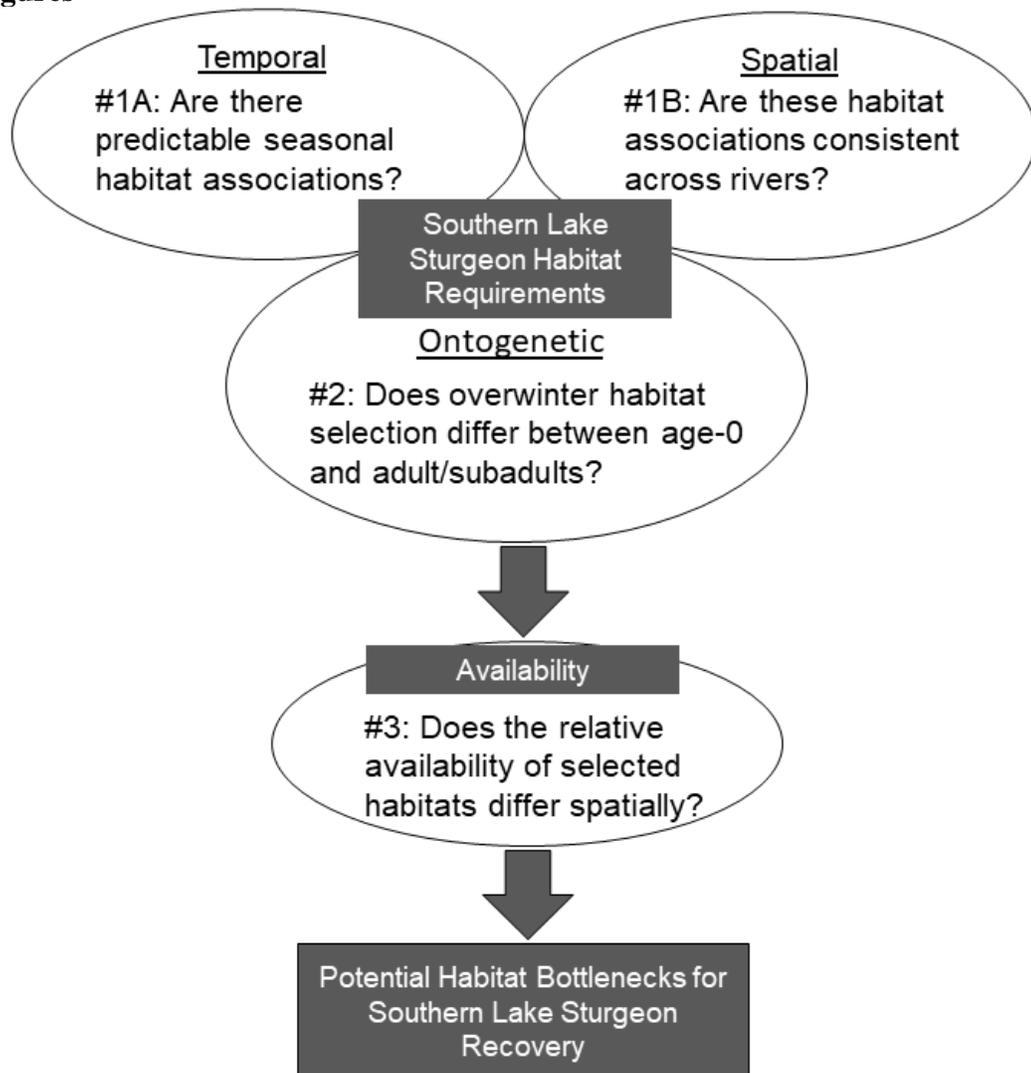


Figure 4.1. Conceptual illustration of how study objectives contribute to our understanding of spatiotemporal and ontogenetic differences in Lake Sturgeon habitat selection and availability to identify habitat bottlenecks for Lake Sturgeon recovery.

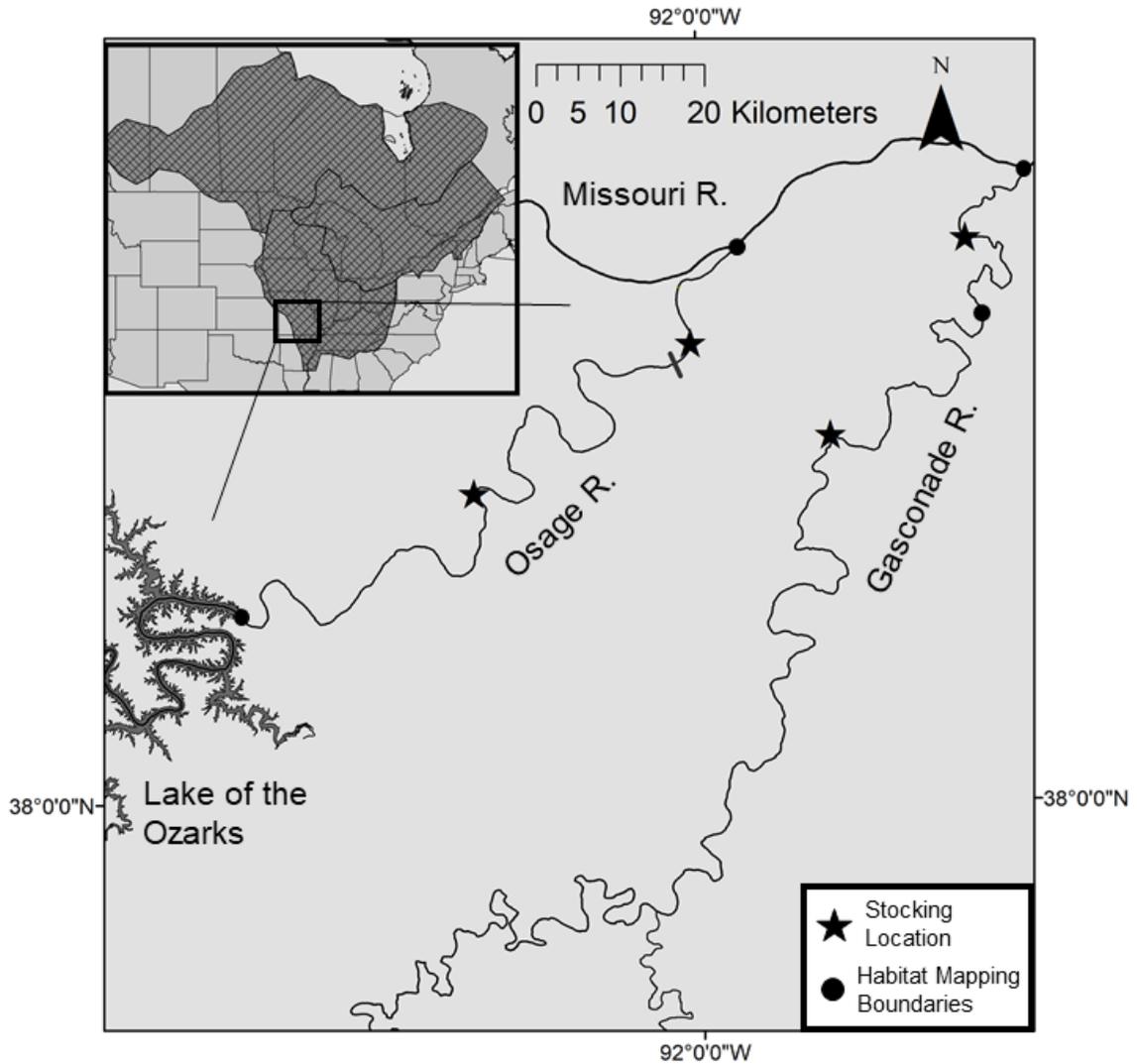


Figure 4.2. Map of study area. The inset shows the location of the study area in relationship to the Lake Sturgeon's native range. Manual tracking occurred across the entire occupied areas of both the Osage and Gasconade rivers shown above during each month from May 2017 to June 2020. Stars depict juvenile Lake Sturgeon stocking locations and dots the boundaries of habitat maps and suitability analyses.

