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ARTICLE

Male lake sturgeon (*Acipenser fulvescens*) migratory and spawning behaviors are associated with sperm quality and reproductive success

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Abstract: Intra-annual reproductive investments may not be predictive of male reproductive success because of the effects of intra- and intersexual interactions on sperm depletion. For long-lived iteroparous fish species such as lake sturgeon (*Acipenser fulvescens*), reproductive effort may affect lifetime reproductive success. Radio frequency identification antennas were placed at the mouth of the Upper Black River, Michigan, and downstream of spawning locations to quantify male migratory and mating behaviors, including upstream migration time (UT), river residence time (RT), number of intra-annual spawning migrations (IM), interannual spawning interval, and operational sex ratio during 2017–2018. Computer assisted sperm analysis was used to quantify sperm quality. RT had a strong negative influence on sperm concentration and with measures of sperm quality. RT and the number of females encountered were positively associated with male reproductive success (number of offspring sired) across years. RT, IM, and UT were negatively associated with sperm quality, indicating sperm depletion is a reliable measure of sexual activity. Results demonstrate trade-offs between benefits and costs associated with current reproductive effort on future reproduction.

Résumé : Les investissements dans la reproduction au cours d'une année pourraient ne pas prédire le succès de reproduction des mâles en raison des effets d'interactions intra- et intersexuelles sur l'appauvrissement du sperme. Pour les espèces de poissons itéropares longévifs tels que l'esturgeon jaune (*Acipenser fulvescens*), l'effort de reproduction pourrait avoir une incidence sur le succès de reproduction sur toute la durée de vie. Des antennes d'identification par radiofréquence ont été placées à l'embouchure de la rivière Upper Black (Michigan) et en aval de lieux de frai afin de quantifier les comportements migratoires et de reproduction des mâles, dont la durée de la montaison (UT), le temps de résidence en rivière (RT), le nombre de migrations de frai au cours d'une même année (IM), l'intervalle de frai interannuel et le rapport de masculinité opérationnel, en 2017–2018. L'analyse du sperme assistée par ordinateur a été utilisée pour quantifier la qualité du sperme. RT avait une forte influence négative sur la concentration du sperme et sur les mesures de la qualité du sperme. RT et le nombre de femelles rencontrées étaient positivement associés au succès de reproduction des mâles (nombre de jeunes engendrés) pour les deux années. RT, IM et UT étaient négativement associés à la qualité du sperme, ce qui indique que l'appauvrissement du sperme est une mesure fiable de l'activité sexuelle. Les résultats illustrent les compromis entre les avantages et les coûts associés à l'effort de reproduction actuel sur la reproduction future. [Traduit par la Rédaction]

Introduction

Fish exhibit different mating behaviors (reviews in Baylis 1981; Komers 1997; Avise et al. 2002). Within species and populations, there can also be considerable behavioral plasticity that is related to demographic and physical environmental variables. For example, individuals within populations often show considerable plasticity in behaviors when exposed to different environmental conditions (Warren and Morbey 2012; Mittelbach et al. 2014). Male phenotype and demographic conditions (e.g., operational sex ratio (OSR); Emlen and Oring 1977) or age–size structure (Wootton and Smith 2014) can also elicit plasticity in behaviors, including the timing and location of reproduction that in turn can affect individual reproductive success (RS) (Jørgensen et al. 2008; Lowerre-Barbieri et al. 2016). Behavioral plasticity is likely to be increasingly important to population dynamics and persistence in situations where formerly reliable migratory and reproductive cues are no longer predictive of positive fitness outcomes (Schlaepfer et al. 2002).

Reproductive effort and energy expenditures also vary widely across species (Wootton and Smith 2014). For long-lived iteroparous species, reproductive costs can be high, and maximum reproductive output across all ages is highly variable (Partridge and Harvey 1988). Life history theory predicts that optimal reproductive effort in the current year will depend on the reduction in future reproductive output over an individual's lifetime (Gadgill and Bossert 1970). Male decisions to invest in current reproduction may have important effects on future reproductive frequency and success (Pianka and Parker 1975).

Migration is energetically demanding (Binder et al. 2011), and for many species, migration is part of reproductive energy expen-

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ditures (Jonsson et al. 1997; Pollock 1984; Wootton and Smith 2014). Timing of spawning migrations into streams and the timing and duration of reproduction by fishes are influenced by environmental cues, including photoperiod (Quinn and Adams 1996; Bizzotto et al. 2009), and other environmental variables, including stream discharge and temperature (Kamler 2002; Forsythe et al. 2012*a*). Timing of migration and spawning optimally occurs under favorable environmental conditions that affect resource expenditures allowing allocation of resources for intra- and intersexual interactions (Wootton and Smith 2014). Time of reproduction also affects the likelihood of offspring being produced under circumstances suitable for incubation and posthatch growth and survival (Einum and Fleming 2000).

Across teleost species, fertilization rates can be highly variable (Kowalski and Cejko 2019), particularly in broadcast spawning species that reproduce in rivers and where gametes are extruded into the water column. Duration of proximity to females, number of female encounters, and sperm quality traits likely also affect fertilization rates (Stoltz and Neff 2006).

Males that produce and expel highly concentrated and (or) high volumes of sperm should have higher RS (i.e., number of offspring sired) than males with lower sperm quality or concentration. Sperm concentration is related to fertilization rate and is a reliable predictor of male RS (Parker 1990). Sperm motility (Kime et al. 1996) and velocity (Gage et al. 2004) have been widely shown to be useful parameters to quantify sperm quality and as a predictor of egg fertilization (Gage et al. 2004; Rurangwa et al. 2004; Gallego and Asturiano 2018). Technological advances allow for detailed characterizations of sperm quality traits, allowing for the assessment of additional factors believed to be associated with male RS (Boschetto et al. 2011; Burness et al. 2004).

RS of males in many polygamous species, including fishes, (DeWoody and Avise 2001; Avise et al. 2002) is associated with access to mates, whereby RS increases with increasing mate number (Bateman 1948; Trivers 1972) and mate quality (Arnold and Duvall 1994; McGuire et al. 2011). For example, availability of males, along with environmental factors such as water velocity and temperature, have been shown to affect spawning behaviors and female RS in lake sturgeon (*Acipenser fulvescens*) (Dammerman et al. 2019).

Lake sturgeon are a long-lived, iteroparous, and potamodromous (lake to river spawning migration) species that exhibits natal philopatry (Bemis and Kynard 1997; Homola et al. 2012). Spawning migrations from large lakes into river occurs in the spring (Bruch and Binkowski 2002; Forsythe et al. 2012*a*, 2012*b*; Peterson et al. 2007). Male lake sturgeon can make multiple spawning migrations to upstream spawning areas during a single reproductive season and repeatedly over a lifetime (Auer 1996; Bemis and Kynard 1997; Rochard et al. 1990).

Lake sturgeon exhibit considerable variability in migratory and reproductive behavior, including timing of initiation of spawning migration, river residence time, upstream migration time, and number of intra-annual spawning migrations (Forsythe et al. 2012*a*, 2012*b*). This variability is attributed to environmental conditions such as water temperature and discharge and intraspecific interactions including number of potential mates and OSRs (Bruch and Binkowski 2002; Dammerman et al. 2019; Forsythe et al. 2012*b*; Thiem et al. 2013). Males often arrive in the spawning grounds before females and may remain as long as females are present (Bruch and Binkowski 2002; Peterson et al. 2007). Spawning periodicity (the number of years between spawning runs) is variable within a sex and between males and females (Forsythe et al. 2012*a*). Lake sturgeon operational sex ratios vary among populations, across years, and intra-annually within populations. Sex ratios are typically male-biased, largely due to sex differences in interspawning interval (Forsythe et al. 2012*b*). Polygynous and polyandrous spawning behaviors have been observed, resulting in two to eight males participating in spawning bouts with a female (Bruch and Binkowski 2002; Peterson et al. 2007). Genetic determination of parentage in the Upper Black River (hereinafter UBR) has shown that over a spawning season, offspring from a single female may be sired by over 30 males (Duong et al. 2011*a*). Competition is high among males to gain access to females (Bruch and Binkowski 2002).

