Canadian Journal of
**Fisheries and
Aquatic Sciences**

OPEN ACCESS | Research Article

# Reproductive contribution of lake sturgeon transferred upstream of dams on a Great Lakes tributary

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## Abstract

Dam construction contributes to declines in the distribution and abundance of many fishes. Increasing connectivity through adult transfer can be demographically and genetically beneficial, but assessing the effects resulting from transfer can be difficult if resident fish exist upstream. Genotypes of adult and larval lake sturgeon (*Acipenser fulvescens*) were used to quantify contributions to larval recruitment from adults transferred upstream of dams on the Menominee River, USA. We evaluated whether transfer timing, sex, and adult size were associated with the odds of reproduction. Elevator transfer operations in Fall 2019, Fall 2020, and Spring 2021 resulted in 152 male and 81 female lake sturgeon transferred upstream. In 2020 and 2021, 580 and 518 larvae were genotyped. We found that 86% (201/233) of adults reproduced and 62.3% (684/1098) of offspring had transferred parents. In total, we estimated that 392 resident adults contributed to offspring production. Mixed matings accounted for 53% of offspring genotyped, increasing levels of offspring genetic diversity relative to offspring produced from resident-only matings. Transferring adults may be a viable restoration alternative for other iteroparous fish in river systems where connectivity to spawning areas has been impeded.

**Key words:** genetic parentage, stream connectivity, Green Bay, fish passage, fish migration, Lake Michigan

## Introduction

Metapopulation persistence is directly related to demographic and genetic connectivity among habitats that are used during critical life stages associated with reproduction, migration, and foraging (Taylor et al. 1993; Hanski 1998). However, anthropogenic activities have resulted in habitat fragmentation and reduced connectivity globally (Donald and Evans 2006; Fischer and Lindenmayer 2007). Accordingly, loss of habitat connectivity is expected to decrease population abundance and species distributions, increase extinction risk, and decrease levels of genetic diversity for many species (Waltert et al. 2004). Barriers to aquatic connectivity are considered the most significant threat to freshwater biodiversity worldwide (Thieme et al. 2021). In freshwater aquatic systems, reduced hydrologic connectivity attributed to dams, road culverts, and road crossings is a threat to ecosystem composition, function, and stability (Baras and Lucas 2001; McAllister et al. 2001; Baumgartner et al. 2022). For instance, in the United States, two million barriers negatively impact mollusks, macroinvertebrates, and resident fish (McAllister et al. 2001). Barriers have contributed to 40% of migratory fishes being listed as imperiled (Jelks et al. 2008), primarily attributed to the obstruction of rivers used historically for spawning migrations and limitations associated with downstream juvenile rearing habitat.

While the number of efforts to remove barriers that impede aquatic connectivity has increased (Bellmore et al. 2017), such an approach is not feasible for many situations associated with hydropower generation and flood control, necessitating the development and application of alternative strategies. One such strategy focuses on using dedicated transfer systems (equivalent to trap-and-transfer and translocation in the fisheries literature; Anderson et al. 2014) as a tool to increase river connectivity (George et al. 2009; Fullerton et al. 2010). Importantly, there is evidence (i.e., genetic rescue effect, Whiteley et al. 2015; Fitzpatrick et al. 2016) that increasing connectivity for populations of conservation concern can enhance recruitment and increase measures of genetic diversity (e.g., Anderson et al. 2015; Evans et al. 2016; Kronenberger et al. 2017). However, a limited set of fish taxa have been studied thus far, which results in uncertainty associated with transfer operations such as when to move fish, the number and sex ratio, and reproductive status. Similarly, measures of transfer success are difficult to quantify, especially if individuals from the same species reside in source and destination locations.

The Laurentian Great Lakes are one of the largest freshwater systems in the world and contain nearly 100 000 barriers that fragment aquatic habitats (Moody et al. 2017). A complex and diverse assemblage of 179 fishes exists in the system; however, many are imperiled because of pollution, overharvest, invasive species, and habitat fragmentation due to dams (Roth et al. 2013). Specifically, as humans exploited the Great Lakes ecosystem, dams were constructed in larger tributaries for processing lumber and improving river navigation (Hayes et al. 2017), and for electricity generation. Many of these dams were situated within a short distance of their confluence with the Great Lakes (see Auer 1996*a*, table 4). As a result, dams are a contributing factor (Auer 1996*a*, 1996*b*; Holey et al. 2000; Coscarelli et al. 2011) to numerical declines in adult abundance and recruitment of many imperiled Great Lakes fishes by blocking access to historical spawning locations (e.g., Reid et al. 2008; Homola et al. 2012; Dymond et al. 2019; Bunnel et al. 2023).

Lake sturgeon (*Acipenser fulvescens*) are a long-lived iteroparous, highly fecund, adfluvial species that migrates seasonally from lacustrine habitats in the Great Lakes into tributaries to reproduce. The life history requirements of lake sturgeon include obligatory spawning migrations, and a diversity of river and lacustrine habitats are required at different life stages, which increase lake sturgeon vulnerability to negative influences of habitat fragmentation (Auer 1996*a*, 1999; Haxton and Findlay 2008; Haxton et al. 2008, 2015). As a result, natural recruitment has decreased largely due to dams blocking access to historical upstream spawning habitats (Auer 1996*a* and references therein; Jager et al. 2001). Dams can also impede downstream migration of larval lake sturgeon from spawning areas to suitable larval rearing habitats (Hegna et al. 2020). Lake sturgeon distribution and abundance throughout the Great Lakes has been reduced to <1% of historic levels (Auer 1999; Hay-Chmielewski and Whelan 1997; Holey et al. 2000; Vélez-Espino and Koops 2009), and the species has become a subject of rehabilitation efforts including regulation of river flows (Auer 1996*b*), harvest regulation (Bruch 1999; Theumler 1997; Hayes and Caroffino 2012), and stocking using streamside rearing facilities (Holtgren et al. 2007; Crossman et al. 2011) and adult transfer (Koenigs et al. 2019; Isermann et al. 2022). Increasing habitat connectivity, including assisted movements of adults above dams to provide access to currently inaccessible spawning and juvenile-rearing habitats, has also been identified as a viable restoration approach (Coscarelli et al. 2011). However, traditional fish passage structures (i.e., ladders) designed for other species (i.e., salmonids) have not generally performed well for sturgeons due to behavioral, phenotypic and physiological limitations (i.e., swimming performance and large size; Peake et al. 1997; Jager et al. 2016; Katopodis et al. 2019).

Adult lake sturgeon have been collected downstream and transferred or allowed to pass upstream of migration barriers to evaluate post-movement behavior with positive results (McDougall et al. 2013; Olach 2015; Boothyroyd et al. 2019; Koenigs et al. 2019; Isermann et al. 2022). Transferred and passed individuals completed upstream migrations to spawning habitats and remained on the spawning grounds for one reproductive season before dispersing downstream (McDougall et al. 2013; Olach 2015; Isermann et al. 2022). However, questions remain regarding which metrics should be used to evaluate the success of transfer and passage operations. Specifically, high mortality during early life (Caroffino et al. 2010; Forsythe et al. 2013) means that the relationship between spawning adult abundance and recruitment measured at early life stages can be difficult to define (Vélez-Espino and Koops 2009; Duong et al. 2011; Burchfield et al. 2022). Transfer and passage also occur in situations where resident adults already exist in receiving waters located upstream of dams. Thus, managers cannot predict increases in expected offspring production based on the number of adults transferred or numbers of larvae captured, as both resident and transferred fish may be contributing to recruitment. Furthermore, determining whether the timing (fall vs. spring or early vs. late spring, etc.), the number of adults transferred, or the sizes and sex ratios of transferred or passed fish influence recruitment success is difficult to quantify unless pedigrees that reconstruct parent–offspring relationships are inferred.