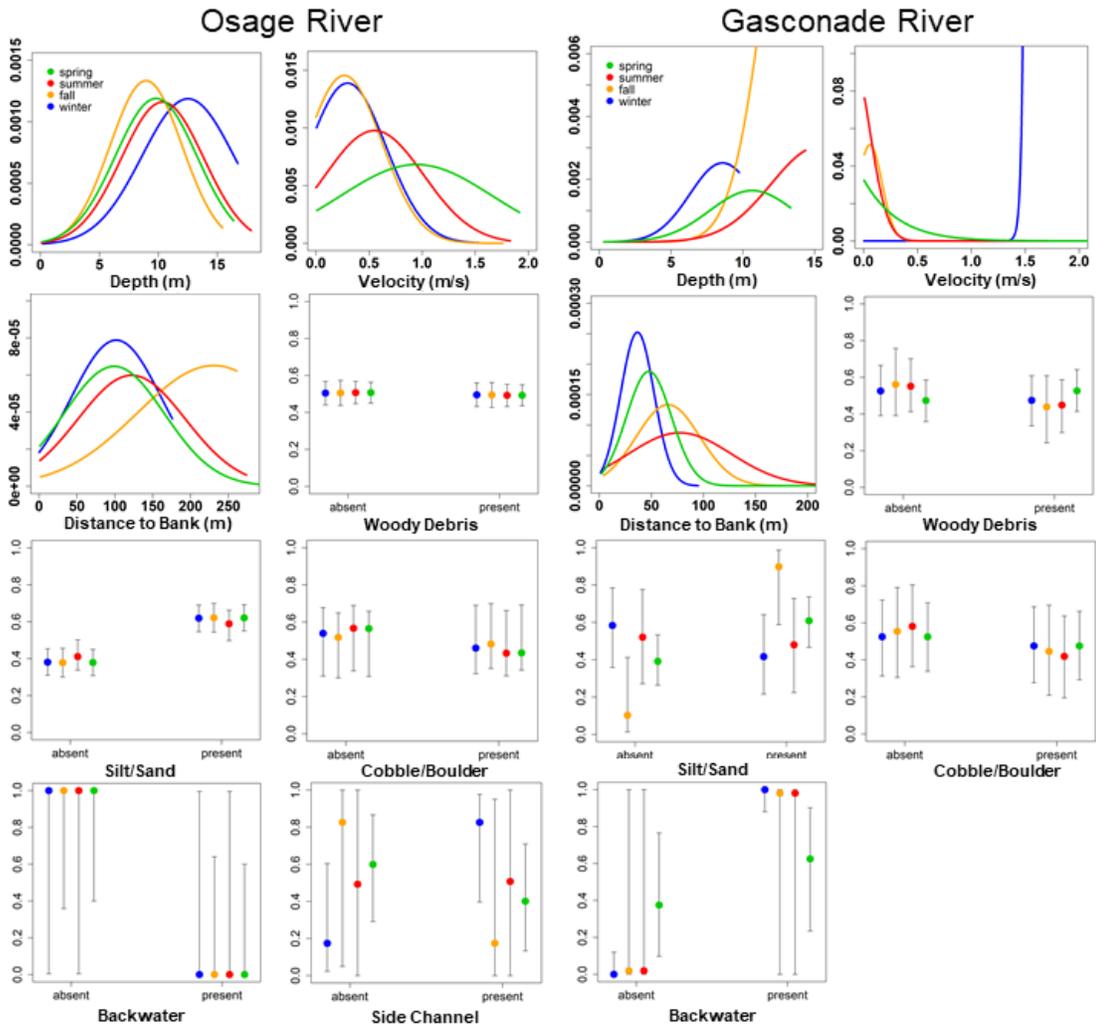


Figure 4.3. Predicted seasonal relative probability of selection for each habitat variable included in adult and subadult global discrete choice models. For each plot the other variables in the model are held at their mean value.

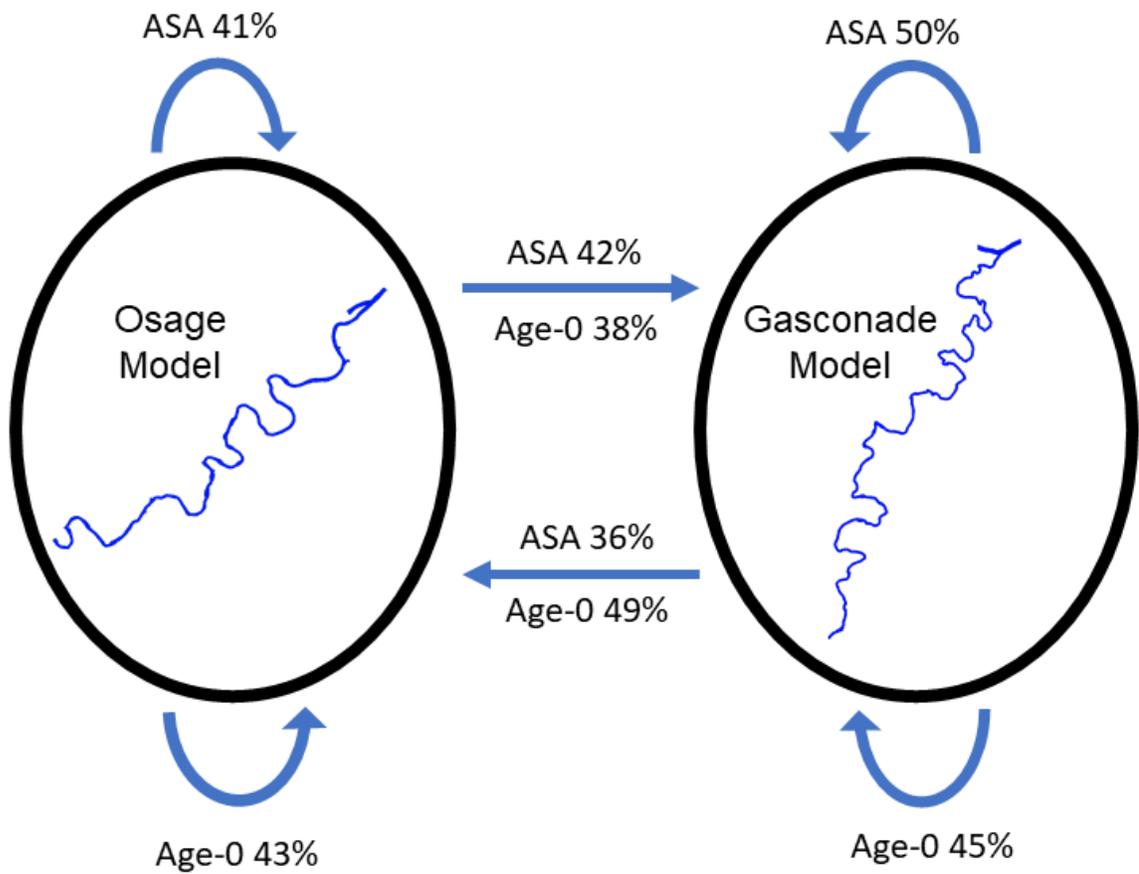


Figure 4.4. Within and across river adult/subadult (ASA) and age-0 model validation. Labels are the percent of choice sets where the used point was correctly classified as having the greatest selection probability.

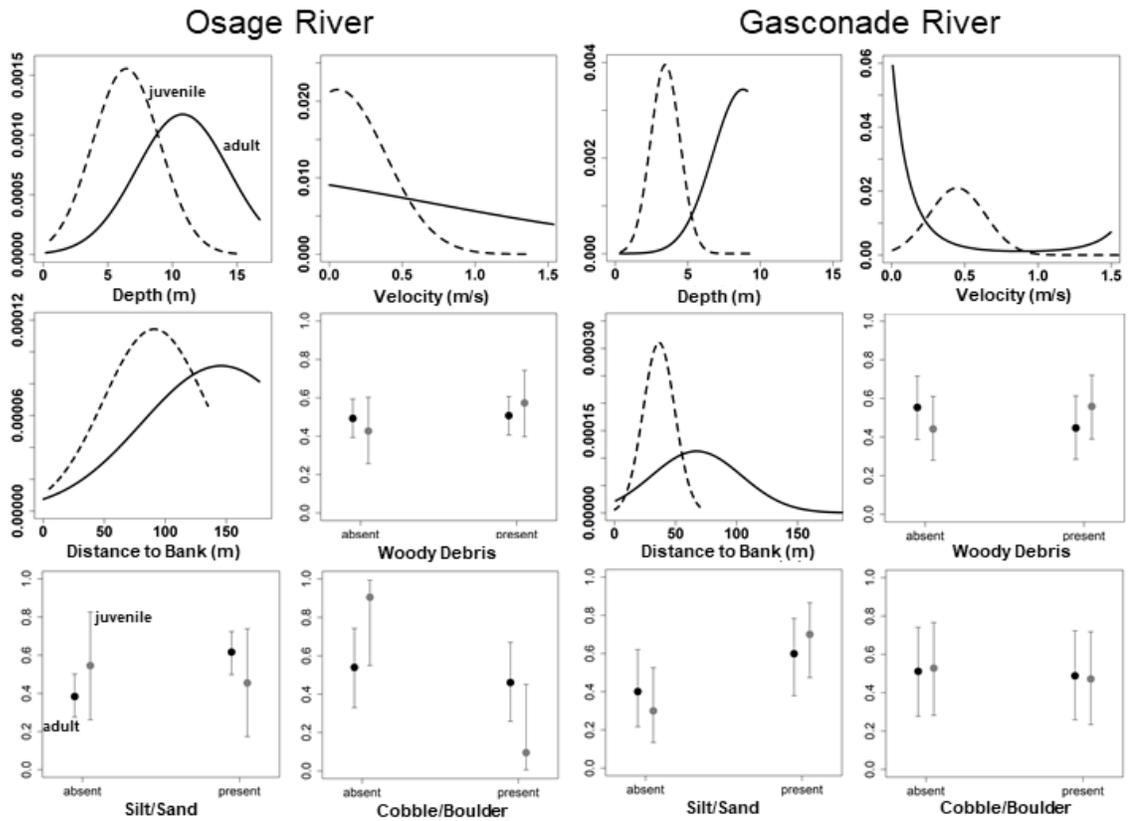


Figure 4.5. Predicted seasonal relative probability of selection for each habitat variable included in juvenile adult and subadult fall/winter global discrete choice models. For each plot the other variables in the model are held at their mean value.