Males that engage in behaviors and expend resources to access females during spawning migrations may increase fertilization opportunities, but potentially reduce fertilization success as the spawning season progresses. Extended male reproductive activity may result in greater intermale variability in sperm quality and concentration. Bruch and Binkowski (2002) documented sperm to be more dilute near the end of the lake sturgeon spawning season.

This study characterizes effects of different prespawning migratory and mating behaviors on measures of sperm quality and concentration, male RS, and reproductive interval during each of two years in the UBR, Cheboygan County, Michigan, for a well-studied population of lake sturgeon. Monitoring data on physical stream features, radio frequency identification (RFID) tagging and monitoring of male movements, estimates of sperm concentration and quality, and genetic determination of parentage were jointly used to determine how current year migratory and spawning behaviors (measures of current year reproductive investment) affected sperm concentration and quality and male RS.

The objectives of this study were to (*i*) characterize associations between lake sturgeon sperm concentration and quality (velocity and motility duration) and migratory and spawning behaviors (river residence time, upstream migration time, the number of intra-annual migrations, and the interspawning interval between spawning years as measures of current year reproductive investment), (*ii*) assess whether male migratory and spawning behaviors associated with current year reproductive effort were positively associated with the number of females encountered during a spawning season, and (*iii*) determine whether increased reproductive investment within a year resulted in higher RS. Implications of associations between physical environmental features (temperature and discharge) and biotic responses (migratory and reproductive behaviors) will be discussed in the context of current and future environmental change and variability and the species conservation status.

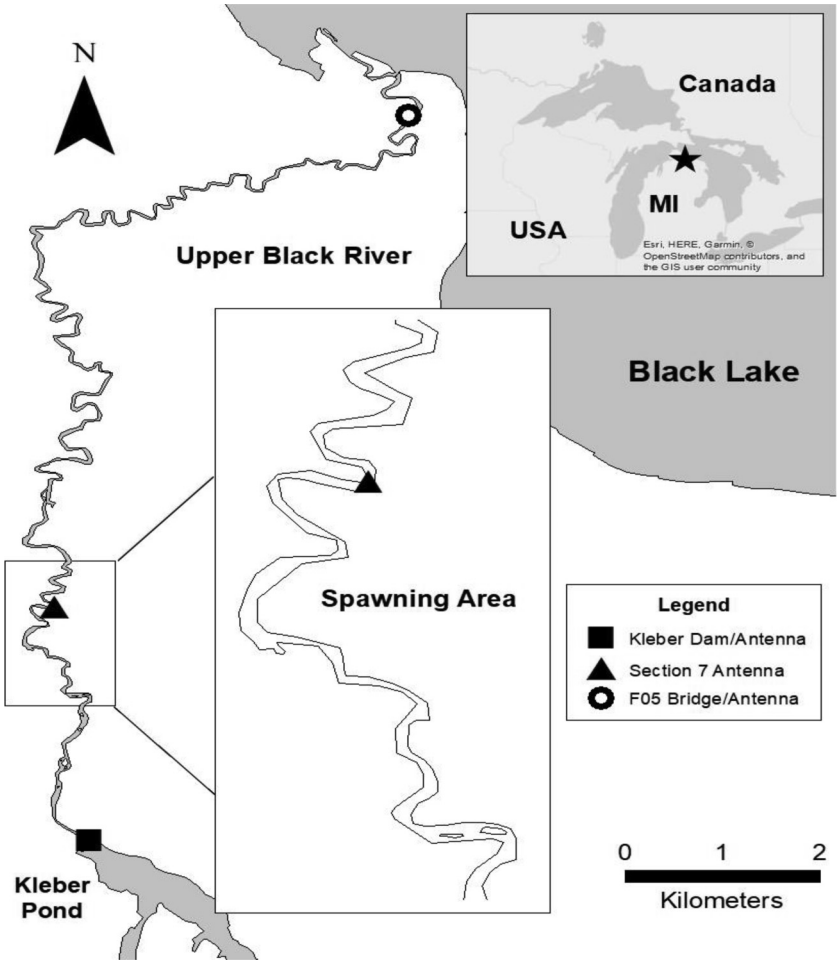
Materials and methods

Study site

The study was conducted during 2017 and 2018 in the UBR, a fourth-order tributary of Black Lake, located in Cheboygan County, Michigan (Fig. 1). The lake sturgeon population in Black Lake is isolated from other populations by Alverno Dam on the Lower Black River. Kleber Dam on the UBR restricts lake sturgeon to the lower 11 km of the river (Baker and Borgeson 1999). The main spawning areas are shallow (~1–3 m) and reasonably narrow (~25 m), allowing for daily access and high levels of detection and tracking using RFID technology to enumerate spawner abundance.

Black Lake has an estimated adult population of 1197 individuals (Pledger et al. 2013; Michigan State University (MSU) and Michigan Department of Natural Resources (MDNR), unpublished data), of which an estimated 660 are male and 537 are female. The annual number of spawning adults identified in the river since the onset of RFID data collection were 268, 349, 343, and 413 individuals from 2016 to 2019, respectively (MSU and MDNR, unpublished data). The timing of spawning by individual males and females in the UBR is repeatable across years (Forsythe et al. 2012*b*). The duration of the spawning season on the UBR during 2017 and 2018 was 48 days (16 April 2017 – 3 June 2017) and 31 days (2 May 2018 – 2 June 2018), respectively.

Fig. 1. Study site on the Upper Black River, Cheboygan County, Michigan. The circle indicates radio frequency identification (RFID) antennas at the highway FO5 Bridge (0.5 km from Black Lake). The triangle indicates locations of the RFID antennas at the downstream-most portion beginning of the spawning area (7 km from Black Lake). The square indicates the location of the RFID antenna at Kleber Dam (11 km from Black Lake).



Adult capture and sperm collection

Spawning lake sturgeon were physically captured in known spawning areas (Forsythe et al. 2012*a*, 2012*b*) in the UBR above the upstream RFID antenna arrays (Fig. 1). Fish were captured by divers in wetsuits using long-handled landing nets. Captured individuals were sexed by examining cloacal and gross morphology as described in Forsythe et al. (2012*a*). Total length (TL, cm), fork length (FL, cm), girth (cm), mass (kg), and capture location were documented at time of capture. Variance inflation scores (car library, R Studio 3.5.1) indicated that variables were correlated. Fork length was chosen as the representative body size variable for subsequent analyses. Fish were checked for RFID tags, and untagged fish were tagged with a 12 mm, full-duplex 134.2 kHz PIT tag (BioMark, Inc.), a 23 mm (0.6 g) or 32 mm (0.8 g) half-duplex 134.2 kHz RFID tag (Oregon RFID, Inc.), and an external Floy tag (Floy Tag & Manufacturing, Inc.) so that individuals could be identified visually and using passive PIT tag receivers. Previous work indicated PIT tag retention in adult lake sturgeon exceeds 95% (Donofrio 2007). Adult lake sturgeon in the UBR began receiving full-duplex PIT tags in 2001 and half-duplex RFID tags in 2012. Since adding RFID tags to the annual adult assessment, 1118 individuals (88.44% of the estimated spawning population; Pledger et al. 2013; MDNR unpublished data) have been captured and tagged. The 2-year duration of this study is appropriate to address our objectives because research at our Black River study site has demonstrated that 43% and 57% of adult males spawn at 1- and 2-year intervals, respectively, based on annual estimates from a repeat-spawning open population estimation model (Pledger et al. 2013). Additionally, a 2-year sampling period is consistent with other studies of lake sturgeon RS (e.g., Dammerman et al. 2019).