Adaptive management necessitates that restoration actions, like trap-and-transfer operations, be quantitatively evaluated to improve conservation efforts. Combining ecological and genetic data can provide important information to evaluate the outcomes of management actions. Genetic data has been widely used to document the demographic and reproductive effects of barriers to movements (Wofford et al. 2005), and gene flow and benefits of restoration and maintenance of migratory connectivity (Raeymaekers et al. 2008). Multi-generational parentage analyses, including parentage-based tagging (Anderson and Garza 2006; Steele et al. 2019) and close-kin capture-mark-release analyses (Rawding et al. 2014), are widely used to characterize aspects of species' reproductive ecology, including measures of reproduction at the individual level for fish including lake sturgeon (Wang and Scribner 2014; Hunter et al. 2020; Scribner et al. 2022).

The 154 km long Menominee River (MR) flows into the upper western portion of Green Bay in northern Lake Michigan, and is the boundary between Wisconsin and Michigan's Upper Peninsula, USA (Fig. 1). Prior to dam construction, lake sturgeon had access to ~133 km of unimpeded river habitat below a natural barrier at Sturgeon Falls (Thuelmer 1997; Elliott and Gunderman 2008). Five dams constructed in the late 19th century fragmented the MR into six sections of lengths ranging from 2.1 to 35.1 km (Daugherty et al. 2009). The MR as a whole supports the largest population of lake sturgeon across the Lake Michigan basin with an estimated 5272 adults in all river segments (Hayes and Caroffino 2012). Inter-annual variation in natural recruitment within

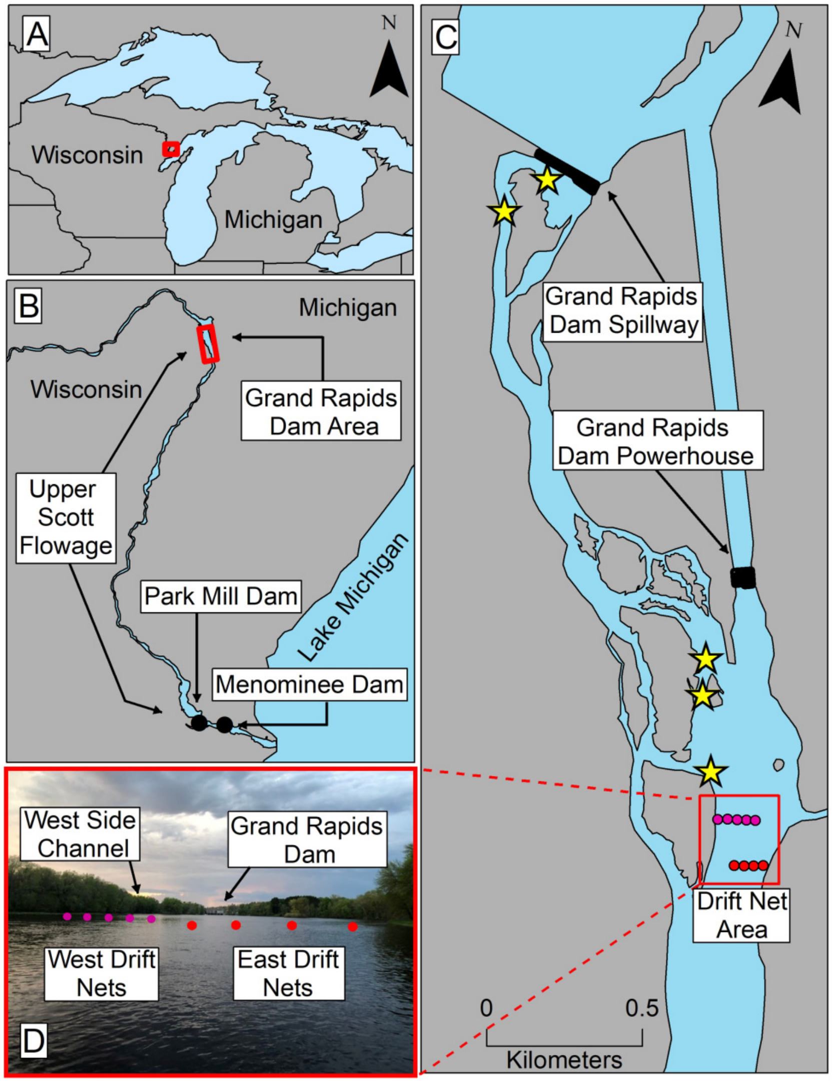


**Fig. 1.** Map of the Menominee River study area located in NW Wisconsin (Panel A). Staging and sexually mature adult Lake sturgeon that entered the fish elevator in the Menominee Dam were lifted into holding tanks within the dam. Within the dam, each fish was processed and then transferred via tank trailer such that the fish could be released into the Upper Scott Flowage 1 km upstream of the Park Mill Dam (Panel B). Fish then migrated upstream to the Grand Rapids Dam where spawning in 2020 and 2021 was observed in the western side channel below the Grand Rapids dam spillway (yellow stars, Panel C). Drift nets were deployed across the river width (Panel D), where river flows from the western side channel and main flows from the Grand Rapids Dam are concentrated. These drift nets were used to sample larval Lake sturgeon emerging and dispersing downstream.

upstream sections of the MR are largely unknown but may be negatively affected by depensatory (Allee effects) effects seen in other lake sturgeon populations (e.g., Black River, Michigan; Dammerman et al. 2020).

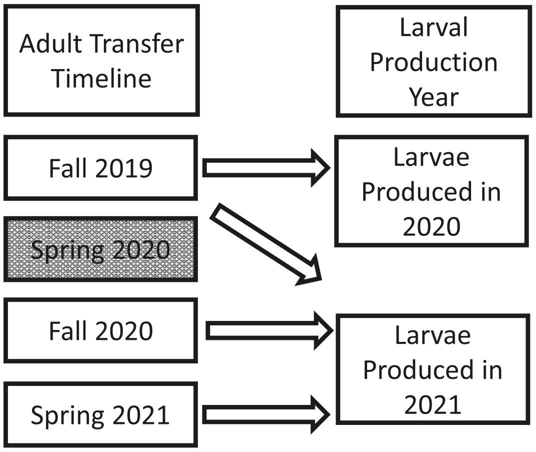
Lake sturgeon migrate into the lower MR from Green Bay and spawn immediately below the Menominee Dam (Fig. 1) where annual adult spawner abundance is ∼800 individuals annually (Hayes and Caroffino 2012) or about 2–3 times greater than the spawning run size of nearby Lake Michigan tributaries (e.g., Peshtigo, Oconto, and Fox Rivers; Donofrio et al. 2018; Tucker et al. 2021), and similarly estimated to be 3–4 times greater than spawning run numbers in the river section upstream of the Park Mill dam (E. Baker, Michigan DNR, written personal communication, 10 July 2023). Recent work shows that annual production of drifting larvae is common and can be substantial within this lower MR section (Lawrence et al. 2020), but the reach is short and highly industrialized, with limited downstream nursery habitat (Daugherty et al. 2009).

The Upper Scott Flowage (USF) is a 31 km river reach ranging from downstream of Grand Rapids Dam to upstream from the Park Mill Dam (Fig. 1). The USF provides several locations of suitable spawning habitat and approximately seven times the amount (or area) of high quality larval/juvenile nursery habitat in contrast to the MR reach below Menominee Dam (Daugherty et al. 2009). Based on capture-markrecapture methods, the USF supports a resident population of lake sturgeon with an estimated 448 resident adults (238–657 95% CI; E. Baker, Michigan DNR, written personal communication, 10 July 2023) that are ≥106 cm in length. A small degree of one-way downstream migration of resident adults through the Park Mill and Menominee Dams is expected from the USF to the lower river section, for example, over the dam spill-ways during periods of high precipitation. However, natural upstream migration is no longer possible since construction of the Menominee Dam ca. 1925.