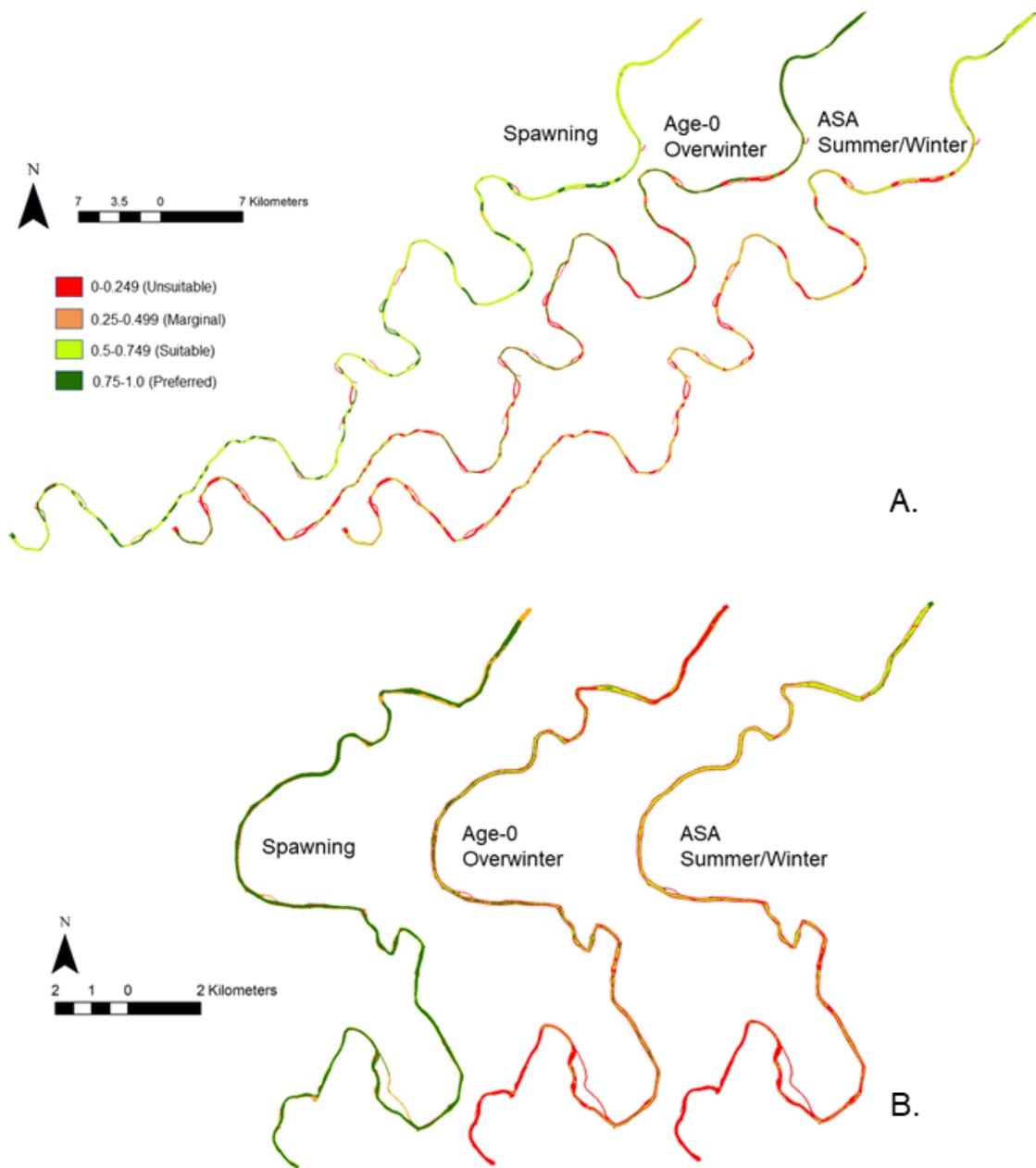


Figure 4.6. Lake Sturgeon habitat suitability maps for spawning, age-0, and adult and subadult (ASA) summer/winter refugia the lower 131 kms of the Osage River (A.) and the lower 36 km of the River Gasconade (B.).

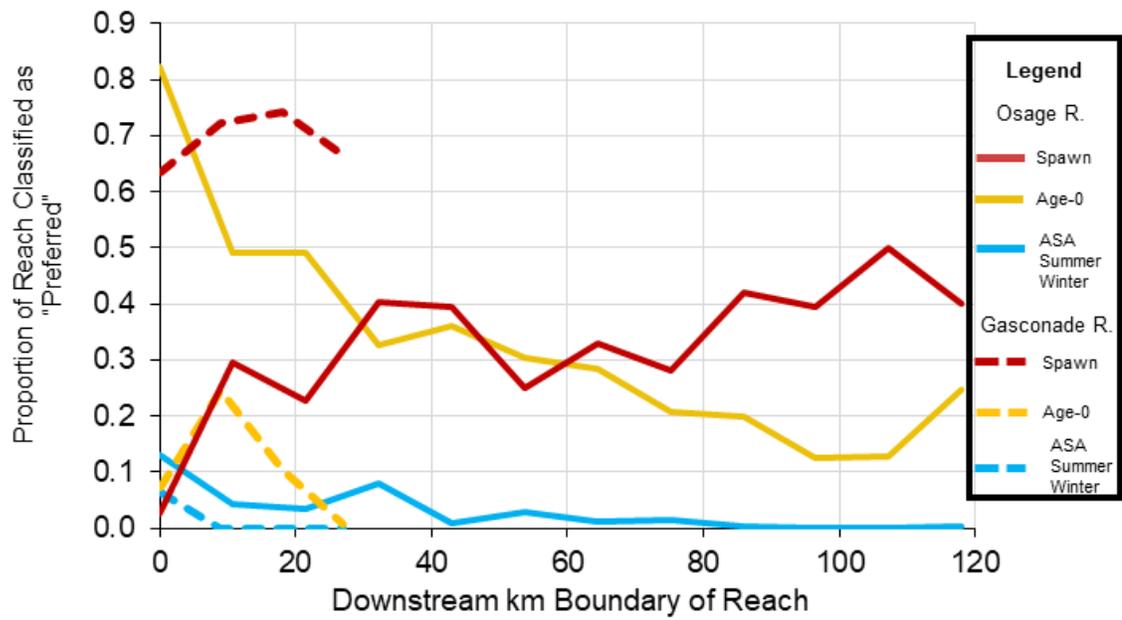


Figure 4.7. Longitudinal trends in the proportion of each reach classified as preferred spawning, age-0 fall/winter, and adult/subadult (ASA) summer/winter habitat.

Appendices

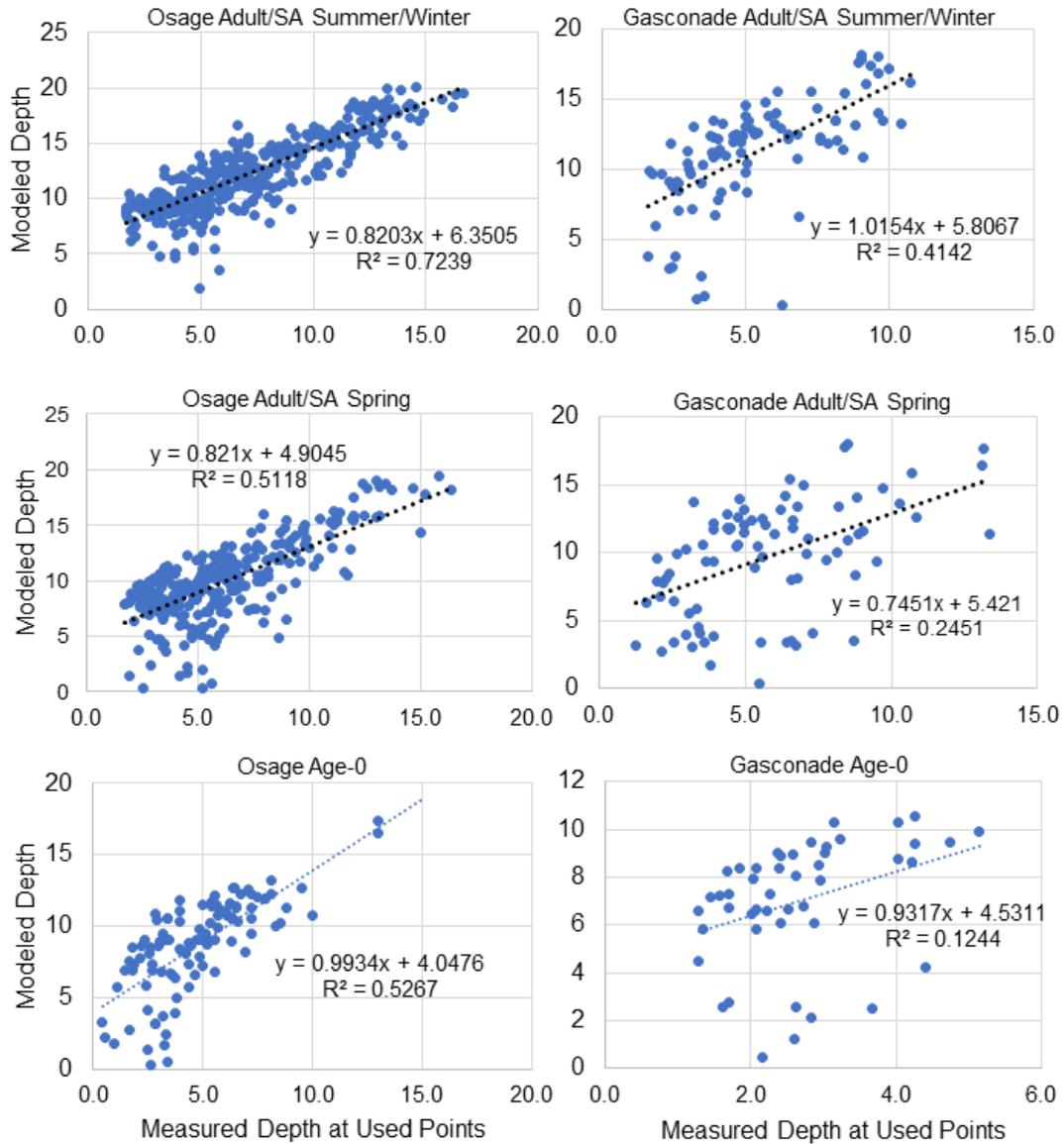
Appendix 4.1. Substrate classification validation results.

Validated Category	Correctly Classified Osage	Correctly Classified Gasconade
Sand/silt	21/30	7/13
Gravel	96/105	16/17
Cobble+	10/15	6/9
Overall	127/150	29/39

Appendix 4.2. Definitions of main- and secondary- channel macrohabitat units used in habitat suitability models and maps. Habitat suitability indices for the spawning season are also shown and based on hypothesized current velocity differences in macrohabitat units and spawning velocities described in Baril et al. (2018).

Habitat Unit	Spawning Suitability	Definition (Lobb & Leukenhoff 2013)
Main Channel		
Riffle	1	Shallow, swift area with surface turbulence and obvious drop in water surface elevation from upstream to downstream.
Run	1	Shallow to deep with moderate to swift velocities, with little to no surface turbulence.
Glide	1	Shallow to moderate depth with slow to moderate velocities and no surface turbulence. A glide was often the transition from a pool to a riffle or run.
Dam Tailwater	1	Hydraulically complex areas immediately downstream of Bagnell Dam and Lock & Dam #1
Pool	0.2	Shallow to deep with slow velocities.
Secondary Channel		
Backchannel/SideChannel	0.5	Secondary channel with flowing water along an island or gravel bar. Could consist of glide, riffle, run, pool, and other habitats
Backwater	0	Pool with little or no velocity and connected to the main channel at the downstream end of an island or gravel bar

Appendix 4.3. Regression of measured and modeled depths to develop linear equations to transform selection curves to better align with conditions in bathymetry maps.