Prior to sperm collection, the urogenital opening and the surrounding area were dried to avoid premature activation. Sperm was collected using a sterile 10 mL Luer slip tip plastic syringe (Medline Industries, Inc.) by applying pressure anterior to the urogenital opening and drawing expelled sperm into the syringe (Crossman et al. 2011). Syringes were placed in labeled ziplock bags and immediately placed on ice and transported to the lab. Measures of sperm quality and concentration were made within 12 h of collection (Ciereszko et al. 1996, 2006; Alavi et al. 2012).

Migration studies of prespawning lake sturgeon have typically used telemetry to track individuals (Auer 1999; Donofrio et al. 2018). High costs of radio or acoustic telemetry technology have limited the number of fish tracked (Lucas and Baras 2000). Advances in RFID technologies have made available less costly methods of identifying and tracking individuals to characterize behavior using smaller, individualized numeric tags (Gibbons and Andrews 2004). Use of recent technologies that allow large proportions of wild populations to be tagged and followed permit accurate inferences to be made about population-level processes from individual observations.

Five pass-over RFID antennas that span the entire width of the river were installed to detect half-duplex RFID-tagged adult lake

sturgeon during spawning migration. Three antennas were installed 0.5 km upstream of the mouth of the river, and two antennas were installed at the downstream end of the spawning area (Fig. 1). Replicate antennas were installed at each site to increased detection efficiency. RFID antennas were constructed with 8-gauge pure oxygen-free copper wire with 805 tinned strands. To provide protection and support, wire was housed inside 3.81 cm diameter PVC pipe. Antennas were 60.96 cm wide and varied in length between 18 and 27.5 m, depending on river width.

Each RFID antenna system consisted of a single-antenna, a half-duplex reader (Oregon RFID, Portland, Oregon) to power the antenna and record data, a tuner board to achieve proper electromagnetic resonance, and a power source to power the system. At the mouth of the river, we used commercial electrical grid power; at the spawning grounds site, we used two 200 W solar panels (Zamp Solar, Bend, Oregon) and a single battery to provide power. Half-duplex RFID antenna systems constantly switch their electromagnetic fields on and off to wirelessly charge and detect RFID tags. RFID antennas were set to have a charge and listening cycle of 50 ms, which results in a net scan rate of 10 times per second. Because the antennas at each site were in proximity, the paired antennas were synchronized to prevent charge–listening cycle interference. Two antennas are synchronized by adjusting the charge pulse of the antenna so that both readers charge at the same time and thus read tags at the same time. When two antennas are not synchronized, one antenna will attempt to listen for a tag response while the other attempts to charge a tag. The resulting interference lowers tag detection range.

RFID antennas were inspected weekly to ensure adequate read range and proper functionality. Read range varied from 26 to 50 cm, which was acceptable for lake sturgeon, because half-duplex tags were inserted in the pectoral fin musculature, the river is shallow, and lake sturgeon swim on or in close proximity to the stream bottom (Hay-Chmielewski 1987). By placing RFID antennas at the river entrance and immediately downstream of the spawning grounds, a number of behavioral variables could be quantified, including (1) the number of tagged spawning males and females and OSR on the spawning grounds, (2) time and date of first river entry date and hour, (3) number of intra-annual spawning migrations, (4) river residence time (hours), (5) spawning grounds residence time (hours), (6) upstream and downstream migration times (hours), and (7) interannual migration time (years). The number of spawning migrations was calculated as the number of complete river migrations defined by (*i*) an entry detection at the river mouth, (*ii*) entry detection at the spawning grounds, (*iii*) exit detection at the spawning grounds, and (*iv*) an exit detection at the river mouth. River residence time (hours) represented the total time in the river, including upstream migration to the point of sperm collection. Upstream migration time (hours) was the time an individual male took to migrate from the mouth of the river to the antenna at the downstream end of the spawning grounds (Section 7, Fig. 1).

Differences among upstream time (hours), river residence time (hours), fork length (cm), sperm concentration (no.·mL^{-1}), and OSR (no. males/no. females) of all fish that migrated in 2017 and (or) 2018 were quantified using Wilcoxon–Mann–Whitney tests (WMW; Siegel and Castellan 1988). Differences among intraspawning migrations, interspawning interval, upstream time, river residence time, sperm concentration, and OSR for fish that migrated in both 2017 and 2018 (n = 16) were evaluated using WMW tests (1988). OSR was calculated as the number of males per female lake sturgeon upstream of the antenna at the start of the spawning grounds over the period each male occupied the spawning area. RFID data allowed estimation of the amount of time males and females were together in the spawning area, and therefore, male and female combined residency was inferred as "female exposure", which was used as a surrogate of male reproductive opportunity. Fish that were upstream of the antenna for any time during a day were considered present on that Julian day. RFID data were converted to spawning migration data in R (3.5.1; www.r-project.org) using package PITr 1.1.0 (Harding et al. 2018).

Differences in male lake sturgeon exposure to female lake sturgeon as a function of the number of intra-annual migrations (one to three total migrations) were evaluated using a nonparametric Kruskal–Wallis (KW) one-way analysis of variance (ANOVA) (Kruskal and Wallis 1952). Post hoc analysis of difference between number of migrations were analyzed using a Dunn's test (DT) of multiple comparisons (Dunn 1964). Alpha values were corrected using the standard Bonferroni method (Bonferroni 1936). Male lake sturgeon were considered "exposed" to a female when both the male and the female were upstream of the antenna at the downstream end of the spawning grounds (Fig. 1). The relationship between the number of females to which a male lake sturgeon was potentially exposed and time spent in the river (river residence time) was evaluated using a generalized liner model. As potential female exposures were evaluated as a count variable, a Poisson distribution was used.

Estimation of sperm concentration

Two replicates of sperm were collected and averaged for each male to quantify sperm concentration and measures of quality. A dilution of 5 μL of sperm to 200 μL of river water (1:40) was used as a baseline dilution for activation. In cases where concentration of sperm exceeded 5.00 × 10^8 sperm·mL^{-1} and sample could not be effectively counted, a dilution of 0.5 μL of sperm to 200 μL of river water (1:400) was used.

Following activation, 5 μL of sperm was placed on a Neubauer hemocytometer (0.0025 mm^2 grid, Weber Scientific, Inc.). Neubauer hemocytometers have been widely used to measure sperm concentration and motility to standardize dilution and activation data (Mahmoud et al. 1997; Mortimer et al. 1986). Within 10 s of activation, a digital image was recorded to quantify concentration, using the 40× objective of a Nikon Eclipse E100 compound microscope with a Nikon 0.7× DXM relay lens and an optiMOS 16-bit monochrome camera. Still images were recorded using the open-source Micro-Manager software (version 1.4). To calculate concentration, we counted sperm from two 4 × 4 grids of the hemocytometer using the point counting tool in ImageJ 1.51 (US National Institutes of Health, http://rsb.info.nih.gov/nih-image/). The two counts were averaged and converted to a sperm concentration as in eq. 1:

$$\text{Sperm Concentration} = C_{1,2} \times 25 \times 10\,000 \times D_f \quad (1)$$

Variable $C_{1,2}$ is the averaged count of sperm in each 4 × 4 grid, 25 is the number of 4 × 4 squares, 10 000 is the conversion from number of cells counted per mm^2 to 1 mL, and D_f is the calculated dilution factor.

Statistical analysis of sperm concentration

Models analyzing variation in sperm concentration were fitted using the glm function (Gaussian family) in R (3.5.1) (www.r-project.org). Independent variables describing all possible combinations of variables, including a full and null model, were fit. AIC values and weights were calculated for each model using the dredge function of the MuMIn library (Bartón 2017). Model averaging was performed for all models for which the $\Delta AIC_c < 4$ (Burnham and Anderson 2002; Bunnell et al. 2012) using the model.avg function of the MuMIn library (2017).