Passage of adult lake sturgeon to the USF could not easily be accomplished via a traditional fish ladder-based system (Thiem et al. 2011; McDougall et al. 2013). However, an unused turbine bay in the Menominee Dam was ideal for housing a large elevator and hopper with water flow suitable to attract and collect adult lake sturgeon in the fall and spring (see Isermann et al. 2022 for details). Adult male and female sturgeon volitionally entered the elevator below the Menominee Dam, operators periodically closed a trapping gate behind them and they were mechanically lifted in a 3 × 5 × 1 m deep water tank and sluiced into a series of sorting and holding tanks in the dam facility. Individuals were processed for biological data, including sex via ultrasound when possible and sexual maturity stage (Chiotti et al. 2016), and body size (total length). Fish that met maturity (stage F4 black egg females and stage M2 fully developed males; Bruch et al. 2001), size (114 cm for males and 125 cm for females), and health (e.g., no visible sign of disease or injury) requirements were transferred into a tank trailer and transported 1 km upstream of the Park Mill Dam and released into the USF. Fish that did not meet criteria were released back downstream below Menominee Dam. Isermann et al. (2022) reported that most adults (80%; 85 of 106) transferred to USF continued upstream migration and were detected at Grand Rapids Dam generally within 5 days or less. Furthermore, 91% of lake sturgeon transferred upstream remained in USF for at least one spawning season. Collectively, these observations suggested high potential for successful reproduction. However, the contributions to recruitment resulting from these transferred adults were beyond the scope of that study (Isermann et al. 2022).

This study was designed to evaluate reproductive contributions of transferred and resident lake sturgeon adults in the MR, a large Great Lakes tributary where multiple dams have impeded migration to historical spawning areas and population abundance (and presumably recruitment) is greatly reduced compared to historic levels. The joint application of traditional fisheries survey methods and genetic determination of parentage allowed quantification of demographic and genetic contributions of adult lake sturgeon transferred upstream of two dams and released into an existing population. This study focuses evaluation efforts pursuant to installation and initial operation of a large fish passage facility on this river. Specific objectives were to (1) determine the proportional contributions of transferred and resident adult lake sturgeon to annual recruitment within the USF section of the MR, and (2) evaluate whether the timing of adult transfer, sex ratio, and size of transferred adults were associated with the odds of successful reproduction. We also predicted that transfer would lead to genetic benefits such as reduced relatedness among offspring.

**Fig. 2.** Diagram describing the chronology of transfer events. Arrows indicate which set of adults could have contributed to larvae sampled each year. Collection and transfer of adult Lake sturgeon occurred during three different periods of elevator operation relevant to this study. Fall 2019 (28 August to 6 September), Fall 2020 (3 September to 17 September), and Spring 2021 (21 April to 6 May). Adult fish transferred in Fall 2019 were approaching ripe condition and thus projected in spawn in Spring of 2020 but hold over fish are likely. Fish transferred in Fall 2020 and Spring 2021 would have spawned in Spring 2021. Lake sturgeon larval collection occurred in Spring 2020 and Spring 2021.



## Methods

### Study area and adult transfers

Adult lake sturgeon for upstream transfer were collected from the section of the MR below Menominee Dam and were released above Park Mill Dam into USF (Fig. 1). Collection of larval sturgeon for parentage assignment occurred in the upper portion of USF, just below Grand Rapids Dam. Transfers of adult lake sturgeon evaluated for this study occurred during three periods of elevator operation (Fig. 2): Fall 2019 (28 August to 6 September), Fall 2020 (3 March to 17 September), and Spring 2021 (21 April to 6 May). Transfer efforts did not occur in the Spring of 2020 due to the COVID-19 pandemic. While most adults transferred in the Fall of 2019 likely spawned in the Spring of 2020 and dispersed downstream back to Green Bay through the dams (Isermann et al. 2022), hold over behavior is possible as well as repeat (i.e., reproduction in two consecutive years) spawning (males) and so Fall 2019 fish were retained in our analysis. Fin clips were collected from all transferred adults for parentage analysis and to genetically confirm sex (Kanefsky et al. 2022; Scribner and Kanefsky 2021).

### Larval collection

Daily water temperature data were collected from a U. S. Geological Survey gauging station downstream of the

Grand Rapids Dam (USGS Site ID 04067500; N 45.325833, W −87.663333). We assumed annual spawning activity was initiated once the water temperature reached 10 °C (Bruch and Binkowski 2002; Forsythe et al. 2012*a*, 2012*b*). We used the Eckes et al. (2015) larval development model to determine when to start larval sampling. Briefly, the timing of spawning events was estimated based on environmental conditions (i.e., water temperature, lunar phase, and river discharge; Forsythe et al. 2012*a*, 2012*b*; Tucker et al. 2021). Egg and larval development and the timing of larval dispersal from spawning areas was also estimated using daily average river water temperature, estimated egg incubation, and larval development indices (Eckes et al. 2015; Tucker et al. 2021). Timing of all suspected spawning events was calculated to guide the timing of larval drift collections. Larval sampling began once the cumulative daily development index (Eckes et al. 2015) reached 50%–75% since the predicted initiation of spawning (i.e., once water temperature reached 10 °C). Larval sampling continued until no larval captures occurred over two consecutive nights.

Standard D-frame drift nets were used to collect larval lake sturgeon dispersing from spawning grounds in 2020 and 2021 (Smith and King 2005; Tucker et al. 2021). Nets were deployed from a boat nightly from 20:00 to 24:00 h during the period of peak drift (Lawrence et al. 2020; Forsythe et al. 2023). Nets were anchored to the river bottom in two transects where the river narrows, and river flow concentrates (Fig. 1). Five nets were deployed along the western shoreline focusing on water flow from the Grand Rapid Dam spillway (water depth range = 0.33–1.40 m; Fig. 1). It is important to note that river flow to the west of the small island complex (Fig. 1; Panel C) was negligible and too shallow to sample with drift nets. Four nets were set along the eastern shoreline sampling river flow from the Grand Rapids Dam powerhouse (water depth range = 0.52–2.74 m). Larval lake sturgeon were collected from drift nets every 2 h, pooled, and enumerated immediately after completion of the final collection each night (after 24:00 h). Larvae retained for parentage analysis were randomly selected from the total nightly catch and stored in 95% ethanol, with a maximum of 250 individuals per night. Additional larvae were released on site each night at their location of capture. Handling and euthanasia protocols were performed under approved University of Wisconsin—Green Bay IACUC protocols (#F105). After completion of larval sampling each spring, larvae were selected for genetic analyses at random such that the final sample ($N \sim 500$) was proportional to the observed distribution of nightly capture totals.

## Microsatellite genotyping

Genomic DNA was extracted from fin clips of all adult and larval tissue using the DNeasy Blood and Tissue kit (QIAGEN, Germantown, MD). DNA samples were quantified using a NanoDrop 1000 spectrophotometer (Nanodrop Technologies, Wilmington, DE) and diluted to 20 ng/μL for use in PCR reactions. Individuals were genotyped at 13 disomic microsatellite loci as described in Hunter et al. (2020) and Scribner et al. (2022): LS-68 (May et al. 1997), Afu68B (McQuown et al. 2002), Spl120 (McQuown et al. 2000), Aox27 (King et al. 2001), AfuG9, AfuG56, AfuG63, AfuG74, AfuG112, AfuG160, AfuG195, AfuG204 (Welsh et al. 2003), and Atr113 (Rodzen and May 2002), as well as 5 polysomic microsatellite loci: Atr100, Atr114, Atr117 (Rodzen and May 2002), AciG35, and AciG110 (Börk et al. 2008). PCR reactions were carried out in 25 μL volumes (see Supporting Information S1 for reaction conditions). Microsatellite fragment visualization and allele size characterization were performed at the Michigan State University Research Technology Support Facility on an ABI 3730xl 96 capillary DNA sequencer (Applied Biosystems Inc., Foster City, CA). Two experienced laboratory staff scored all genotypes independently using the software GeneMarker (SoftGenetics, State College, PA). Ten percent of the samples were randomly re-genotyped at all 18 loci. Re-genotyped scores were compared with the initial scores to estimate scoring error. Scoring error was 0.71% for the 2020 samples and 0.54% for the 2021 samples.