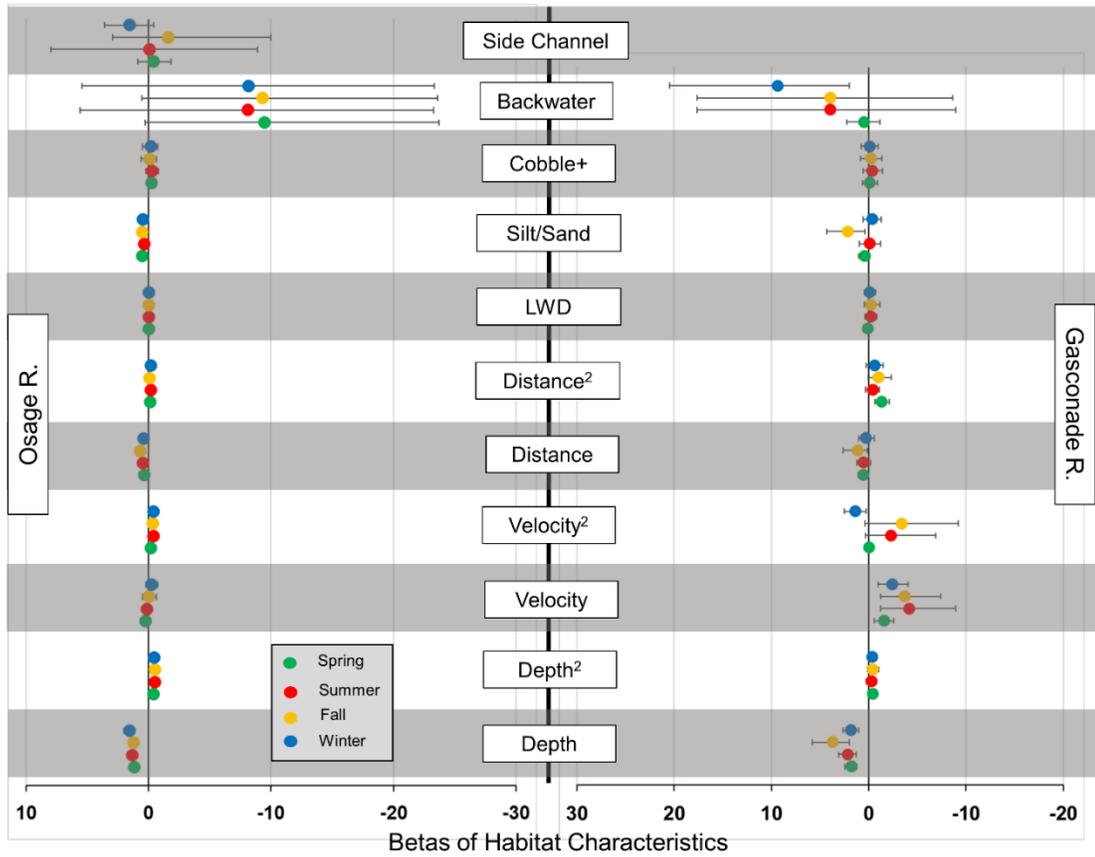
Appendix 4.4. Summary of adult/subadult Lake Sturgeon used habitat (mean and Standard Deviation [SD] in parentheses), availability (mean and SD), and selection (top 1/3 of discrete choice relative probability distributions shown in Figure 4.5 or pos=positive relationship or neg=negative relationship) broken down by variable, season, and river. The column titled * indicates whether global model included a quadratic (Q) or linear (L) relationship. The final column compares whether selected habitat ranges were greater, less than, or not significantly different in the Osage and Gasconade rivers.

Habitat Variable	Season	Osage River				Gasconade River				Os. To Gas. Comp.
		Used	Available	Modeled selection	*	Used	Available	Modeled selection	*	
Depth (m)	Spring	6.1 (3.1)	4.9 (2.9)	8.4-11.3	Q	5.3 (2.7)	4.4 (2.6)	9.6-11.7	Q	(=)
Depth (m)	Summer	6.7 (3.4)	5.2 (3.4)	8.9-11.8	Q	6.5 (2.4)	4.8 (2.4)	13.2-14.4	Q	(-)
Depth (m)	Autumn	6.0 (2.93)	4.9 (3.0)	7.6-10.3	Q	5.0 (2.0)	3.8 (2.3)	10.5-11.4	Q	(-)
Depth (m)	Winter	7.6 (3.5)	5.6 (3.7)	11.1-14.0	Q	4.2 (2.4)	3.5 (1.9)	7.9-9.3	Q	(+)
Velocity (m/s)	Spring	0.67 (0.41)	0.62 (0.43)	0.69-1.19	Q	0.32 (0.32)	0.50 (0.5)	(Neg)	Q	(+)
Velocity (m/s)	Summer	0.49 (0.38)	0.49 (0.44)	0.38-0.71	Q	0.14 (0.13)	0.23 (0.4)	(Neg)	Q	(+)
Velocity (m/s)	Autumn	0.29 (0.28)	0.28 (0.28)	0.17-0.28	Q	0.16 (0.22)	0.24 (0.3)	0.04-0.10	Q	(+)
Velocity (m/s)	Winter	0.39 (0.31)	0.39 (0.33)	0.17-0.41	Q	0.28 (0.22)	0.30 (0.2)	(Pos)	Q	(-)
Distance (m)	Spring	66.2 (32.1)	57.0 (37.5)	73-126	Q	39.6 (18.2)	40.6 (39.3)	39-57	Q	(+)
Distance (m)	Summer	79.3 (37.0)	68.3 (46.6)	94-151	Q	46.7 (19.7)	49.1 (49.0)	57-96	Q	(=)
Distance (m)	Autumn	82.8 (38.7)	63.4 (41.4)	201-253	Q	41.5 (17.2)	41.6 (48.9)	53-79	Q	(+)
Distance (m)	Winter	71.3 (32.1)	59.1 (39.3)	80-123	Q	35.7 (17.10)	31.3 (18.2)	30-43	Q	(-)
Woody Debris	Spring	0.35	0.37	-	L	0.53	0.48	-	L	(=)
Woody Debris	Summer	0.31	0.34	-	L	0.36	0.45	-	L	(=)
Woody Debris	Autumn	0.36	0.41	-	L	0.33	0.42	-	L	(=)
Woody Debris	Winter	0.36	0.38	-	L	0.40	0.43	-	L	(=)
Silt/Sand	Spring	0.19	0.16	(Pos)	L	0.44	0.32	-	L	(+)
Silt/Sand	Summer	0.31	0.32	(Pos)	L	0.45	0.51	-	L	(+)
Silt/Sand	Autumn	0.24	0.22	(Pos)	L	0.36	0.27	(Pos)	L	(=)
Silt/Sand	Winter	0.52	0.40	(Pos)	L	0.47	0.39	-	L	(+)
Cobble+	Spring	0.09	0.11	-	L	0.70	0.08	-	L	(=)
Cobble+	Summer	0.06	0.11	-	L	0.07	0.14	-	L	(=)
Cobble+	Autumn	0.08	0.10	-	L	0.15	0.12	-	L	(=)
Cobble+	Winter	0.04	0.07	-	L	0.13	0.11	-	L	(=)
Backwater	Spring	0.00	<0.01	-	L	0.1	0.01	-	L	(=)
Backwater	Summer	0.00	0.00	-	L	0	0	-	L	(=)
Backwater	Autumn	0.00	0.01	-	L	0	0	-	L	(=)
Backwater	Winter	0.00	0.00	-	L	0.06	0.01	(Pos)	L	(-)
Side Channel	Spring	0.01	0.02	-	L	0.01	0.00	-	L	(=)
Side Channel	Summer	0.00	0.00	-	L	0.00	0.00	-	L	(=)
Side Channel	Autumn	0.00	0.00	-	L	0.00	0.00	-	L	(=)
Side Channel	Winter	0.02	0.01	-	L	0.00	0.01	-	L	(=)
DO (mg/L)	Spring	9.5 (2.5)	9.5 (2.6)	-	-	9.3 (1.7)	9.4 (1.6)	-	-	(=)
DO (mg/L)	Summer	6.2 (1.1)	6.2 (1.2)	-	-	7.2 (0.7)	7.2 (0.9)	-	-	(=)
DO (mg/L)	Autumn	8.7 (1.6)	8.6 (1.6)	-	-	10.2 (2.0)	10.1 (2.2)	-	-	(=)
DO (mg/L)	Winter	12.4 (1.0)	12.4 (1.1)	-	-	12.5 (1.0)	12.5 (1.0)	-	-	(=)
Temperature C	Spring	16.0 (6.8)	16.0 (6.8)	-	-	16.7 (6.4)	16.7 (5.6)	-	-	(=)
Temperature C	Summer	27.0 (1.7)	27.0 (1.8)	-	-	27.4 (1.6)	27.4 (1.6)	-	-	(=)
Temperature C	Autumn	15.3 (4.7)	15.3 (4.7)	-	-	13.3 (6.6)	13.2 (6.6)	-	-	(=)
Temperature C	Winter	5.7 (2.0)	5.7 (2.0)	-	-	5.7 (1.9)	5.7 (1.9)	-	-	(=)