Sperm concentration data were analyzed using a general linear model including body size at the time of capture, river residence time, upstream swimming time, years between spawning migrations, the number of migrations within a season, and spawning year (2017 and 2018). The full model included six variables, including year, for which the interactions with other variables were

considered. All variables were tested for normality using Shapiro–Wilk tests.

Estimation of sperm quality

Sperm samples collected during 2018 were assessed using a computer assisted sperm analyzer (CASA) system using the ImageJ CASA plugin (1.0) described in Wilson-Leedy and Ingermann (2007). Image stacks (16-bit, 480 × 270 pixels) were created using the Multi-Dimensional Acquisition tool each representing one frame of video collected at 100 frames·s^{-1}. A total of 3000 frames were collected representing 30 s of sperm video 10 to 40 s postactivation. Video was recorded using the 40× objective of a Nikon Eclipse E100 compound microscope with a Nikon 0.7× DXM relay lens and an optiMOS 16-bit monochrome camera. One second of sperm movement (frames 1–100) was analyzed for each replicate of each male sample (Wilson-Leedy and Ingermann 2007; Purchase and Earle 2012). CASA (2006) software produced five correlated sperm quality variables, including motility (MOT), curvilinear velocity (VCL), velocity along the average path (VAP), straight line velocity (VSL), and linearity (LIN).

All image-stack files accumulated from Micro-Manager were converted to AVI files after being uploaded one at a time to program ImageJ. The CASA (2006) plugin requires that the threshold of all frames be adjusted so that only the sperm heads appear black on a white background. Once the threshold value was set, the video file was analyzed. Optimal settings were adapted from Wilson-Leedy and Ingermann (2007) and Toth et al. (1997) and modified by a macro created with instructions described in Xu (2012). Frame rate was determined from the microscope camera used, and micrometres (μm) per 1000 pixels was determined using the set scale tool on the 0.05 mm hemocytometer gridlines in ImageJ. A table of CASA plugin parameters is provided in online Supplementary Table S1[1].

Statistical analysis of sperm quality

CASA (Wilson-Leedy and Ingermann 2007) produced five correlated variables, each describing variation in sperm quality. As no one candidate variable encompasses sperm quality better than the others, a principal components analysis (PCA; Hotelling 1933) was used to create orthogonal dependent variables that encompass the variability in all CASA variables. Eigenvalues, factor loadings, and the selection of significant axes were done in R (3.5.1) (www.r-project.org) using the Factoextra library (Kassambara and Mundt 2017). Axes of significance were determined using a Scree test (Cattell 1966), where the cumulative variance explained exceeded 90% of the total variance and where the axes also exceeded the average eigenvalue for each of the five produced axes. Pearson correlations were used to identify variables associated with each principal component. Correlations and axes contributions can be found in Table 4 (Afifi et al. 2004).

Models analyzing variation in sperm quality (as characterized by principal components 1 and 2: PC1 and PC2) for males sampled in 2018 were fitted using the glm function (Gaussian family) in R (3.5.1) (www.r-project.org). Independent variables describing all possible combinations of variables, including a full and null model, were fit. AIC values and weights were calculated for each model using the dredge function of the MuMIn library (Bartón 2017). Model averaging was performed for all models for which the $\Delta AIC_c < 4$ (Burnham and Anderson 2002; Bunnell et al. 2012) using the model.avg function of the MuMIn library (2017).

Sperm quality data were analyzed using a general linear model including body size (FL) at the time of capture, river residence time (RT), upstream swimming time (UT), years between spawning migrations (SI), and complete river migrations in a season (IM). The full model included all five variables for which the interactions with other variables were considered. All variables were tested for normality using Shapiro–Wilk tests.

Male RS

Genetic data and analyses have contributed greatly to understanding of reproductive and social behavior of fishes (DeWoody and Avise 2001; Avise et al. 2002; Flanagan and Jones 2019). Estimates of male RS were quantified using genetic determination of parentage as described in the Black River system by Duong et al. (2011*a*, 2011*b*, 2013) and Dammerman et al. (2019). DNA was extracted from fin samples collected from all spawning adults. DNA was also extracted from fin clips of a random subset of drifting larvae that was collected nightly during larval dispersal and was proportional to total numbers collected on each night. A total of 500 and 462 larval lake sturgeon were genotyped from the 2017 and 2018 larval drift periods, respectively. During the 2017 larval drift period, we captured 19 315 larval lake sturgeon and genotyped 500 (2.61%). Of the 46 931 larval sturgeon collected during the larval drift period in 2018, we genotyped 472 (1.01%). Data used in this study to characterize male RS is comparable to previous research in the Black River system that characterized female RS using a 2-year data set (2012 and 2013) and genetic parentage analysis based on genotyping 1%–2% of larvae captured using the program COLONY (Dammerman et al. 2019). Results were unequivocal and consistent across years, in part due to the unparalleled control we have relative to comprehensive data collection for adults and larvae in the system. Results comparing parentage assignment across programs and of simulations demonstrating statistical power and confidence in pedigree assignment are reported in Duong et al. (2011*a*, 2011*b*), Dammerman et al. (2019), and Hunter et al. (2020), respectively.

Laboratory analyses

DNA extraction protocols followed manufacturer's recommendations (QIAGEN DNeasy Blood & Tissue Kits, QIAGEN Inc.). DNA concentration was estimated using a NanoDrop ND-100 spectrophotometer (Nanodrop Technologies, Wilmington, Delaware, USA). Samples were diluted to a DNA concentration of 20 ng·μL^{-1} using sterile water prior to polymerase chain reaction (PCR).

To ensure sufficient power for UBR parentage including paternal assignment (details in Duong et al. 2011*a*, 2011*b*, 2013; Dammerman et al. 2019), sample DNAs were amplified for genotyping at 13 disomic microsatellite loci, including *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).

PCR was conducted in 25 μL reactions using 100 ng DNA and PCR conditions specified in Dammerman et al. (2019). Single locus PCR products were multiplexed. Genotyping was performed at the MSU Research Technology Support Facility (https://rtsf.natsci.msu.edu/) on an ABI 3730xl DNA analyzer. Allele sizes were characterized using size standards (MapMarker, and BioVentures Inc.). Three samples of known genotypes were included on each microtitre plate as allele size standards. Genotypes were visualized using GeneMarker software (Softgenetics, State College, Pennsylvania). All genotypes were scored by two experienced lab personnel to ensure consistency. Ten percent of individuals were blindly genotyped a second time as an additional measure of quality control. Mean allelic error rates were calculated at 2.67% and 1.80% in 2017 and 2018, respectively.

Parentage analyses

Genotypes were analyzed using the full-likelihood implementation of Program COLONY (Wang 2004) to assign larvae to maternal

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2020-0124.

and paternal parents and parental pairs. Analysis with Program COLONY was performed in two replicate runs with different random number seeds as per Jay et al. (2014). The COLONY full-likelihood implementation (ML) approach considers all of the possible relationships (i.e., full-siblings, half-siblings, and non-siblings) between each pair of individuals, such that the entire sample pedigree is determined that maximizes the probability of the entire genotype data set (Wang 2004).

User-provided parameters for COLONY included mutation rates (Talbot et al. 1995; Wang 2004). Program COLONY accounts for class 1 error (allelic dropout during PCR amplification) and class 2 error (mutation, genotyping, contamination, and data entry) (Wang 2004). Analyses assumed a slightly higher error rate than empirically observed: 2% for allelic dropout and 0.1% for all other sources of error. All COLONY runs allowed for multiple mates for both sexes (polyandry for females and polygyny for males). Allele frequencies were considered unknown and were not updated. No sibship prior was used. Parentage assignments were reconstructed using a "long" run with "high" precision options. We note that there could be type I and II errors in the ML parentage assignments; for example, a sibling pair might be inferred as non-sibs or a non-sib pair might be inferred as siblings. However, these two types of errors are naturally balanced and minimized in the full likelihood inference framework (Wang 2004; Hunter et al. 2020).