## Genetic confirmation of passed adult sex assignment

Genetic sex assignment was carried out on adult lake sturgeon using a PCR assay with the AllWSex2 primers (Kuhl et al. 2021), as described in Scribner and Kanefsky (2021) and Sanfilippo et al. (2022). The DNA quality check employed by Sanfilippo et al. (2022), using the primers for microsatellite locus AfuG160, was also performed on 10% of samples assigned as male based on the PCR assay. Sex was assigned to 153 out of 233 adult lake sturgeon via ultrasound at the time of passage. Ultrasound-based sex determination and PCR-assigned sex agreed for 148 of the 153 fish. Five fish identified as F4 (black-egg) females via ultrasound (Chiotti et al. 2016) were classified as male by the PCR-based assay. These five fish were assigned as males in the parentage analyses. The remaining 140 transferred adults were assigned sex based on PCR based assay and molecular sex was used for statistical analyses.

## Inferring parental contributions

We first delineated the potential familial genetic relationships (or lack thereof) between trap-and-transferred adults and lake sturgeon larvae collected in 2020 and 2021 (i.e., pedigree reconstruction). In brief, parent—offspring pedigrees were reconstructed for transferred adult and larval offspring genotypes using the Linux installation (colony2s.ifort.out) of Colony (Jones and Wang 2010; see also Supporting Information S2). Adults transferred in Fall 2019 were assigned to offspring collected in Spring 2020 and Spring 2021. Adults passed in Fall 2020 and Spring 2021 were assigned to offspring genotypes observed with dispersing larvae collected in Spring 2021. All pedigrees were reconstructed in parallel on the High-Performance Computing Cluster at the Michigan State University Institute for Cyber-enabled Research.

Estimates of reproductive success per transferred adult were inferred based on the number of larvae assigned to each parent. Colony also infers unsampled parental genotypes. Thus, we could estimate reproductive success for each inferred parent in the reconstructed pedigree, and in this context, inferred parents were assumed to be unsampled lake sturgeon that were residents of USF (this assumption is supported by simulations; see Results below). We then partitioned the entire pool of sampled larvae using reconstructed pedigrees into one of three different mate-pair categories: (1) larvae from USF residents (Resident × Resident; R × R), (2) larvae from transferred adults (Transferred × Transferred; T × T), and (3) larvae having mixed parentage (Transferred × Resident). Note that because the sex of transferred adults was known, larvae with mixed parentage could be genetically delineated as the result of Transferred male × Resident female (T × R) or Resident male × Transferred female (R × T) mating types.

We analyzed the matings of resident fish (R × R matings), inferred in the reconstructed pedigrees, and found that in 2020 most Colony-inferred resident females (70%) and males (61%) reproduced with at least one transferred adult, which enabled the resident fish's sex to be inferred. We found similar results in 2021 (females: 87% and males 85%). Moreover, the proportion of female and male resident fish that mated with only other residents as compared to all resident fish inferred by Colony did not significantly differ in either 2020 (Fisher Exact Test, $P = 0.40$) or 2021 ($P = 0.83$). These results suggest that if Colony made errors in inferring sex among resident-only mating adults, they were rare and direction of those errors (falsely inferring a female as male or falsely inferring a male as a female) were not strongly biased.

We estimated mean (±1 standard deviation) adult male and female reproductive success (RS) and the effective number of breeders via the sibship method (Wang 2007) provided as part of pedigree reconstructions conducted within Colony (See Supporting Information S2 for further explanation of reproductive success methods). Given that some adults with RS > 0 may not be detected due to pedigrees being reconstructed with a sample of offspring, we estimated the asymptotic total number of successfully breeding adults (i.e., parents) via the pedigree accumulation method (Sard et al. 2021; $N_s$), which considers the total number and relative frequency of parents detected among offspring in the sampled pedigree (Chao 1984).

## Factors related to reproductive success

Multiple logistic regression using backwards variable selection was used to determine if reproductive success of transferred lake sturgeon (i.e., defined here as the probability of producing at least one larval fish collected in drift; similar to Davis et al. 2024) was related to total length (cm), sex, and season of transfer (spring vs. fall). We focused on comparisons using 2021 produced larvae with 2020 Fall and 2021 Spring adults. All statistical analyses were conducted in R version 4.2.2 (R Core Team 2022).

## Resident mating and associated genetic effects

Randomization tests were used to answer two questions. First, we tested if the observed number of offspring assigned to each "category" of adult mate-pairs (♀ × ♂: R × R, T × T, T × R, or R × T) was expected by chance (i.e., based on the joint probability of occurrence). The randomization procedure accounted for the number of transferred and resident parents in the system annually (see also Supporting Information S3). Second, we evaluated whether offspring produced from transferred adults reduced the median offspring relatedness ($R_{xy}$) in the 2020 and 2021 juvenile cohorts collected in USF. Specifically, a randomization procedure was used to test if median $R_{xy}$ statistically differed between offspring produced by different types of mate pairs (Supporting Information S3). Two-tailed tests were used to determine whether observed results were expected by chance ($\alpha = 0.05$) after false-discovery rate corrections (Benjamini and Hochberg 1995).

## Pedigree accuracy and uncertainty

Simulations were used to evaluate the effects of errors associated with pedigree reconstruction (i.e., false negative rate and pedigree assignment accuracy; Sard et al. 2020). All simulated datasets were created using the simulation module developed for polypoid species in Colony (Wang and Scribner 2014; see detailed description in Hunter et al. 2020 and Scribner et al. 2022). Importantly, two key uncertainties associated with reproductive dynamics within the MR system were the number of resident adults contributing to recruitment and the proportion of transferred adults that successfully reproduced. In short, both uncertainties were evaluated via simulations where the number of resident parents varied from 0 to 300, and the proportion of transferred adults that did not reproduce varied (i.e., 25%, 50%, and 75%). Detailed methods associated with pedigree reconstruction simulations and how simulations were used to account for these uncertainties when estimating parameters of interest are described in Supporting Information S3 and see Supporting Information S4/S5 for an overview and schematics.

# Results

## Lake sturgeon adult transfer and larval collection

Elevator operations from Fall 2019 through Spring 2021 (Fig. 2) resulted in 152 male and 81 female adult lake sturgeon transferred upstream into the USF (Total $N = 233$; Table 1). Total length of transferred females ranged from 124.5 to 174.0 cm and males ranged from 110.5 to 154.9 cm. Transferred females (mean ± 1 SD: 151.8 ± 10.6 cm) were significantly ($F_{[1,231]} = 215.1$, $P < 0.001$) longer than males (mean ± 1 SD: 130.4 ± 9.8 cm). On 2 May 2020, the water temperature below the Grand Rapids Dam reached 10 °C, and adult lake sturgeon were observed staging for spawning in shallow reaches on the river's western free-flowing portion below the dam spillway (Fig. 1; yellow stars on Panel C). Larval sampling began on May 25, when egg/larval development of potential spawned eggs on 2 May reached an estimated 75%, and lasted for 9 consecutive days, encompassing one peak of larval drift (Supporting Information S6 and S7). A total of 985 lake sturgeon larvae were captured, and 580 individuals were retained for genetic analysis in 2020 (Table 2). In 2021, water temperatures exceeded 10 °C on 10 April, nearly 1 month earlier than in 2020. Larval collection began on 6 May when larval development reached 50%, and drift persisted for 20 consecutive nights concluding on June 1 (Supporting Information S6 and S7). A total of 9563 lake sturgeon larvae were captured,

**Table 1.** Total number of male and female adult Lake sturgeon trapped and transferred above the Menominee and Park Mill Dams in 2019, 2020, and 2021.

| | | Number transferred | | Total length range (mean ± SD cm) | |
|---|---|---|---|---|---|
| Year | Season | Female | Male | Female | Male |
| 2019 | Fall | 28 | 59 | 125–169 (148 ± 11.2) | 113–150 (129 ± 9.7) |
| 2020 | Spring | NA | NA | NA | NA |
| 2020 | Fall | 12 | 20 | 141–165 (153 ± 7.3) | 114–151 (129 ± 11.5) |
| 2021 | Spring | 41 | 73 | 133–174 (152 ± 10.9) | 111–155 (131 ± 9.4) |

**Note:** Lake sturgeon were not transferred in Spring 2020 due to COVID-19 pandemic restrictions. Measures of total body length of transferred adults is provided for each sex.