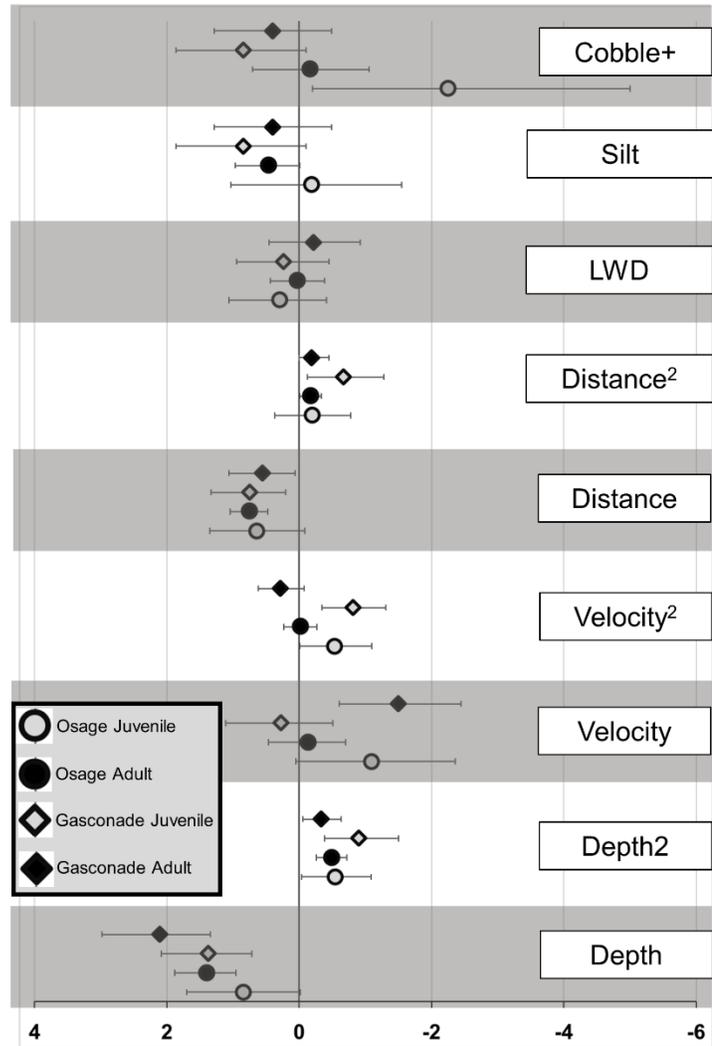
Appendix 4.5. Mean and 95% credible intervals of seasonal beta estimates for Osage and Gasconade adult/subadult discrete choice models.

Habitat Variable	Life Stage	Osage River				Gasconade River				Os. To Gas. Comp.
		Used	Available	Modeled selection	*	Used	Available	Modeled selection	*	
Depth (m)	Age-0	4.60 (2.6)	4.23 (2.8)	5.3-7.5	Q	2.76 (1.2)	2.29 (1.4)	3.0-3.9	Q	(+)
Depth (m)	ASA	7.01 (3.4)	5.24 (3.5)	9.3-12.2	Q	4.15 (1.6)	3.16 (1.7)	8.1-9.1	Q	(+)
Velocity (m/s)	Age-0	0.35 (0.27)	0.42 (0.36)	0.01-0.16	Q	0.41 (0.18)	0.40 (0.26)	0.37-0.52	Q	(-)
Velocity (m/s)	ASA	0.31 (0.31)	0.29 (0.29)	0.00-0.39	Q	0.25 (0.20)	0.27 (0.25)	0.0-0.07	Q	(=)
Distance (m)	Age-0	52.00 (27.6)	47.48 (26.2)	76-106	Q	31.79 (12.7)	26.88 (15.4)	31-42	Q	(+)
Distance (m)	ASA	76.27 (33.8)	55.8 (37.7)	127-164	Q	38.69 (17.2)	32.34 (24.05)	52-83	Q	(+)
Woody Debris	Age-0	0.51	0.44	-	L	0.37	0.38	-	L	(=)
Woody Debris	ASA	0.36	0.40	-	L	0.38	0.43	-	L	(=)
Silt/Sand	Age-0	0.21	0.17	-	L	0.18	0.19	-	L	(=)
Silt/Sand	ASA	0.39	0.33	-	L	0.38	0.38	-	L	(=)
Cobble+	Age-0	0.03	0.11	(Neg)	L	0.10	0.15	-	L	(-)
Cobble+	ASA	0.05	0.08	-	L	0.15	0.12	-	L	(=)

Appendix 4.6. Mean and 95% credible intervals of seasonal beta estimates for Osage and Gasconade adult/subadult discrete choice models.



Appendix 4.7. Mean and 95% credible intervals for beta estimates from combined juvenile and adult/subadult fall/winter discrete choice models.



CHAPTER 5- IMPLICATIONS FOR THE CONSERVATION AND MANAGEMENT OF SOUTHERN LAKE STURGEON POPULATIONS AND FUTURE RESEARCH

Summary

To our knowledge, this is the first telemetry study to investigate movement behavior and habitat selection for multiple life-stages of Lake Sturgeon near its southern range boundary. We began by reviewing the abiotic factors influencing reintroduction success of migratory large river fishes such as temperature, habitat condition, and tributary influences in Chapter 1. In Chapter 2, we identified the spatial extent and environmental factors that explain adult and subadult Lake Sturgeon movement. In Chapter 3, we estimated overwinter survival and dispersal of age-0 Lake Sturgeon released at four tributary sites. Finally, in Chapter 4 we explored Lake Sturgeon habitat selection and used models to classify suitable habitats for adult and stocked age-0 Lake Sturgeon in Missouri River tributaries.

In Chapter 2, we found that (1) in all months > 70% of tagged Lake Sturgeon occupied a Missouri River tributary, (2) upstream tributary (i.e., Osage and Gasconade river) migrations are most common in the spring and may be associated with spawning, (3) tributary-specific hydrologic and thermal conditions likely drive migration timing, migration duration, and summer habitat use. These results underscore that tributaries are key habitats for Lake Sturgeon population recovery in the degraded Missouri River basin. Lake Sturgeon may be drawn to the Osage River for its large areas of gravel or cobble substrate for spawning and its deep, productive, cooler waters for feeding. Yet, hydrologic regulation could negatively affect the Osage River's suitability for spawning,

and oxy-thermal suitability during stressful periods. Habitat restoration and institution of ecological flows at Bagnell Dam like those that occur in the Gasconade River, may further increase habitat suitability for reproduction in the lower Osage River.

Research presented in Chapter 3 examined similar questions but focused instead on stocked age-0 juveniles during their first fall and winter. Our results revealed that (1) age-0 overwinter survival was not significantly different (~ 40%–55%) among all four stocking sites in our two tributaries, (2) stocked Lake Sturgeon exhibit high fidelity to stocking tributaries, (3) Lake Sturgeon stocked at upstream sites usually disperse further than those stocked at downstream sites, but individuals from both sites converge to overwinter in similar areas in the lower 50 km of the tributaries. We confirmed that hatchery-reared fingerlings are selecting habitats in Missouri River tributaries and are surviving there at rates comparable to those documented in other Lake Sturgeon populations.

The movements examined in chapters 2 and 3 are likely driven by transitions among habitat patches for feeding, growth, and reduction of physiological stress. Therefore, in Chapter 4 we investigated the variables influencing habitat selection in the age-0 juvenile and subadult/adult life stages. We discovered that: (1) in the Osage River, adult and subadult Lake Sturgeon selected deep (> 8 m), low velocity main-channel pools with fine silt/sand substrates during the summer, fall, and winter, (2) in the Gasconade River, adult and subadult Lake Sturgeon selected similar deep, slow velocity habitats in the summer, fall, and winter, only selected for silt/sand substrates in the fall, and selected for backwaters during the winter, (3) in both tributaries, spawning habitat information was likely not available because individuals were commonly located during migrations,

(4) selection models were spatially transferable and could be used to predict used habitats in the other river, (5) suitability models suggested that suitable conditions for spawning may be widespread upstream of rkm 10 in both tributaries, (6) age-0 habitat was most common in lower reaches of both tributaries, and (7) deep pools for summer and winter refugia were rare and confined to the downstream portions of both tributaries. These results challenge the notion that Lake Sturgeon are large river habitat generalists and identifies potential habitat bottlenecks, as well as areas of opportunity for future habitat conservation and restoration.

Conservation and Management Recommendations

Our study addresses information needs established in Missouri's Lake Sturgeon recovery plan and may be useful in Lake Sturgeon conservation for information-deficient southern populations related to hydrologic regulation, habitat fragmentation, monitoring for natural reproduction, adult/subadult population assessment, management of a future fishery, stocking practices, and habitat restoration or protection.

Hydrologic regulation and habitat fragmentation

Completed in 1931, Bagnell Dam increased flow variability and reduced flow seasonality in the natural hydrologic regime of the lower Osage River. Whereas the Gasconade River is unregulated and lacks major barriers to fish passage. Therefore, we focus on actionable applications of our research for flow management on the Osage River. The Federal Energy Regulatory Commission's (hereafter, FERC) relicensing process requires negotiations between the Bagnell Dam's operator, Union Electric

Company (AmerenUE) and environmental agencies such as the U.S. Fish and Wildlife Service (USFWS), the U.S. National Park Service, the Missouri Department of Conservation (MDC), and the Missouri Department of Natural Resources (DNR) to establish operational guidelines at this facility. Comments are also solicited from the public and private stakeholder groups such as Osage River Flood Control Association. Bagnell Dam’s license was renewed in 2007 and will not need to be renewed again until 2047. Although most amendments to the dam’s operations occur during relicensing negotiations, the agreement provides some flexibility to adjust operations when significant impacts occur (e.g., “if fish protection measures are determined to be ineffective, then the licensee shall take reasonable actions to improve the performance and/or effectiveness of protection measures and shall in good faith consider recommendations of the FWS, the Missouri DC, and the Missouri DNR to improve fish protection”).

Economic and environmental tradeoffs exist in dam management. Historically, the dam’s generation schedules have tracked electricity demand 94% of the time (FERC 118 ¶ 62,247). This operational strategy results in dynamic flows that fluctuate (up to 5 m change in river level in a day) between high generating discharges when electricity demand is high, and low discharges when demand is low. In contrast, a more natural “run-of-river” operation style would release water at rates equivalent to reservoir inputs. This approach has been used to increase Lake Sturgeon spawning success in several smaller northern rivers including the Sturgeon River, MI downstream of Prickett Dam (Auer, 1996). There were also greater abundances of Lake Sturgeon in Ontario rivers that were unregulated or had run-of-river dam operations than in rivers with large-

hydropeaking impoundments (Haxton et al., 2015). Less drastic modifications to dam operations could be made to better approximate a natural condition while accommodating economic considerations. For instance, the 2007 license agreement proposed measures aimed at improving aquatic habitats in the lower Osage River that include: “(a) lake level restrictions, (b) variable minimum flows, (c) ramping rates, (d) DO enhancement program, (e) fish protection measures, (f) measures to enhance aquatic habitat in the lower Osage River, including reducing erosion and sedimentation,” (FERC 118 ¶ 62,247). Our research suggests that aspects of these five categories of proposed management actions may serve a workable framework to promote migration and increase seasonal habitat suitability for Lake Sturgeon.