Statistical analysis of male RS

Male RS was defined as the number of larvae assigned to each male lake sturgeon (Duong et al. 2011*a*, 2013; Dammerman et al. 2019). Owing to differences between the variance and mean of the sample data, a negative binomial regression was used to evaluate variables associated with RS. Negative binomial error distributions were used for 2017 and 2018 given the overdispersion of count data (Long 1997; Burnham and Anderson 2002; Pradhan and Leung 2006).

Independent variables used to evaluate associations with RS included river residence time (hours), upstream swimming time (hours), number of intra-annual migrations, interspawning interval (years), and the number of females to which a male was exposed. Sperm concentration and quality were not included in this analysis because they were correlated with river residence time. All possible combinations of variables, including a full and null model, were fit with AIC values, and weights were calculated for each model using the dredge function of the MuMIn library (Bartón 2017). Model averaging was performed for all models for which the $\Delta AIC_c < 4$ (Burnham and Anderson 2002; Bunnell et al. 2012) using the model.avg function of the MuMIn library (2017).

In each year, the number of larvae assigned to a male can vary proportionally as a function of the number of males in the river, the number of larvae captured during the larval drift period, and the number of fish genotyped per night of larval drift capture. Because the number of adults and proportion of larvae genotyped of the total number captured differed between years, male RS (the number of genotyped larvae sired) was evaluated separately for 2017 and 2018. Number of larvae produced was regressed against sperm concentration (sperm·mL^{-1}) independently for 2017 and 2018. Variables were analyzed for normality using Shapiro–Wilks tests. Given the lack of normality, generalized linear models were used to evaluate the predictive value of sperm concentration.

Results

Estimates of spawning adult composition

In total, 349 lake sturgeon entered the spawning grounds in 2017, while 343 lake sturgeon entered the spawning grounds in 2018, based on RFID detections at the RFID antenna immediately below the spawning area. During the 2017 spawning period, 255 male lake sturgeon (73.1% of migrating adults) were detected by the RFID antenna migrating into the spawning areas. Complete RFID migratory data (i.e., without missing detections) and at least one sperm sample were collected from 68 males. In 2018, 248 males (72.3% of migrating adults) were detected by RFID migrating into the spawning grounds, including areas 11 km upstream of spawning areas used in 2017 below Kleber Dam (Fig. 1). Complete RFID migratory data and at least one sperm sample were collected from 103 males. Of the total number of spawning adults that were detected by RFID in 2017, 94 (26.9%) were females, and in 2018, 95 (27.7%) were females.

Table 1. Summary of male lake sturgeon body size and migration parameters during the spawning season in 2017 and 2018.

		2017		2018	*W*	*p*
Fork length (cm)	μ	138		139		
	±SD	13		13		
	Min.	110	~	101	3823.5	0.984
	Max.	168		168		
River residency (h)	μ	128.41		110.39		
	±SD	106.23		79.76		
	Min.	2.38	>	8.54	5710	<0.001*
	Max.	508.39		299.58		
Upstream time (h)	μ	53.53		34.14		
	±SD	47.66		43.35		
	Min.	11.07	>	8.35	5666	<0.001*
	Max.	215.59		260.42		
Interspawning interval (years)	μ	2.59		1.99		
	±SD	1.19		1.28		
	Min.	1.00	>	1.00	5120.5	0.0011*
	Max.	5.00		7.00		
Intra-annual migrations (count)	μ	1.66		1.34		
	±SD	0.83		0.63		
	Min.	1.00	>	1.00	4729	0.0027*
	Max.	4.00		3.00		
Sperm concentration (no.·mL^{-1})	μ	2.00×10^9		3.82×10^9		
	±SD	1.39×10^9		2.93×10^9		
	Min.	9.50×10^7	<	2.32×10^8	2415	<0.001*
	Max.	5.95×10^9		1.23×10^{10}		

*Indicates significant difference between 2017 and 2018 using Wilcoxon–Mann–Whitney test.

Mean (±SD) male residence time was significantly higher in 2017 (128.41 ± 106.23 h) than in 2018 (110.39 ± 79.76 h; WMW, $W = 5710$, $p < 0.001$; Table 1). Mean (±SD) male upstream migration time was also significantly higher in 2017 (53.53 ± 47.66 h) than in 2018 (34.14 ± 43.35 h; WMW, $W = 5666$, $p < 0.001$; Table 1). Mean ± SD interspawning interval was longer for males spawning in 2017 (2.59 ± 1.19 years) than in 2018 (1.99 ± 1.28 years; WMW, $W = 5120.5$, $p = 0.0011$; Tables 1–2; Supplementary Fig. S2[1]). The mean (±SD) number of intra-annual upstream migrations was also higher in 2017 for male lake sturgeon (1.66 ± 0.83 migrations) than in 2018 (1.34 ± 0.63 migrations; WMW, $W = 4729$, $p = 0.003$; Tables 1–2; Supplementary Fig. S3[1]). In 2017, males had significantly lower sperm concentration (mean ± SD: $2.00 \times 10^9 \pm 1.39 \times 10^9$ sperm·mL^{-1}, range: $9.50 \times 10^7 - 5.95 \times 10^9$ sperm·mL^{-1}) than in 2018 ($3.82 \times 10^9 \pm 2.93 \times 10^9$ sperm·mL^{-1}, range $2.32 \times 10^8 - 1.23 \times 10^{10}$ sperm·mL^{-1}; WMW, $W = 2415$, $p < 0.001$; Table 1; Fig. 2). Mean ± SD temperature was higher in 2018 (16.46 ± 3.93 °C) than in 2017 (13.32 ± 2.65 °C; WMW, $W = 247\,340$, $p < 0.001$). Finally, mean ± SD discharge (m^3·s^{-1}) was higher in 2018 (20.25 ± 11.62 m^3·s^{-1}) than in 2017 (12.87 ± 5.29 m^3·s^{-1}; WMW, $W = 255\,340$, $p < 0.001$). Collectively, when comparing migratory and spawning behavioral characteristics of spawning males between years, male spawners in 2017 expended more resources on reproductive activities, as seen in longer river residence times, longer upstream migration times, and higher average numbers of migration events from the lake to the spawning site, compared with males spawning in 2018.

Fig. 2. Boxplot of male lake sturgeon sperm concentration (sperm·mL^{-1}) and river residence time (hours) in 2017 and 2018.

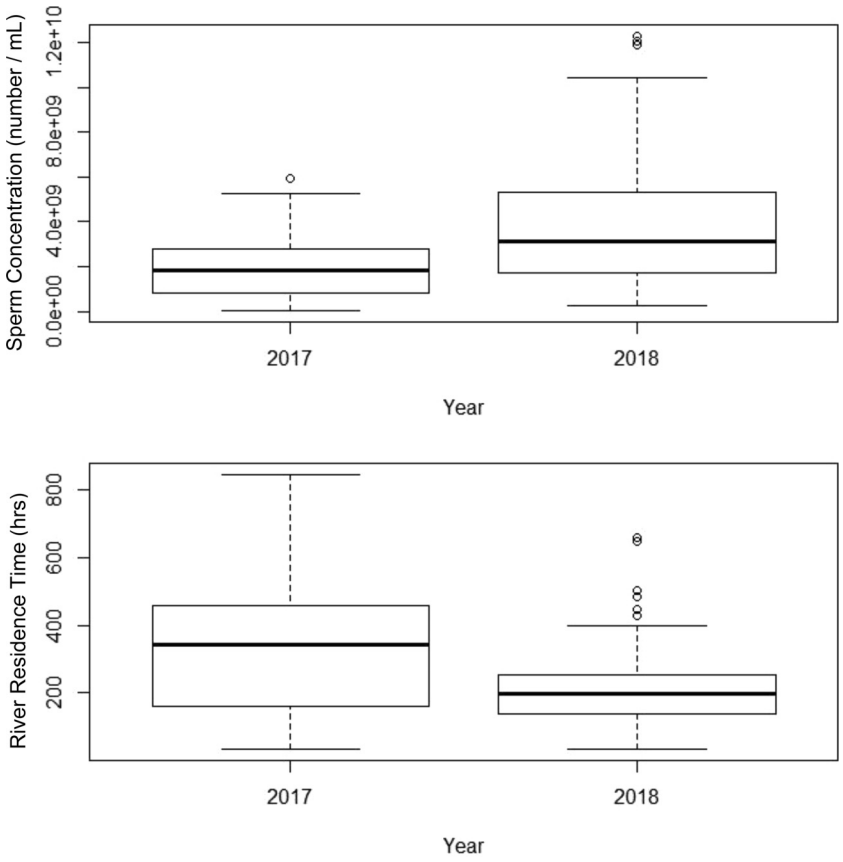


Table 2. Summary of male lake sturgeon interspawning interval and intra-annual migrations during the spawning season in 2017 and 2018.