**Table 2.** Sample sizes ($N$) for female (F) and male (M) adults transferred above the Park Mill and Menominee Dams, as well as offspring ($N$off) sampled in the Spring of 2020 and 2021.

| Year | Sex | Type | $N$ | $N$off | RS | Parents | $N_s$ | LM Est. | $N_b$ |
|---|---|---|---|---|---|---|---|---|---|
| 2020 | F | Transferred | 28 | 580 | 5.2(2.9) | 28 | 28 (28–32) | – | 254 (213–305) |
| | | Resident | – | | 4.1(2.6) | 106 | 108 (107–117) | 87 (75–99) | |
| | M | Transferred | 59 | | 3.8(1.8) | 52 | 52 (52–64) | – | |
| | | Resident | – | | 4.1(2.4) | 94 | 97 (95–108) | 118 (83–153) | |
| 2021 | F | Transferred | 53 | 518 | 4.9(2.8) | 52 | 53 (52–61) | – | 262 (219–312) |
| | | Resident | – | | 3.8(2.2) | 68 | 71 (69–84) | 55 (43–67) | |
| | M | Transferred | 93 | | 3.0(1.8) | 63 | 68 (64–80) | – | |
| | | Resident | – | | 3.1(1.8) | 104 | 107 (105–117) | 132 (97–167) | |

**Note:** In addition, several parameters, based on reconstructed pedigrees are reported. First, counts (Parents), as well as mean and ±1 SD for reproductive success (RS) are reported for both transferred and inferred, resident parents. Estimates of the number of successfully reproducing adults using the pedigree accumulation method ($N_s$) are reported as well. The table also includes estimates of the total number of resident parents, inferred via linear models point estimates (LM Est.) and 95% confidence intervals are reported. Finally, the effective number of breeders ($N_b$) is reported.

and 1753 individuals were retained in 2021 and 518 larvae from the 2021 cohort were genotyped, respectively (Supporting Information S6). Only 20 of the total 10 548 larvae collected across both years were collected in the drift nets set on the east side of the river channel below the powerhouse.

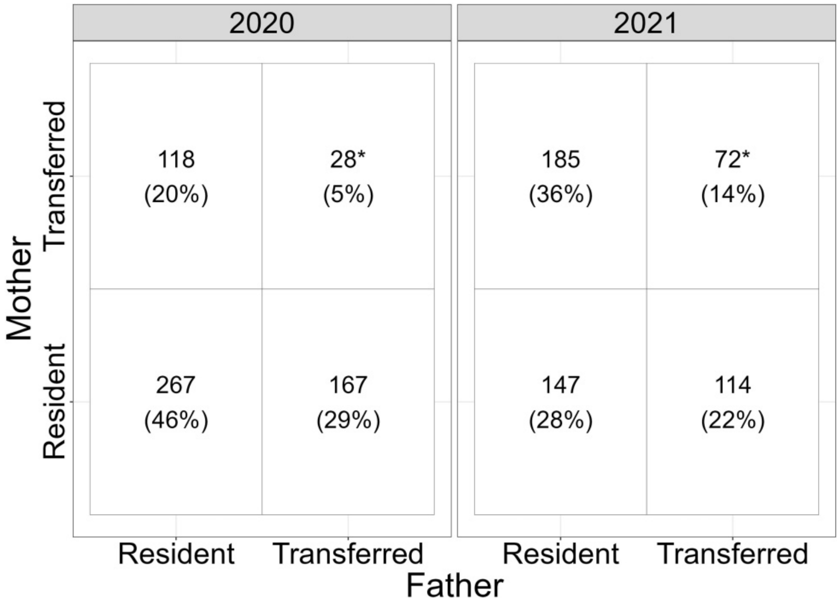
## Assessment of adult transfer success

Overall, 86% (201/233) of transferred adults were assigned as parents for at least one larvae collected during the 2020 and 2021 spawning seasons (Table 2). However, this estimate is naïve because it does not account for offspring sample size, which could falsely infer that an adult was not successful at reproduction because none of its offspring were sampled. Based on null distributions generated via simulation, which account for bias associated with offspring sample size, the probability of adult lake sturgeon successfully spawning after transfer in the MR system was at least 75% for both males and females across both study years.

Mean (±1 SD) individual reproductive success of transferred adults ranged from 3.0 ± 1.8 to 5.2 ± 2.9 offspring, which was similar to resident adults (3.0 ± 1.8 to 4.1 ± 2.6; Table 2) (see Supporting Information for further explanation of reproductive success results). Transferred females, especially those transferred in the Fall of 2019 and Fall of 2020, had the highest mean reproductive success in 2020 and 2021 (5.5 ± 2.9 and 4.5 ± 2.8 larvae per adult), respectively. Males transferred in the Fall of 2019 had a mean reproductive success of 3.3 ± 2.1 larvae/male (2020 larval production) and those passed in Fall 2020 produced 1.8 larvae on average (±2.3) in 2021. We found that 8.7% of the 2021 offspring were produced by fish passed in Fall of 2019. Estimates of the effective number of breeding adults, which is in part influenced by sex ratio and mean and variance in reproductive success (RS, Table 2) for both transferred and resident fish in 2020 and 2021, were not considerably different between 2020 ($N_b = 254$, 213–305, 95% CI) and 2021 ($N_b = 262$, 219–312, 95% CI; Table 2).

Factors associated with successful reproduction (yes/no or RS $> 0$) for transferred adults differed between years. For adult fish transferred upstream in the Fall of 2019, total length, sex, and transfer season were unrelated with the odds of successful reproduction based on larval pedigree assignments in Spring 2020. In contrast, both sex and total length significantly explained variation in the odds of successful reproduction (RS $> 0$) for adults transferred in the Fall of 2020 and Spring of 2021. First, we found that transferred males were 27% (12%–58%; $z = -3.3$, $P = 0.001$) less likely to reproduce than females, supporting randomization results. In addition, we found that larger fish were more likely to reproduce (0.055 ± 0.015; $z = 3.80$, $P < 0.001$). However, the two-way interaction between sex and total length did not explain variation in the odds of success ($z = -0.22$, $P = 0.826$), indicating that regardless of sex larger fish were more likely to reproduce. Both the total length and sex logistic regression models had similar AIC scores (178.3 and 183.7, respectively). When placed in a single additive model, only total length significantly explained variation in the odds of reproductive success, which was expected given that females are larger

**Fig. 3.** Lake sturgeon larvae genotyped in 2020 ($N = 580$) and 2021 ($N = 518$) that were assigned to one of three different parentage categories based on a reconstructed pedigree: (1) larvae from adult lake sturgeon resident to the Upper Scott Flowage (Resident × Resident), (2) larvae from transferred adults (Transferred × Transferred), and (3) larvae having mixed parentage (Resident × Transferred). Larvae with mixed parentage could be the result of resident female × transferred male or resident male × transferred female matings. Statistical significance (*) was assessed via a randomization procedure; see supplemental materials for more details.



than males. Thus, based on the final model, for each 1 cm increase in total length, we found that odds of successful reproduction increased by a factor of 1.06 (1.03×–1.09×, 95% CIs).

## Matings between transferred and resident adults and associated genetic effects

Both pedigree accumulation-based ($N_s$) and linear model-based (LM) estimates, which relied on simulated data to construct a linear model, indicated that more resident adult lake sturgeon (i.e., unsampled parental genotypes inferred by Colony) contributed to larval production in both 2020 and 2021 compared to transferred adults. For the 2020 offspring, the number of female and male resident parents was 106 and 94. After accounting for bias in pedigree reconstruction using linear models, we estimated that 87 (75–99, 95% CI) female and 118 (83–153, 95% CI) male resident parents were successful parents. We found similar linear model estimates for resident females (55, 43–67) and males (132, 97–167) that produced offspring in 2021. Estimates of the number of successfully reproducing adults (resident and transferred) were similar using the pedigree accumulation method (see Table 2). Results collectively support the conclusion that approximately 170–200 residents spawned annually across the study period (Table 2).