In some cases, rigid lake level restrictions (action “a”) may be replaced by complex optimization algorithms that incorporate both reservoir surface elevation and natural precipitation events in the watershed to more closely approximate natural hydrologic regimes downstream of hydroelectric dams (Yin et al., 2012). Truman Reservoir further upstream provides flood control protection for Lake of the Ozarks and offers additional flexibility in balancing recreational, economic, and ecological concerns in the Osage River basin. Increased sustained flow releases during spring and fall may trigger upstream migrations. These flow pulses may also facilitate upstream passage over L&D#1 allowing sturgeon to access spawning sites. Although the ecological role of fall migrations for Lake Sturgeon remains unclear, they may be important in scouting spring spawning habitats or accessing foraging grounds (Chapter 1).

Next, by increasing minimum flow requirements (action “b”) and decreasing maximum down-ramping rates (action “c”), AmerenUE could reduce short-term

discharge variability that disrupts migration signals and degrades water quality and physical habitats in the lower Osage River. Upstream spring migrations in the unregulated Gasconade River were positively correlated to above average but declining flows at temperatures from 12-20 °C. These hydrologic conditions rarely occur in the Osage River due to rapid ramp down rates that follow generation. Reduced flow variability during the spring may decrease the number of directional changes during prolonged spring migrations in the Osage River relative to the Gasconade River and increase Lake Sturgeon reproductive success (Auer, 1996). Furthermore, more stable river levels could reduce risk of desiccation for demersal eggs and larvae (Ontario Department of Natural Resources, 2009).

For action “d”, the 2007 license contains provisions to increase water quality through aeration of discharged water. Chapters 2 and 4 suggested that Lake Sturgeon remain sedentary in slow velocity pools which serve as refugia during periods of potentially physiologically stressful oxy-thermal conditions. Cool hypolimnetic discharges during the summer can lower water temperatures and may increase habitat suitability in the Osage River for coolwater fish like the Lake Sturgeon (Li et al., 2015; Lyons et al., 2010). However, summer hypolimnetic discharges at Bagnell Dam often contain low concentrations of dissolved oxygen causing the Osage River to regularly drop below 5.0 mg/L in the summer, a minimum standard established by Missouri DNR’s minimum to support aquatic life (Farless & Landwer, 2020; Missouri Code of Regulations 10 CSR 20-7.031). During hydropeaking, off-channel habitats can have reduced dissolved oxygen relative to main channel habitats (Farless et al., 2018) and may explain why Lake Sturgeon rarely used pools near Bagnell Dam or off-channel habitats

throughout the Osage River compared to the Gasconade River where backwater use was common.

Actions “e” and “f” are mitigation projects for sensitive aquatic taxa and are separate from dam operation. Variable discharges limit Paddlefish (*Polyodon spathula*) reproductive success below Bagnell Dam (Lallaman, 2012). Therefore, the license stipulates that AmerenUE must pay MDC \$134,000 a year to fund propagation and stocking of sport fishes above and below the dam (FERC 118 ¶ 62,247). Similarly, AmerenUE could provide funds to support long-term stocking program for Lake Sturgeon if further research suggests that dam operations are preventing natural recruitment in the Osage River. The Endangered Species Act (ESA) requires that the federal agencies do not engage in actions that will present risks to the existence of listed species or their designated critical habitats. AmerenUE also contributes \$175,000 funding for ecological restoration projects such as the captive propagation of federally listed mussels such as the Pink Mucket (*Lampsilis abrupta*), the Pearly Mussel (*Lampsilis higginsii*), and the Scaleshell Mussel (*Leptodea leptodon*). Similarly, the petitioned listing of the Lake Sturgeon under the ESA may provide additional leverage in flow negotiations (Fink, 2018).

Fortunately, movement data presented in chapters 2 and 3 suggest that Bagnell Dam itself is not a major barrier for adult and age-0 Lake Sturgeon movement. L&D#1 can block Lake Sturgeon movements at low discharges that are influenced by Bagnell Dam. The combined discharge at the Osage River gage station at Bagnell Dam (Bagnell, MO: 0692600, rkm 129) and the Missouri River gage station at Boonville (Boonville, MO: 06909000) must exceed $\sim 2,900 \text{ m}^3/\text{s}$ to permit upstream passage of L&D#1 by

Paddlefish and Lake Sturgeon (Lallaman, 2012; Brandon Brooke, personal communication, Missouri Department of Conservation). Lallaman (2012) found that passable conditions occurred between March 1st and May 31st (the spawning season for Paddlefish and Sturgeon) in 69% of years. Under median historical conditions during the spring migration period the Osage River contributes a small but important 8% to 18% of this minimum passable flow threshold, whereas the Missouri River provides 81% to 91% of the threshold. For comparison, the minimum flow releases prescribed by the license agreement at Bagnell Dam are < 1% of 2,900 m³/s. By increasing minimum flows, except during periods when water retention is needed to mitigate property damage from downstream flooding, we may increase the number of passable days at L&D#1 for migratory fishes. Removal of L&D#1 is a second option to facilitate migration. The dam would likely need to be replaced with an engineered riffle-pool complex to overcome the bed elevation drop and avoid disturbance of upstream mussel beds containing endangered species.

Monitoring for Natural Reproduction

This project was the first to assess Lake Sturgeon putative spawning migrations in Missouri River tributaries and provides guidance on when and where biologists should direct their monitoring effort for Lake Sturgeon reproduction. Chapter 1 indicated that biologists should monitor for Lake Sturgeon reproduction in the Osage River during a migratory period that on average lasts from April 10th to May 26th, whereas in the Gasconade River monitoring should begin and end earlier between March 28th and April 29th. Water temperatures during spring migrations were similar in both rivers and ranged

from 13 °C to 20 °C, which bounds the mean water temperature of 16.4 °C observed during Lake Sturgeon spawning in Mississippi River basin populations (Baril et al., 2018). Elevated discharge was correlated with upstream movement, but our study was not designed to determine how flow metrics influence fine scale movement and spawning behavior near spawning shoals.

In the Osage River during April and May when water temperatures were likely suitable for reproduction we identified areas of frequent Lake Sturgeon use from rkm 48 to 65. This reach contained patches of coarse substrates including riprap training structures, moderate depths, and faster flows that were classified as “preferred” spawning habitats by models developed in Chapter 4. MDC has been developing two-dimensional hydrodynamic models to predict depth and current velocity at various flows in 10 2-km to 4-km reaches. All 10 reaches being modeled by MDC contain potentially suitable spawning habitat according to our model and two of these reaches include areas of high springtime use by tagged Lake Sturgeon. Paired with substrate maps, biologists could use high resolution flow velocity fields from hydrodynamic models to determine where to position egg mats or larval drift nets to validate reproduction under different discharge conditions. Biologists could also refine hormone assays for physiologic markers such as vitellogenin, testosterone, estradiol, and ketotestosterone (Craig et al., 2009) or utilize new genotyping techniques (Scribner & Kanefsky, 2021) to assign sex and reproductive condition to adult fish captured near these sites during the spring. Finally, sonar technology such as Sound Metrics Aris (<http://www.soundmetrics.com/Products/ARIS-Sonars>) or Garmin Panoptix Livescope (<https://explore.garmin.com/en-US/panoptix/>) can produce high-resolution real-time underwater imagery that may allow biologists to

observe Lake Sturgeon spawning behavior in turbid conditions. Interannual variability in upstream migration distance in the Gasconade River precluded the identification of potential spawning sites and further research will be needed to find the location of putative spawning sites.

Adult/Subadult Population Assessment and Management of a Future Fishery

Establishment of harvest quotas or tag sales under a future limited-entry recreational fishery requires long-term monitoring of recruitment, growth, and mortality. Information from our sampling experiences and results of chapters 2 and 4 can be used to inform those sampling efforts. CPUE abundance indices from trotlines or gillnets may be used to monitor Lake Sturgeon population trends in some tributaries. Our results suggested that capture rates were higher with gill nets in the Gasconade River, but we never evaluated sampling efficiency of gill nets in the Osage River (Appendix 2.1). During winter and early spring, most Lake Sturgeon are concentrated the lower 15 km of both tributaries near their confluence with the Missouri River. Lake Sturgeon can also be captured in the gravel-dredging pool at rkm 35 in the Osage River. Catch rates declined in April as Lake Sturgeon migrated upstream. Biologists could deploy gill nets across the mouths of large backwaters in the Gasconade River to intercept Lake Sturgeon as they enter or exit these habitats during spring migrations. Information on seasonal habitat suitability and sturgeon distribution will be provided in GIS layer formats for biologists to reference when conducting sampling.

Attaining abundance estimates of adult Lake Sturgeon in Missouri River tributaries will likely be challenging due to low recapture rates and violation of closure

assumptions (Haxton & Friday, 2019). We only recaptured 4 of the 97 telemetry-tagged Lake Sturgeon during 37 days sampling with setlines or gillnets. Single-season mark-recapture sampling may be most feasible when recapture rates are highest and movement is lowest. For example, in Chapter 1 we found the 2 km long gravel dredging pool at rkm 35 in the Osage River contains high densities of Lake Sturgeon with low immigration or emigration during the winter. Our research also suggests that there may be fairly strong fidelity of individuals to portions of the Missouri River basin near the Osage and Gasconade rivers and mixing of individuals between the Osage and Gasconade rivers suggest that harvest targets should be established collectively for the two rivers. Yet movement into and out of the study area was common enough to violate assumption of population closure for multi-year mark-recapture studies. Mark-recapture population assessments should also consider the impacts of temporal, behavioral (trap-shyness), or individual differences in recapture probabilities (Otis et al., 1978). Lake Sturgeon do not seem to exhibit recapture avoidance in gill nets (Haxton & Friday, 2019), but the trap-response to baited setlines has not been investigated. Some studies have used side scan sonar imagery counts of sturgeon to generate population estimates (e.g., Thomas & Haas, 2002). In our experience mapping habitats for Chapter 4, the image resolution obtained with a Lowrance HDS9 side-scan sonar transducer operated at 455 kHz was insufficient to discriminate Lake Sturgeon from the many other large-bodied fishes (e.g., Paddlefish (*Polyodon spathula*), Blue Catfish (*Ictalurus furcatus*), Flathead Catfish (*Pylodictus olivarius*), Black Carp (*Mylopharyngodon piceus*), Longnose Gar (*Lepisosteus osseus*) etc.).