	Spawning interval (years)		Spawning migrations (no.·year^{-1})	
Count	2017	2018	2017	2018
1	11 (16.18%)	42 (40.38%)	36 (52.94%)	78 (75.00%)
2	25 (36.76%)	44 (42.31%)	23 (33.82%)	18 (17.31%)
3	11 (16.18%)	6 (5.77%)	6 (8.82%)	8 (7.69%)
4	18 (26.47%)	4 (3.85%)	3 (4.41%)	—
5	3 (4.41%)	4 (3.85%)	—	—
6	—	3 (2.88%)	—	—
7	—	1 (0.96%)	—	—
Mean	2.59	1.99	1.66	1.34
±SD	1.19	1.28	0.83	0.63
Min.	1.00	1.00	1.00	1.00
Max.	5.00	7.00	4.00	3.00
N_{total}	68	104	—	—

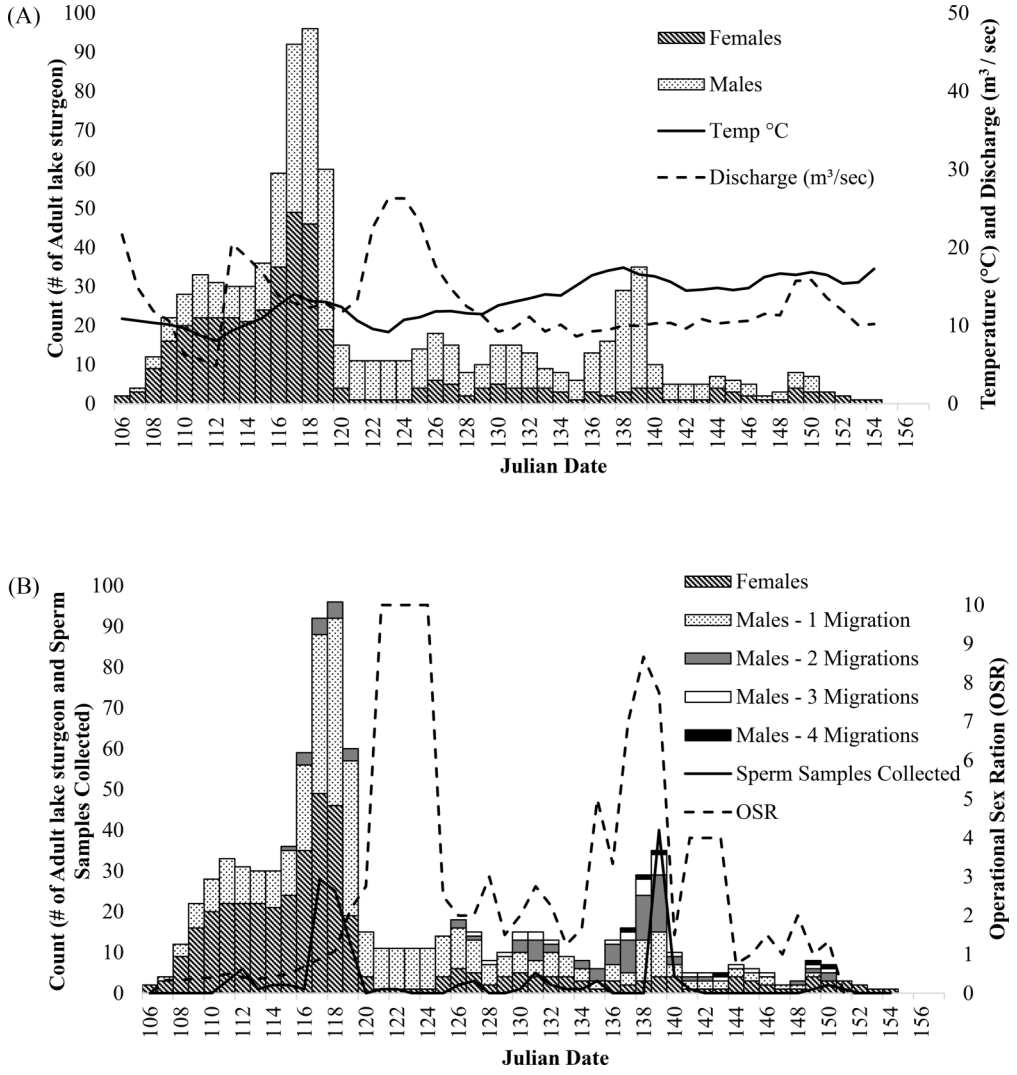
Note: Values in parentheses indicate percentage of male lake sturgeon that exhibited each strategy (interspawning interval or intra-annual migrations) relative to the total number of migrations in each respective year.

The mean (±SD) daily OSR in 2017 was 2.57 (±2.96) males per female and 2.84 (±2.44) males per female in 2018. OSR did not differ significantly between years (WMW, W = 672, p = 0.527; Fig. 3). The range in daily OSR varied between 0 (16 April 2017) and 10 (4 May 2017). In 2018, daily OSR varied between 0 (2 May 2018, 29 May 2018, 2 June 2018) and 8 (22 May 2018) (Fig. 3). Mean (±SD) male FL was not significantly different between years (2017: 138 ± 13 cm FL and 2018: 139 ± 13 cm FL; WMW, W = 3823.5, p = 0.894; Table 1). Additionally, Figs. 3B and 3D show the number of male and female lake sturgeon in the river on a given day, which provides a visual representation of the peak spawning activity days and the relative day of the spawning season that sperm samples were collected.

The number of possible exposures of male lake sturgeon to female lake sturgeon in the spawning grounds increased as a function of male river residence time in 2017 and 2018 (GLM, z = 10.37, p < 0.001; Fig. 4). When compared with female exposures in 2017 (GLM for 2017, z = 19.42, p < 0.001; Fig. 4), fewer female exposures occurred at commensurate river residence time in 2018 (GLM for 2018, z = –14.7, p < 0.001; Fig. 4). The number of females to which a male was exposed also varied as a function of the number of migration events within a year in both 2017 and 2018 (Fig. 4). During 2017, a male that undertook a single migration was exposed to (mean ± SD) 83.14 ± 68.70 females in spawning areas. Males undertaking two or three migrations were exposed to 164.78 ± 80.74 females and 158.67 ± 85.11 females, respectively. Males that made one spawning migration were exposed to significantly fewer females (KW: χ^2 = 14.43, p < 0.001, df = 2) than those that migrated twice (DT: z = 3.59, p < 0.001) or three times (DT: z = –2.19, p = 0.029). The number of females to which a male was exposed did not differ between males that migrated twice and those that migrated three times (DT: z = 0.37, p = 0.713; Fig. 4). This relationship was not evident in 2018 (KW: χ^2 = 0.13, p = 0.936, df = 2), where males that migrated once were exposed to 96.79 ± 52.38 females, while males that migrated twice were exposed to 86.64 ± 38.99 females, and males that migrated three times were exposed to 90.63 ± 50.02 females (Fig. 4).