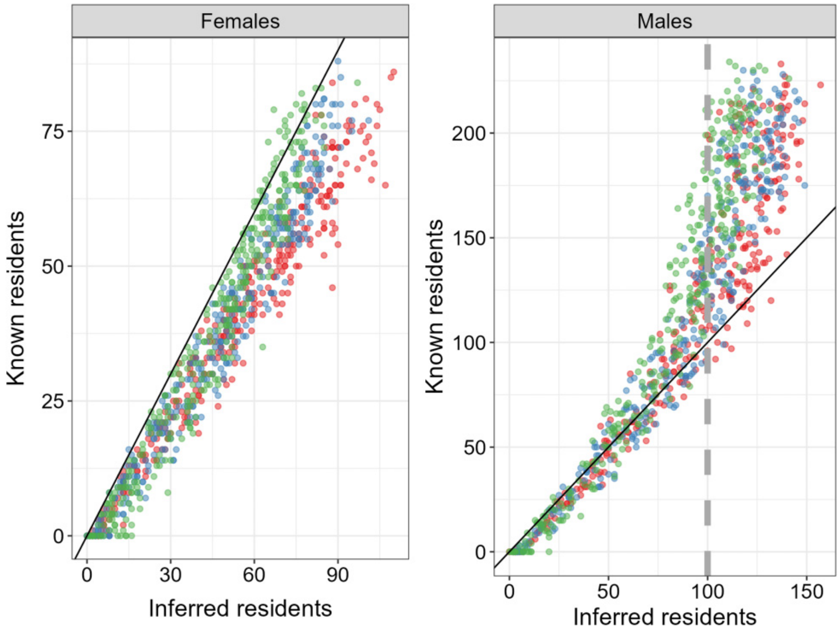
The number of offspring produced by the four mate pair types (R × R, T × T, T × R, or R × T; R refers to resident and T refers to transfer adult) varied from random expectations in some cases. R × R mating pairs produced 46% (267/580) and 28.4% (147/518) of 2020 and 2021 larvae genotyped, respectively (Fig. 3). In contrast, 4.8% (2020: 28/580) and 13.9% (2021: 72/518) larvae were produced by T × T mate pairs across the study period, which was fewer offspring than expected by chance ($P < 0.05$) in both years. Most offspring genotyped in 2020 (49.1%, 285/580) and 2021 (57.7%, 299/518) were produced by either R × T or T × R mate pairs.

The analysis of pair-wise offspring relatedness ($R_{xy}$) estimates between offspring produced in the system indicated comparisons were sensitive to the number of transferred fish placed in the system. For example, given that few transferred fish contributed to recruitment in 2020, median $R_{xy}$ values for offspring produced by only transferred parents were consistently higher (13% ± 8%) than all other comparisons (Supporting Information S8). However, offspring produced by only transferred parents had consistently lower median $R_{xy}$ estimates (7% ± 5%) for the same comparisons in 2021. When focused on offspring produced by only resident parents, the same general trends remained. Specifically, offspring produced by only resident parents had lower (12% ± 8%) median $R_{xy}$ values in 2020 but significantly higher (5% ± 3%) or comparable (i.e., not statistically different) levels of relatedness in 2021 (Supporting Information S8) when comparatively fewer adults contributed.

## Pedigree accuracy

Genotypic data collected from transferred adults and offspring provided the necessary statistical power to reconstruct pedigrees with little error based on the simulation results (Supporting Information S5). Across the parameter space evaluated, most full-siblings (96% ± 3%, mean + 1 SD) and half-siblings (87% ± 7%) were correctly inferred. The largest pedigree errors occurred when known half-siblings

**Fig. 4.** Scatterplot showing the relationship between the number of resident parents (females or males) compared to the known number of parents, determined via simulations, based on reconstructed pedigrees. The solid black line depicts the 1:1 line, and the vertical gray dashed lined, highlights that a truncated simulated dataset was needed to meet the assumption of linearity when fitting a linear model to the data. The model based on the truncated dataset was used to estimate the true number of residents fathers in 2020 and 2021. The colors (red, blue, and green) represent 25%, 50%, or 75% of transferred parents successfully spawned, respectively.



were incorrectly inferred as unrelated individuals (13% ± 7%). The direction of pedigree misassignment modestly inflated the number of adults contributing to the sampled pedigree. Across most parameter space, the number of males was overestimated, with most simulated datasets producing estimates less than 1.5 times known values. The number of females plateaued at 1.25 times that of actual when assuming 25% successful reproduction among transferred females; however, bias declined at both 50% and 75% success as the number of unsampled (residents) adults increased (Supporting Information S9).

Across 25%, 50%, and 75% successful reproduction among males, the number of males contributing offspring declined as the number of unsampled adults increased. Regardless of simulation assumptions, we found that the inferred number of parents can be biased high when few residents contributed to recruitment (Fig. 4). Importantly, this bias was addressed using the linear model approach (LM-$N_s$) described in the Supporting Information when estimating how many resident parents contributed to recruitment in the system. Finally, when no residents contributed to recruitment, Colony never incorrectly inferred a sampled offspring's transferred parents, and at most, Colony falsely inferred one resident parent (Fig. 5).