Although no formal catch-and-release season exists for Lake Sturgeon, anecdotal reports indicate that several Missouri anglers have learned how and where to reliably catch-and-release Lake Sturgeon. Therefore, angling effort may be rapidly directed to seasonal congregation areas, which may impact management decisions. More anglers may be able to participate in a Lake Sturgeon season managed using a harvest quota system, however biologists would need to monitor harvest closely to ensure quotas are not exceeded before closing the season. Alternatively, a tag-system would allow biologists more control over the number of individuals legally harvested, but fewer anglers may be able to participate. Minimum length limits or inverted slot limits would protect subadults or young adults or largest fish in the population (Moore, 2021). Protection of the seasonal refugia we identified in Chapter 1 with spatial restrictions on angling methods is not likely to be well-received by stakeholders and may draw attention to these areas as targets for poachers.

Increasing Lake Sturgeon's recreational value through the promotion of an official catch and release season may inadvertently draw attention to its commercial value as well and increase the risk of poaching for its valuable caviar. MDC has already documented instances of Lake Sturgeon poaching and "egg-checks" where poachers make a slit in the abdomen to check for ripe eggs before releasing the fish (Moore, 2021). Catch and release angling mortality is likely low for Lake Sturgeon. Only two sturgeon in our study shed a tag or died within a week of tag implantation, and our capture and tagging procedure in this study would likely be more stressful to Lake Sturgeon that catch and release angling at water temperatures < 20 °C. Similarly, other studies suggest that sturgeon post-release survival from traditional hook-and-line catch

and release angling is high, although the stress response to handling is dependent on environmental conditions (McLean et al., 2020). MDC may develop programs to educate anglers on appropriate times of the year to fish for sturgeon and proper handling and release practices for Lake Sturgeon.

Our study also indicated that it is possible to capture juvenile Lake Sturgeon using a 2.5 m long mini-Missouri benthic trawl (Appendix 3.1). Using information on movement and habitat selection of juveniles from Chapter 3 to select sampling locations, we were able to capture 12 age-0 or age-1 juvenile Lake Sturgeon including four telemetry-tagged individuals over 3 days in February 2020. Biologists could validate that natural reproduction had occurred by capturing juveniles that lack hatchery markings or during years when MDC has not stocked.

Stocking Practices

Juvenile movement and survival results in Chapter 3 can inform reintroduction practices. Our overwinter survival estimates of 40% to 50% are higher than those reported in other studies and support MDC's decision to stock Missouri River tributaries to establish adult populations there. These estimates of demographic parameters also can inform the establishment of attainable stocking goals. Missouri's latest recovery plan for Lake Sturgeon identified a need to reevaluate initial cumulative stocking goals of 12.5 fish per acre in large rivers, goals which would take an estimated 176 years to attain at current stocking rates (Moore, 2021). Adult and juvenile survival and emigration rates estimated in our study may be used to develop future population viability analyses (Wildhaber et al., 2017) and rough estimates of population size (Ganus et al., 2017).

However, information on natural recruitment is still lacking to inform population models, and current recovery program guidance is to continue stocking until natural recruitment is documented that can sustain the Lake Sturgeon population long-term.

Our results showing high overwinter fidelity to stocking tributaries contrasted with previous studies that documented rapid downstream movement in the Meramec River and emigration into the mainstem Mississippi River (DeLorenzo & Moore, 2017). Fidelity to Missouri River tributaries may make it easier to establish adult population in other large Missouri River tributaries such as the Lamine and the Grand rivers. Although the Chariton River has relatively shallow homogenous habitats from agricultural landuse and channelization that may be unsuitable for Lake Sturgeon occupation throughout the year, the spring detection of Lake Sturgeon at Rathbun Dam in Iowa and multiple captures of Lake Sturgeon including a black-egg female near the town of Yarrow, MO in 2016 suggest that Lake Sturgeon may be attempting to spawn in the Chariton River. Stocking the Chariton River may allow Lake Sturgeon to imprint on this river and increase densities of migrating reproductive individuals in the future.

Habitat Restoration or Protection

The habitat suitability maps we developed predicted that > 77% of the Osage and the Gasconade rivers contained suitable depths and substrates for spawning and it is unknown whether habitat augmentation could increase reproductive success in this population. Variable long-distance migration events in the Gasconade River may indicate interannual variability in the location of optimal spawning habitat or a lack of exceptional spawning habitat that would draw the attention of large aggregations Lake Sturgeon year

after year. Spawning habitat restoration for lithophilic fishes can sometimes be accomplished by restoring habitat forming processes. An example is restoring natural sediment transport processes downstream of dams by adding coarse substrate to the river, which is then naturally distributed by the river's flow (McManamay et al., 2010). Alternatively, spawning reefs can be actively engineered using natural and manmade materials. Lake Sturgeon have successfully spawned on reefs constructed from natural rock or coal clinkers from past industrial activities in the St. Clair River system (Fischer et al. 2018). Geomorphological data can help select the optimal location to construct spawning sites to ensure use and minimize the need for future maintenance to remove silt or algal accumulation (Fischer et al., 2020).

Some spring aggregations of Lake Sturgeon in the Osage River occurred near manmade shoals formed by riprapped training structures which may provide suitable habitat for spawning and egg deposition, and larval development in the Osage River (Bruch & Binkowski, 2002). The two-dimensional hydrodynamic models being developed by MDC at some sites could be paired with fine scale movement studies using an Innovasea Vemco VPS receiver arrays (<https://www.innovasea.com/fish-tracking/fine-scale-movement/>) to confirm whether spawning is occurring there and whether modifications to these structures would increase their suitability for spawning. For instance, these are long linear structures with abrupt depth changes along either side. Perhaps Lake Sturgeon would reproduce more effectively on large patches of cobble with more uniform depths and current velocities. Training structures could also be modified to provide habitat complexity and velocity refuges for Lake Sturgeon to rest between spawning bouts as has been done with notching of wing dikes by the United States Army

Corps of Engineers in the mainstem Missouri River (e.g., Papanicolaou et al., 2011).

Multiagency partnerships between the MDC, USFWS, and landowner associations may be able to develop around restoration or construction at spawning shoals that may benefit sport fish; non-game fish; and mussel habitats while also minimizing bank erosion.

In many Lake Sturgeon populations spawning occurs immediately downstream of dams or natural rapids that are barriers for further upstream migration (Baril et al, 2018). During the spring of 2019 Lake Sturgeon aggregated immediately downstream of L&D#1 until water levels rose to permit them to pass in May. Chapter four's model suggests there is little preferred spawning habitat downstream of L&D#1. However, some of the western bank downstream of the structure has been reinforced by large rip-rap, cinderblocks, and paving tiles. As long as this barrier remains in place, perhaps restoring more shallow rocky habitats to areas near the base of the dam could facilitate spawning of Lake Sturgeon during dry springs when they couldn't access sites further upstream. There may be other reasons for Lake Sturgeon selecting of sites further upstream such as proximity to larval drift and juvenile nursery habitats.

Our research also identifies opportunities to preserve or enhance existing habitat patches that our selection models suggest may be critical for Lake Sturgeon reproduction, growth, or survival. Conservation of deep off-channel habitats appear to be important for overwintering and during migration in the Gasconade River. Limiting floodplain development will allow the river channel to meander naturally and form complex secondary channel habitats. Maintaining habitat diversity is also important to provide the range of habitats Lake Sturgeon selected at different life stages. While adults and subadults seem to overwinter in deep pools, age-0 Lake Sturgeon were often located in

the transitional areas between low and high current velocities and fine and coarser substrates that occurred on the downstream and on the inside of river bends at moderate depths (Appendix 3.2). Options to create deep water habitats seemingly preferred by Lake Sturgeon in the summer and winter are limited. Due to the other negative ecological effects such as increases in suspended fine sediments and channel entrenchment, dredging where it is not currently occurring may not be a suitable strategy to create deep-water habitats for Lake Sturgeon. Instead, efforts to promote water quality and mitigate the impacts of global warming will be important for the conservation of this coolwater species. Dams may reduce summer water temperatures in some systems to moderate the influences of climate change for coolwater fish if sufficient dissolved oxygen is present in dam effluent (Li et al., 2015). Other actions to preserve summer or winter habitats for Lake Sturgeon include maintaining riparian corridors that shade tributaries and intercept nutrients from floodplain agriculture and urban development (Trimmel et al., 2018). Reducing inputs of sediments and nutrients that may cause silt or algal accumulation on spawning sites will also be key to helping maintain suitable spawning habitat for Lake Sturgeon (Fischer et al., 2020). Implementing more gradual ramping rates would help reduce bank erosion that may degrade spawning sites and water quality for aquatic organisms (Mohammed-Ali, Mendoza, & Holmes 2020).

Future Research

There remain many opportunities to build on our research to improve Lake Sturgeon in Missouri. Therefore, we developed a list of the 20 top new or enduring questions related to our chapter themes that could help set a course for future research

endeavors. For each question we consider the urgency of the answer and the likely difficulty of attaining that answer.