Males that migrated in both 2017 and 2018 had shorter (mean ± SD) river residence times in 2018 (169.82 ± 76.70 h) than in 2017 (362.55 ± 209.13 h, WMW, W = 0.88, p = 0.002). These males also engaged in fewer spawning migrations in 2018 (1.44 ± 0.73 migrations) compared with 2017 (1.69 ± 0.79 migrations, WMW, W = 0.78, p < 0.001) and thus encountered fewer females in 2018 (32.94 ± 16.14 encounters) than in 2017 (42.06 ± 22.13 encounters,

Fig. 3. (A) Description of the number of adult male and female lake sturgeon present above the RFID antenna below the known spawning grounds and the daily average temperature (°C, solid line) and discharge ($m^3 \cdot s^{-1}$, dashed line) as a function of Julian day in 2017. (B) Description of the number of adult male and female lake sturgeon present above the RFID antenna below the known spawning grounds and the operational sex ratio (OSR) during the 2017 (48 days) spawning season as a function of Julian day. The dashed line represents daily operational sex ratio (males per female) in the stream spawning area above the Section 7 RFID antenna. The solid line represents the daily number of sperm samples collected. (C) Description of the number of adult male and female lake sturgeon present above the RFID antenna below the known spawning grounds and the daily average temperature (°C, solid line) and discharge ($m^3 \cdot s^{-1}$, dashed line) as a function of Julian day in 2018. (D) Description of the number of adult male and female lake sturgeon present above the RFID antenna below the known spawning grounds and the operational sex ratio (OSR) during the 2018 (35 days) spawning season as a function of Julian Day. The dashed line represents daily operational sex ratio (males per female) in the stream spawning area above the Section 7 RFID antenna. The solid line represents the daily number of sperm samples collected.



WMW, $W = 0.88$, $p = 0.002$; Table 3). When comparing reproductive expenditures in 2017 to 2018, those males that engaged in behaviors consistent with comparatively higher reproductive investments in 2017 (multiple runs and extended river residence time) ultimately encountered more females in 2017. Males that did not invest heavily in a single year spawning efforts, opting to expend resources in back-to-back reproductive seasons, ultimately exerted a lower effort in 2018 when compared with 2017.

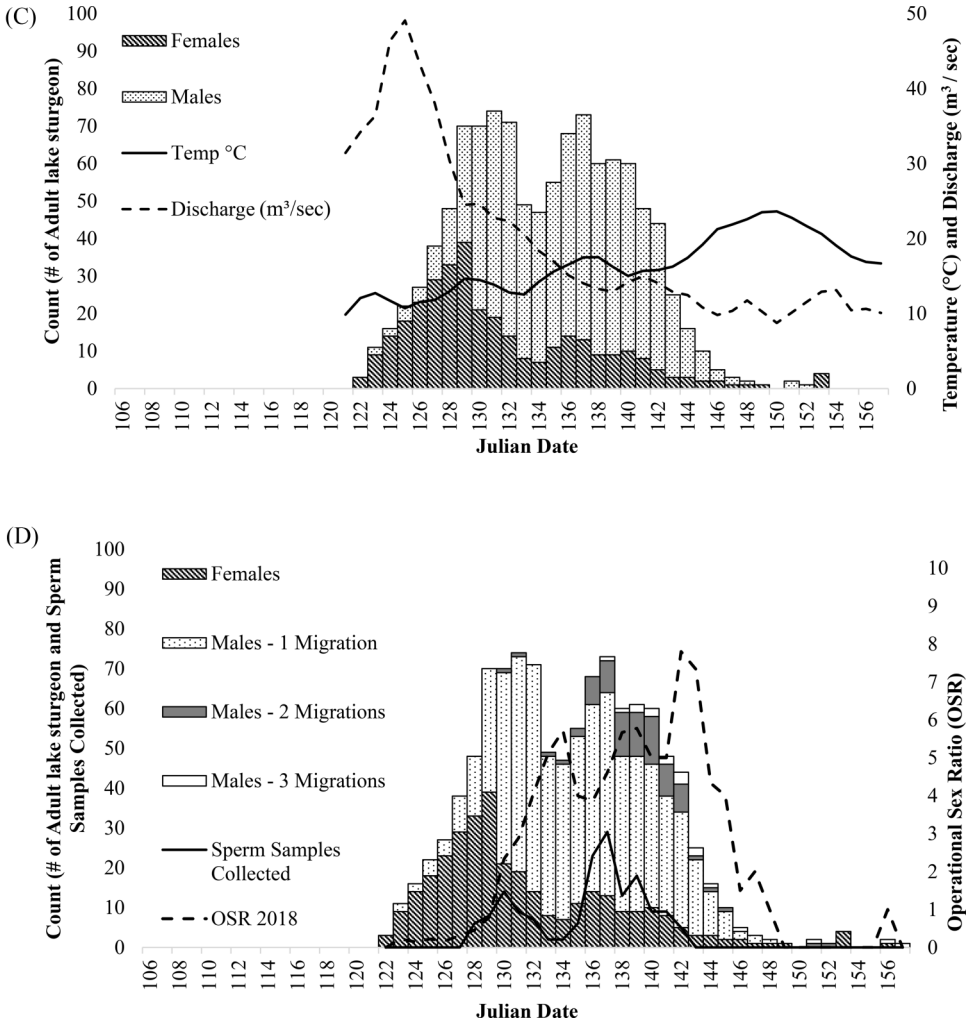
Model selection — sperm concentration

For sperm concentration, the AIC_c-selected model included year and strong negative relationship with residence time. As variability among models (as emphasized by the number of models with a ΔAIC_c <4) was minimal, we averaged the top candidate models. An increase of 1 h in the river equated to a drop in sperm concentration of 5.17×10^6 sperm·mL^{-1} (GLM, $z = 2.42$, $p = 0.02$; Table 4; Supplementary Table S3[1]). Spawning interval, upstream travel time, and number of intra-annual migrations appeared in more than half the averaged models but did not significantly impact sperm concentration (Table 4, Supplementary Table S3[1]). Fork length only appeared in four of the twelve candidate models (Table 4, Supplementary Table S3[1]) and did not impact sperm concentration.

Sperm quality

PCA indicated five axes explaining the variation in sperm concentration, motility, curvilinear velocity, velocity along the average path, straight line velocity, and linearity. PC1 and PC2 cumulatively explained greater than 90% of the variation in sperm quality and based on Cattell's Scree test (Cattell 1966) were retained for analysis (Table 5).

Fig. 3 (*concluded*).



PC1 described 60.48% of the variation in sperm quality variables derived from the CASA plugin (Table 5). PC1 grouped males by velocity straight line, velocity averaged path, linearity, motility, and velocity curvilinear; however, the factor loadings indicating the greatest negative correlation with PC1 were VSL and VAP (Table 5). These values indicate that the variables that predominately explained the variability on the first axis of the PCA were sperm velocity and the maximum distance sperm traveled along an average straight line path during the segment of video analyzed.

PC2 described 30.17% of the variation in sperm quality variables. Like PC1, PC2 grouped males by VSL, VAP, LIN, MOT, and VCL. The factor loadings indicating the greatest correlation to PC2 were VCL and LIN (Table 5). VCL was negatively correlated to PC2, while LIN was positively correlated to PC2 (Table 5). VCL (a measure of movement when in a nonlinear path), LIN (the measure of path curvature during the analyzed video segment), and MOT (how functionally active a sperm is) were all best described by PC2. All variables computed by the CASA plugin were represented on at least one of the two main PCs.