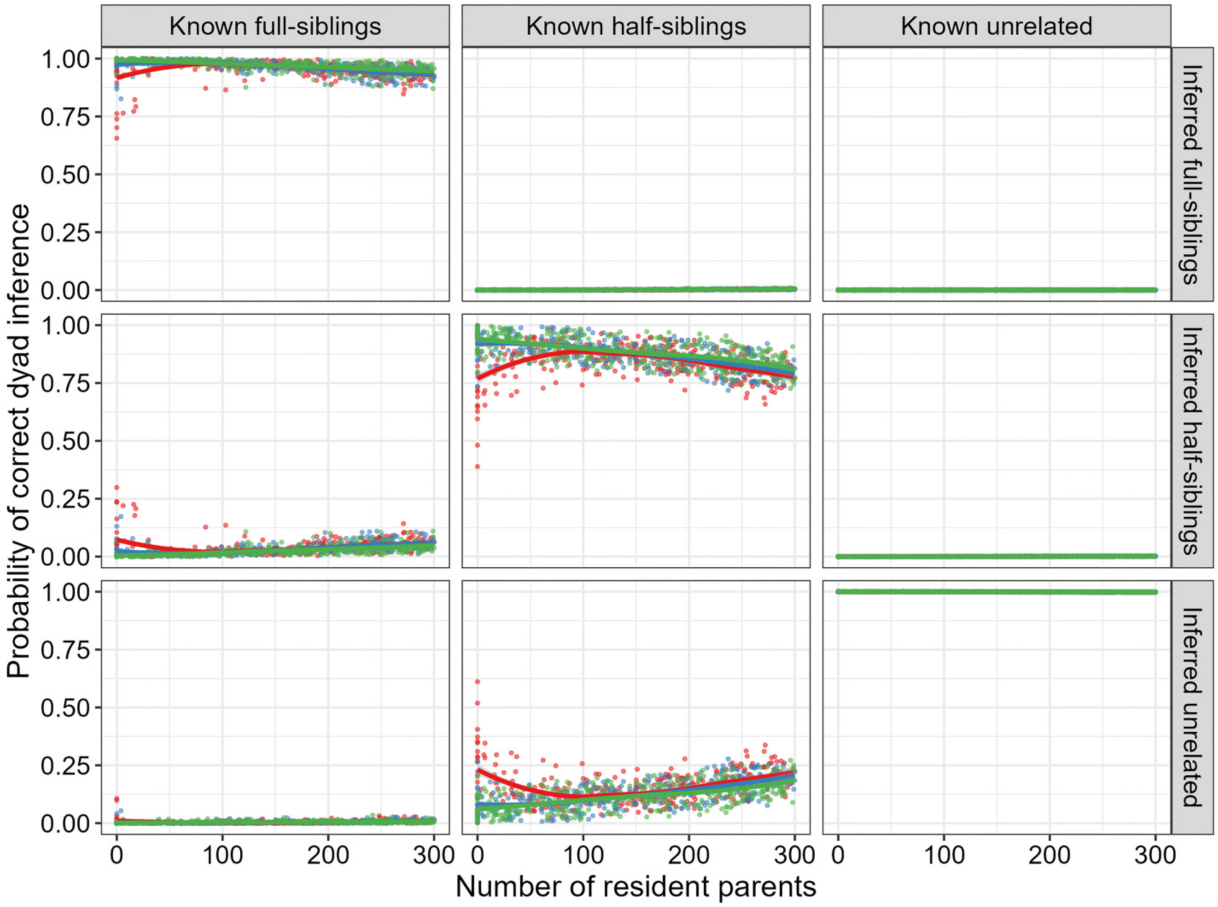
# Discussion

Parent-offspring relationships inferred using genetic pedigree reconstruction, combined with novel modeling and simulation methods, indicated that 233 adult lake sturgeon transferred above the two lowest dams on the MR increased the number of parents that contributed to lake sturgeon recruitment in 2020 and 2021 by ∼40%, with most offspring produced by mate pairs that included at least one transferred adult (51.1% in 2020 and 57.7% in 2021; Fig. 3). The addition of transferred parents reduced median relatedness among offspring with at least one transferred parent as compared to those produced by only resident parents (Supporting Information S8). Collectively, there were demographic and genetic benefits to transferring the 233 adult lake sturgeon above dams to provide them access to additional spawning and offspring-rearing habitat and the ability to mix with the estimated 170–200 annual resident spawners.

## Demographic effects

Empirical and modeling genetic results expand recent translocation studies by demonstrating that adults will complete upstream migrations to spawning habitat that had never been used (McDougall et al. 2013; Boothroyd et al. 2018; Koenigs et al. 2019), and successfully reproduce (Boothroyd et al. 2018). The finding that most (≥73%, based on comparisons to null distributions) transferred adult male and female lake sturgeon consistently contributed to larvae produced during both study years is notable because successful reproduction can vary considerably (35%–80%) across years, based on results in another well-studied system on the Black River, Michigan, USA (Duoug et al. 2023). Similarly, the proportion of adult steelhead (*Oncorhynchus mykiss*), another iteroparous fish species, that successfully reproduce ranged 48%–95% (Seamons et al. 2007). In contrast to iteroparous fish species,

**Fig. 5.** Scatter plots showing results of simulations estimating the probability of correct offspring dyad pedigree relationships (full-siblings, half-siblings, and unrelated) as a function of the number of resident parents represented in the pool of simulated spawning adults. The colors (red, blue, and green) represent 25%, 50%, or 75% of transferred parents successfully spawned, respectively.



pedigree-based studies for transferred Chinook salmon (*Oncorhynchus tshawytscha*; semelparous) consistently estimated that ~50% of all sexually mature adults did not successfully spawn (e.g., Sard et al. 2015; Nuetzel et al. 2023). While the studies compared here were not specifically associated with transferring adults after collection in fish elevators, they do suggest there can be considerable inter-annual variation in successful reproduction and highlight the high probabilities of successful reproduction among transferred adults in the MR. The consistent success of transferred adults is likely due to efforts to only reintroduced sexual mature individuals into the system. However, additional years of evaluation may provide for better characterization of inter-annual variability in spawning success among transferred and resident adult lake sturgeon in this system.

The timing and location of spawning for migratory fish species has a variable effect on measures of fitness (Morbey and Ydenberg 2001), which has become important in the context of fish passage. For instance, Sard et al. (2015) empirically reported that the reproductive success of adult Chinook salmon declined for individuals transferred upstream later in the spawning season; however, the result was inconsistent among years evaluated. Van Leeuwen et al. (2016) for example show that in both European grayling (*Thymallus thymallus*) and brown trout (*Salmo trutta*), a high degree of mismatch between the opening/closing of fishways for species can result in strong eco-evolutionary consequences. Our sample size of seasonal based transfer was small. However, we show evidence that adult lake sturgeon transferred in the spring can have lower than average reproductive success than adults transferred in the fall. It is important to note that a few spring-collected-fish were transferred to the USF less than 10 days before the initiation of that year's spawning activity. It is possible that fall transferred adults may benefit physiologically from reduced post-transfer stress and ecologically from over-winter acclimation facilitating a proper response to the prevailing environmental cues (water temperature, discharge, and lunar effects; Forsythe et al. 2012*a*, 2012*b*) before needing to arrive on the upstream spawning grounds the following spring.

Two hypotheses may explain why the logistic regression analysis of transfer factors indicated that larger lake sturgeon were more likely to successfully reproduce (RS > 0). First, female lake sturgeon transferred from 2019–2021 were at least 125 cm in total length, which is likely larger, on average, than females resident to the USF (Sloss and Kittel 2007).

Thus, increased reproductive success among larger females could be due to individual egg production potential, due to the likely relationship between body size and fecundity described in other systems (i.e., an increase of ∼2000 eggs is expected per cm of fish on average; Bruch et al. 2006). Another hypothesis, which is not mutually exclusive, is that more eggs from larger females could be fertilized because these females may attract more males to mate with (Dammerman et al. 2019). Similarly, larger males may have reproductive success benefits because they may be better competitors in male–male interactions, and in the case for lake sturgeon, may optimally position themselves next to females during egg release into the water column (Bruch and Binkowski 2002).

## Genetic effects of transfer

Translocations are a means of promoting gene flow, which is a tool widely used in conservation biology that can increase genetic diversity, and potentially benefit populations demographically by increasing recruitment (Fitzpatrick et al. 2016; Kronenberger et al. 2017). Offspring produced by transferred and resident parents, which represented most offspring in the system, varied in median $R_{xy}$ estimates, and were sensitive to the number of fish transferred above the dams. Mean relatedness of offspring generally was lower when more adults were transferred and contributed to reproduction.

The simulation framework applied here was novel because it incorporated uncertainty in the number of resident parents contributing to recruitment, as well as the uncertainty associated with the proportion of transferred adults that successfully reproduced. Simulations estimated the magnitude of pedigree assignment error and identified the sources of classification errors (half-siblings misclassified as unrelated). Importantly, the inferred number of males and females were used in a linear modeling framework to provide an estimate that, importantly, included 95% confidence intervals. In addition, simulation framework provided a means to estimate the proportion of females and males that successfully reproduced that incorporated the possibility that not all transferred parents would be detected among a sample of ∼500 offspring annually.

Overall, the effective number of breeder estimates were high ($N_b > 200$) across the study period. Estimates of $N_b$ were comparable to several artificial reefs sampled in the St. Clair-Detroit River system (Hunter et al. 2020), which is a considerably larger system that connect Lake Huron to Lake Erie. $N_b$ estimates in the MR were also larger than the annual population spawning in the Black River, Michigan ($N_b$ range: 63–167) documented in Duong et al. (2023), and the annual lake sturgeon population ($N_b$ range: 17–43) in the Manistee River, Michigan (Scribner et al. 2022).

While effective population size ($N_e$) estimates are more challenging for iteroparous species (Waples et al. 2011, 2013, 2014*a*, 2014*b*), it is expected that $N_e$ will be larger than cohort specific $N_b$ estimates, but below the product of generation time and the harmonic mean of $N_b$ because some individuals will breed in multiple years. Given that $N_b$ estimates were above 200, the MR system is not at risk of severe inbreeding depression associated with populations with $N_e < 50$ (Frankham et al. 2014). A potential disadvantage of assisted gene flow is the possibility of outbreeding depression and decreased overall levels of biodiversity through the mixing of genetically different gene pools. In the MR system, outbreeding depression is very unlikely because the above and below dam subpopulations are part of a historically panmictic population, the abundance of adults below the lower Menominee Dam are at least in part the result of gradual downstream emigration of both juveniles and adults from upriver populations, which include fish originating from many years of past stocking up-river sections with hatchery reared fish, and adults in these river sections currently do not differ genetically (Sloss and Kittel 2007). Previous genetic assignments have identified that adult lake sturgeon from Peshtigo, Oconto and Fox rivers also constitute a minor portion of lake sturgeon below the MR (Donofrio et al. 2018).