Chapter 2-Environmental Drivers of Adult/Subadult Lake Sturgeon Movement:

- 2.1 Is natural reproduction occurring in Missouri River tributaries? (urgency- high; difficulty- unknown)
- 2.2 How does hydrologic instability affect fine-scale movements and spawning habitat suitability in the Osage River? (urgency- high; difficulty- moderate)
- 2.3 What are the physiological effects (growth, stress, survival) of temperatures > 28 °C and dissolved oxygen < 5 mg/L on adult and juvenile Lake Sturgeon? (urgency- high; difficulty- moderate)
- 2.4 What is the adult Lake Sturgeon population size in the lower Missouri River and its tributaries? (urgency- high; difficulty- high)
- 2.5 Are inferences on spatial population structure influenced by tagging location? (urgency- moderate; difficulty- low)
- 2.6 What factors explain interannual variation in migration distance in the Gasconade River? (urgency- moderate; difficulty- moderate)
- 2.7 What is the ecological role of likely non-reproductive migrations (i.e., adult migrations in consecutive years, subadult migrations, fall migrations)? (urgency- moderate; difficulty- high)
- 2.8 What factors influence the idiosyncratic movements exhibited by some individuals? (urgency- low; difficulty- high)

Chapter 3-Survival and dispersal of age-0 Lake Sturgeon:

- 3.1 Do stocked Lake Sturgeon imprint on stocking tributaries? (urgency- high; difficulty- high)
- 3.2 Are movements of stocked juveniles similar to those of wild spawned cohorts? (urgency- high; difficulty- high)
- 3.3 What is the primary cause of mortality in stocked age-0 Lake Sturgeon? (urgency- moderate; difficulty- low)
- 3.4 Where are the preferred habitats for age-1 Lake Sturgeon located? (urgency- moderate; difficulty- low)
- 3.5 What are the impacts on fitness of increased dispersal distances from upstream stocking sites? (urgency- low; difficulty- high)

Chapter 4-Lake Sturgeon habitat selection:

- 4.1 What habitats do Lake Sturgeon use in the Missouri River? (urgency- high; difficulty- low)
- 4.2 How does flow regulation affect optimal the amount of suitable spawning habitat in the Osage River? (urgency- high; difficulty- moderate)
- 4.3 Do plains tributaries (e.g., Grand River) also have suitable year-round Lake Sturgeon habitat? (urgency- high; difficulty- moderate)
- 4.4 What resource is the greatest limitation to future population growth? (urgency- high; difficulty- high)
- 4.5 Why do Lake Sturgeon use off-channel habitat in the Gasconade River but not the Osage River? (urgency- moderate; difficulty- moderate)

- 4.6 Why are Lake Sturgeon rare in some upstream deep-water pools that models suggest may provide suitable summer and winter habitat? (urgency- moderate; difficulty- moderate)
- 4.7 What is the role of spatial scale and patch configuration in habitat selection? (urgency- moderate; difficulty- moderate)
- 4.8 Why do Lake Sturgeon use Missouri River tributaries more than Mississippi River tributaries? (urgency- moderate; difficulty- high)

References

- Auer, N. A. (1996). Response of spawning lake sturgeons to change in hydroelectric facility operation. *Transactions of the American Fisheries Society*, 125(1), 66-77.
doi:10.1577/1548-8659(1996)125<0066:ROSLST>2.3.CO;2
- Baril, A. M., Buszkiewicz, J. T., Biron, P. M., Phelps, Q. E., & Grant, J. W. (2018). Lake Sturgeon (*Acipenser fulvescens*) spawning habitat: a quantitative review. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(6), 925-933.
doi:10.1139/cjfas-2017-0100
- Bruch, R. M., & Binkowski, F. P. (2002). Spawning behavior of Lake Sturgeon (*Acipenser fulvescens*). *Journal of Applied Ichthyology*, 18(4-6), 570-579.
doi:10.1046/j.1439-0426.2002.00421.x
- Craig, J. M., Papoulias, D. M., Thomas, M. V., Annis, M. L. & Boase, J. (2009). Sex assignment of Lake Sturgeon (*Acipenser fulvescens*) based on plasma hormone and vitellogenin levels. *Journal of Applied Ichthyology*, 25(2), 60- 67.
doi:10.1111/j.1439-0426.2009.01289.x

- DeLorenzo, H. & Moore, T. (2017). *2016 Meramec River Fingerling Lake Sturgeon Telemetry Project Report. Missouri Department of Conservation*. Unpublished draft.
- Farless, N., Baebler, E., Landwer, B., & Lobb, D. (2018). *Evaluation of Habitat for Mussels and Their Fish Hosts in the Lower Osage River*. U.S. Fish and Wildlife Service Task Order No. F11AC01144.
- Farless, N., & Landwer, B. (2020). *Lower Osage River Habitat and Fish Community Evaluation*. U.S. Fish and Wildlife Service Task Order No. F11AF00170.
- Fink, M. (2018). Petition to List U.S. Populations of Lake Sturgeon (*Acipenser fulvescens*) as endangered or threatened under the Endangered Species Act. Center for Biological Diversity. Retrieved from <https://www.biologicaldiversity.org/species/fish/pdfs/Lake-Sturgeon-petition-5-14-18.pdf>
- Fischer, J. L., Pritt, J. J., Roseman, E. F., Prichard, C. G., Craig, J. M., Kennedy, G. W., & Manny, B. A. (2018). Lake Sturgeon, Lake Whitefish, and Walleye egg deposition patterns with response to fish spawning substrate restoration in the St. Clair–Detroit River system. *Transactions of the American Fisheries Society*, *147*(1), 79-93. doi:10.1002/tafs.10016
- Fischer, J. L., Roseman, E. F., Mayer, C., & Wills, T. (2020). If you build it and they come, will they stay? Maturation of constructed fish spawning reefs in the St. Clair-Detroit River System. *Ecological Engineering*, *150*, 105837. doi:10.1016/j.ecoleng.2020.105837

- Ganus, J. E., Mullen, D. M., Miller, B. T., & Cobb, V. A. (2017). Quantification of emigration and habitat use inform stocking rates of Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in the Cumberland River, Tennessee, USA. *Journal of Applied Ichthyology*, *34*, 331-340. doi:10.1111/jai.13568
- Haxton, T., Friday, M., Cano, T., & Hendry, C. (2015). Assessing the magnitude of effect of hydroelectric production on Lake Sturgeon abundance in Ontario. *North American Journal of Fisheries Management*, *35*(5), 930-941. doi:10.1080/02755947.2015.1074962
- Haxton, T. J., & Friday, M. J. (2019). Are we overestimating recovery of sturgeon populations using mark/recapture surveys? *Journal of Applied Ichthyology*, *35*(1), 336-343. doi:10.1111/jai.13795
- Li, H. Y., Ruby Leung, L., Tesfa, T., Voisin, N., Hejazi, M., Liu, L., Rice, J., Wu, H., & Yang, X. (2015). Modeling stream temperature in the Anthropocene: An earth system modeling approach. *Journal of Advances in Modeling Earth Systems*, *7*(4), 1661-1679. doi:10.1002/2015MS000471
- Lallaman, J. (2012). *Factors affecting paddlefish reproductive success in the lower Osage River*. [Doctoral dissertation, University of Missouri, Columbia, Missouri]. Retrieved from <https://mospace.umsystem.edu/xmlui/handle/10355/33041>
- Lyons, J., Stewart, J. S., & Mitro, M. (2010). Predicted effects of climate warming on the distribution of 50 stream fishes in Wisconsin, USA. *Journal of Fish Biology*, *77*(8), 1867-1898. doi:10.1111/j.1095-8649.2010.02763.x
- McLean, M. F., Litvak, M. K., Stoddard, E. M., Cooke, S. J., Patterson, D. A., Hinch, S. G., Welch, D. W., & Crossin, G. T. (2020). Linking environmental factors with

reflex action mortality predictors, physiological stress, and post-release movement behaviour to evaluate the response of White Sturgeon (*Acipenser transmontanus* Richardson, 1836) to catch-and-release angling. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 240, 110618.

doi:10.1016/j.cbpa.2019.110618

McManamay, R. A., Orth, D. J., Dolloff, C. A., & Cantrell, M. A. (2010). Gravel addition as a habitat restoration technique for tailwaters. *North American Journal of Fisheries Management*, 30(5), 1238-1257. doi:10.1577/M10-007.1

Mohammed-Ali, W., Mendoza, C., & Holmes Jr., R. R. (2020). Influence of hydropower outflow characteristics on riverbank stability: case of the Lower Osage River (Missouri, USA). *Hydrological Sciences Journal*, 65(10), 1784-1793.

doi:10.1080/02626667.2020.1772974

Papanicolaou, A. N., Elhakeem, M., Dermisis, D., & Young, N. (2011). Evaluation of the Missouri River shallow water habitat using a 2D-hydrodynamic model. *River Research and Applications*, 27(2), 157-167. doi:10.1002/rra.1344

Rules of Department of Natural Resources, Missouri Code of State Regulations, 10 CSR 20-7.031 (2019).

Scribner, K. T., & Kanefsky, J. (2021). Molecular sexing of Lake Sturgeon. *Journal of Great Lakes Research*. doi:10.1016/j.jglr.2021.03.015

Thomas, M. V., & Haas, R. C. (2002). Abundance, age structure, and spatial distribution of Lake Sturgeon, *Acipenser fulvescens*, in the St Clair System. *Journal of Applied Ichthyology*, 18(4-6), 495-501.

- Trimmel, H., Weihs, P., Leidinger, D., Formayer, H., Kalny, G., & Melcher, A. (2018). Can riparian vegetation shade mitigate the expected rise in stream temperatures due to climate change during heat waves in a human-impacted pre-alpine river? *Hydrology and Earth System Sciences*, 22(1), 437-461. doi:10.5194/hess-22-437-2018
- Ontario Ministry of Natural Resources. 2009. *The Lake Sturgeon in Ontario*. Fish and Wildlife Branch. Peterborough, Ontario.
- Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, 62, 3-135.
- United States Federal Energy Regulatory Commission (2007). Federal energy guidelines 118 ¶ 62,247: FERC reports archive Order Issuing New License Project No.459-128 (March, 30, 2007). Washington, DC.
- Wildhaber, M. L., Albers, J. L., Green, N. S., & Moran, E. H. (2017). A fully-stochasticized, age-structured population model for population viability analysis of fish: Lower Missouri River endangered Pallid Sturgeon example. *Ecological Modelling*, 359, 434-448. doi:10.1016/j.ecolmodel.2015.07.019
- Yin, X. A., Yang, Z. F., & Petts, G. E. (2012). Optimizing environmental flows below dams. *River Research and Applications*, 28(6), 703-716. doi:10.1002/rra.1477

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