## Assessing pedigree reconstruction quality

Genetic reconstructed pedigrees were highly accurate, and associated error rates, inferred through simulations, were similar to other published studies on sturgeons (Hunter et al. 2020; White et al. 2021; Scribner et al. 2022). Multiple studies have attempted to reconstruct pedigrees without parents using a combination of disomic and polysomic loci; as the number of alleles per locus and the number of loci used increased, so too does statistical power to correctly resolve familial relationships (e.g., Jamieson 1994; Christie 2010; Harrison et al. 2013). Genetic variation among disomic and polysomic loci in the MR system provided sufficient information to infer parentage for most sampled offspring (Wang and Scribner 2014) using an established (Hunter et al. 2020) simulation framework.

## Limitations

The number of years where adults and juveniles were sampled provides some insight into the demographic and genetic effects of transferred adults above dams; however, sampling additional cohorts would be particularly beneficial for this long-lived iteroparous species. For instance, USF river conditions during spring migration/spawning were significantly different between 2020 and 2021 (see Supplemental material), which is relevant here because abiotic factors may have affected any number of reproductive features in terms of egg fertilization probabilities, the locations adults are using for spawning, and egg and free embryo survival. Indeed, larval production in the USF was 90% lower in 2020 relative to 2021 despite similar larval netting effort and despite the same number of projected breeding adults. Interannual environmental variability is generally expected to play a role in lake sturgeon reproductive success and larval production to the drift stage (Smith et al. 2017; Dammerman et al. 2019). Thus, future studies evaluating transfer time, numbers and size of transferred adults, and sex ratio are warranted.

## Applications and management implications

Results from this study may help direct future trap-and-transfer efforts for lake sturgeon on the MR and other systems. First, sex determination based on ultrasound (Chiotti et al. 2016) and genetic (Scribner and Kanefsky 2021) techniques were highly concordant. Information pertaining to male and female gamete maturity is currently provided in “real time” only via ultrasound methods, and allow decisions to be made on whether gamete maturity stage is sufficiently advanced to indicate spawning in the next reproductive season. Determination of gamete maturity was likely a significant contributor to the high proportion (>75%) of transferred adults successfully producing offspring. Consequently, we suggest that ultrasound methods could be continued. However, due to the increased handling involved with the ultrasound, it might turn out to be easier on the fish (and the people) to forgo the ultrasound step if nearly all fish collected of a certain size are mature, and if continued evaluation shows that fish moved up stream are finding their way back downstream.

Second, data indicated that adults transferred during the fall are more likely to produce offspring collected in the spring period of larval dispersal than adults transferred during the spring. If resources are lacking, more offspring on average per adult may be expected from fall-transfer efforts if adults are present in sufficient numbers to make increased fall passage logistically feasible. However, recruitment differences between the two different groups of adults were not large and may benefit from further detailed evaluation. Based on research in other rivers (e.g., Black River, Michigan; Forsythe et al. 2012*b*) different groups of adults arrive at spawning areas at different times. However, the number of adults arriving at the elevator during either fall or spring periods is not known in advance and can change quickly within a season and annually. Therefore, we suggest that adult lake sturgeon continue to be transferred and evaluated during fall and spring periods whenever most easily and effectively able, or during whichever season(s) mature adult sturgeon are most available and easiest to logistically pass assuming the same size distribution and sex ratios are available in Fall and Spring.

Third, based on research in other rivers (e.g., Black River, Michigan; Duong et al. 2023) larger males and females will produce more offspring that survive to the period of larval drift. Our data indicate that larger transferred adults will contribute more larvae to the drift stage than smaller adults. However, screening and selection based on phenotype is not advised. Importantly, we found consistently high rates (>75%) of spawning success ($RS > 0$) described here maybe the result of selectively passing adults displaying strong sexual maturity phenotypes. We suggest that in this system where smaller resident adults exist upriver in the receiving waters, that continuing to use the minimum size screening procedure to select predominantly mature adults or continuing to check maturity of all screened fish is a good practice. Adults may be passed based on likelihood of maturity and not based on phenotype.

Fourth, the highly localized nature of available spawning habitat in the USF likely concentrated transferred and resident individuals. Based on the number of offspring captured in nets deployed on the western side of the river and based on trap-and-transferred and resident adults detected in pedigrees, we believe that in these study years, spawning occurred within the western river bypass channel and comparatively little spawning occurred below the east side of the Grand Rapids Dam powerhouse or in other downstream sections. Our research underscores the importance of maintaining appropriate river flows at the Grand Rapids spillway throughout the spawning and incubation season. Collectively, increasing adult connectivity to above-dam habitat in the LSF increased access to ~5876 km$^2$ of spawning and juvenile rearing habitat (Daugherty et al. 2009).

Finally, based on the positive contribution of transferred adult lake sturgeon to the larval production in the UMR, limiting the number of adults passed upstream of the Menominee and Park Mill dams, which has been intentionally and prudently done during the initial years of evaluation of this fish passage facility, may not be necessary. If the management agencies involved in implementing sturgeon passage at these two dams are interested in, and able to increase the number of adult lake sturgeon passed up river, there is certainly data to support doing so, until further evaluation results indicate otherwise.

## Conclusions

Given that hydropower dams exist on most large Great Lakes tributaries including the MR, and complete removal of dams in favor of fish connectivity and passage in the short term is not an option, genetic results from this study were encouraging given that success of transfer and reintroductions of other fishes have been varied (e.g., see Cochran-Biederman et al. (2015) and Kock et al. (2021) for a salmon focused review). Results of this study and those reported in other projects on this river have established that adult lake sturgeon will migrate to known spawning areas after transfer (Isermann et al. 2022), and adults will successfully contribute to larval production (results provided herein). However, lake sturgeon larval survival is low in all river systems (Caroffino et al. 2010; Forsythe et al. 2013; Bruch et al. 2016), and the contribution of transferred fish to early juvenile and later stages will take additional time to determine.

In addition to the upstream fish passage elevator, downstream passage bypass structures were also constructed and have been operated continuously at the Park Mill and Menominee dams to better support downstream passage of adult and juvenile lake sturgeon. While movement of adult fish out of the MR and through the Park Mill and Menominee Dams has been documented (Isermann et al. 2022) and a nominal level might be expected elsewhere (Moore et al. 2021, 2022), future studies could evaluate the extent, timing, and consequences of juvenile downstream movement past and through these structures to Green Bay waters. Collectively, we can conclude that elevator operation is a viable trap-and-transport method for lake sturgeon in this river system. Thus, our results support previous assertions that lake sturgeon transfer over dams is a management action that could improve the likelihood of species rehabilitation in impacted rivers across the species range (Auer 1996*a*,1996*b*; Daugherty et al. 2009; Coscarelli et al. 2011).

## Acknowledgements

We thank staff that contributed to the transfer and evaluation operations that are not included as authors (e.g., Darren Kramer and other MDNR staff, FWS and UWSP staff, other UWGB field staff, etc.). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## Article information

### History dates

Received: 25 July 2024
Accepted: 27 September 2024
Version of record online: 29 January 2025

### Copyright

### Data availability

The data collected as part of this study and affiliated code were reported in part as supplementary information and is available upon reasonable request from the corresponding author. Raw adult translocation data, larval catch and genetic information, data analysis procedures, basic R code for relatedness randomizations, and simulations are also available on Dryad: https://doi.org/10.5061/dryad.dz08kps63.

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### Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Funding information

Funding for this project were provided by the Great Lakes Fish and Wildlife Restoration Act (US Fish and Wildlife Service; F19AP00926-01) and Wisconsin Electric Company via the Mitigation and Enhancement Fund (Project Number MEF20-66). KS and JK were supported through the Partnership for Ecosystem Research and Management (PERM) program between the Fisheries Division of the Michigan Department of Natural Resources (DNR) and Michigan State University and USFWS Sport Fish Restoration Program funds.

## Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0215.

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