Model selection — sperm quality

For PC1, the AIC_c-selected model included a strong positive relationship with river residence time and positive relationship with the number of intra-annual migrations (Table 4). As variability among models, as emphasized by the number of models with a $\Delta AIC_c < 4$ was minimal, we averaged the top candidate models. An increase of 1 h in the river equated to a 0.01 unit increase in PC1 (GLM, $z = 2.42$, $p = 0.02$; Table 6, Supplementary Table S3[1]). The negative correlation of VAP and VSL to PC1 indicates that increased residence time reduced sperm velocity. Of the two variables in the top candidate model, only river residency was identified as significant (GLM, $z = 2.57$, $p = 0.01$; Supplementary Table S3[1]). Spawning interval, upstream travel time, fork length, and number of intra-annual migrations appeared in fewer than half of the averaged models and did not significantly impact sperm quality across PC1 (Table 4, Supplementary Table S3[1]).

For PC2, the AIC_c-selected model included a positive relationship with residence time (Table 6). Again, as the number of models with a $\Delta AIC_c < 4$ was substantial, we averaged the top candidate models. Model averaging and the subsequent analysis of the variables in the top models indicated that river residency did not significantly contribute to PC2 (GLM, $z = 1.47$, $p = 0.014$; Supplementary Table S3[1]), but instead increasing intra-annual migrations slightly decreased PC2 (GLM, $z = 2.41$, $p = 0.02$; Supplementary Table S3[1]). The negative correlation of VCL and LIN to PC2 indicates that increased intra-annual migrations reduced sperm velocity and linearity. Spawning interval, upstream travel time, and fork length appeared in fewer than half of the averaged models and did not significantly impact sperm quality across PC2 (Table 6, Supplementary Table S3[1]).

Male RS

Allelic diversity (mean ± SD) in 2017 genotyped larvae was 5.15 ± 2.31, while in 2018 larval allelic diversity was 5.61 ± 2.81. Estimates

Fig. 4. (Top panel) Mean (±SE) exposure of male lake sturgeon to numbers of female lake sturgeon in the spawning grounds concurrently as a function of the number of intra-annual complete migration events in 2017 and 2018. Nonparametric Kruskal–Wallis one-way ANOVA (2017: $p < 0.001$; 2018: $p = 0.9361$; combined: $p = 0.01206$) indicates that the number of female exposures increased significantly with increased number of migrations within a year (differences from post hoc Dunn's test of multiple comparisons indicated by letter (a and b for 2017, c for 2018). (Bottom panel) The number of female lake sturgeon exposures on the spawning grounds based on concurrent male–female residence in the spawning grounds varied as a function of river residence time in 2017 (GLM, family = "Poisson", $z = 10.37$, $p < 0.001$) and 2018 (GLM, $z = 19.42$, $p < 0.001$). Results from a generalized linear model indicated an increase in the number of female exposures as a function of male residence time ($z = 20.82$, $p < 0.001$) and that the number of female exposures varied significantly for males during 2017 and 2018 ($z = -14.7$, $p < 0.001$).

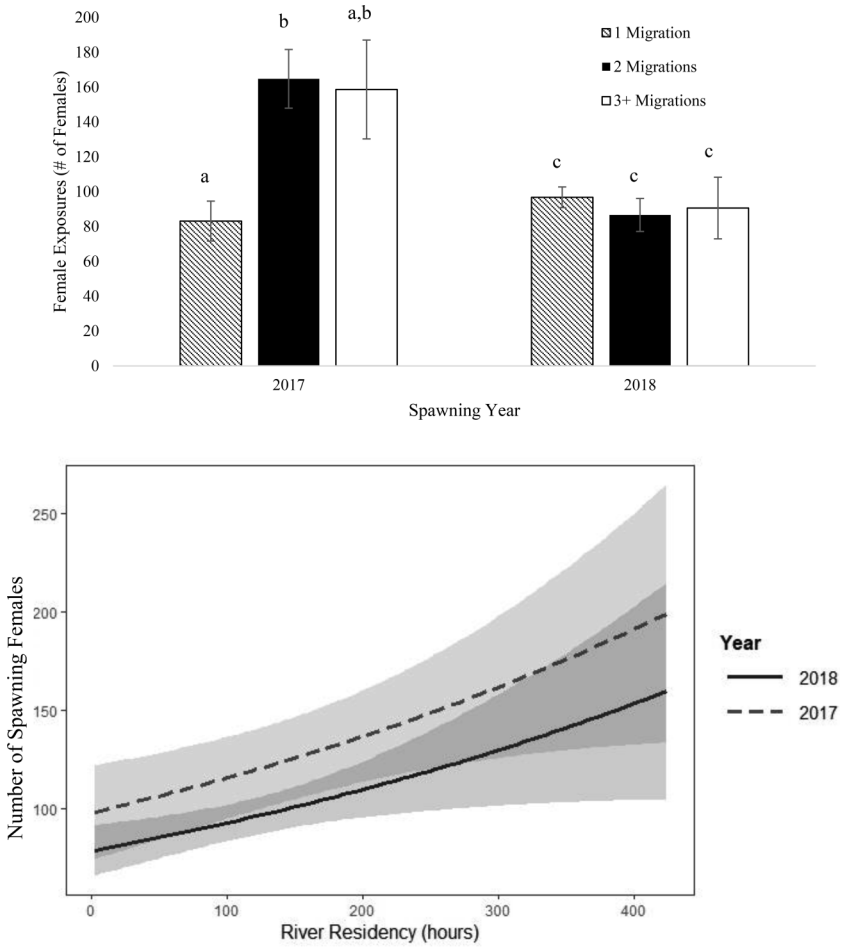


Table 3. Summary of male lake sturgeon migration parameters for those males that spawned in both the 2017 and 2018 spawning season.

		2017		2018	W	p
River residency (h)	μ	362.55		169.82		
	±SD	209.13	>	76.70	0.88	0.002*
	Min.	103.03		54.16		
	Max.	723.88		313.18		
Intra-annual migrations	μ	1.69		1.44		
	±SD	0.79	>	0.73	0.71	<0.001*
	Min.	1.00		1.00		
	Max.	3.00		3.00		
Female encounters	μ	42.06		32.94		
	±SD	22.13	>	16.14	0.88	0.002*
	Min.	5.00		11.00		
	Max.	61.00		61.00		

*Indicates significant difference between 2017 and 2018 using Wilcoxon–Mann–Whitney test.

of heterozygosity were 0.603 and 0.613 in 2017 and 2018 adults, respectively. COLONY successfully assigned an RFID-detected male parent to 74.0% and 72.0% of the genotyped offspring in 2017 and 2018, respectively. Male RS of successfully reproducing males ranged from 1 to 15 offspring (mean ± SD = 4.94 ± 3.21) in 2017 and from 1 to 21 offspring (mean ± SD = 5.43 ± 3.70) in 2018.

The model with the selected AIC_c score that best explained the number of larvae sired by a male lake sturgeon in 2017 was the null model, suggesting that variables other than those considered for this analysis best explained male RS in 2017. Multiple candidate models with ΔAIC_c scores < 4 existed, so all candidate models ($N = 13$) were averaged to generate a single model. As in the AIC_c model of best fit, none of the explanatory variables in the averaged model explained RS with statistical significance (Table 7, Supplementary Table S5[1]).

The model with the selected AIC_c score that best explained the number of larvae sired by a male lake sturgeon in 2018 included the number of female exposures and the interspawning interval prior to spawning. Again, multiple candidate models with ΔAIC_c scores < 4 existed, so all candidate models ($N = 12$) were averaged to generate a single model. As in the AIC_c model of best fit, both increasing female exposures (GLM, $z = 2.04$, $p = 0.04$) and longer interspawning interval prior to spawning (GLM, $z = 5.72$, $p < 0.001$) resulted in greater larval production in 2018 (Table 7, Supplementary Table S5[1]).

Table 4. General linear models explaining sperm concentration as a function of lake sturgeon migratory behavior.

Model	df	AIC_c	ΔAIC_c	$wAIC_c$
Sperm concentration ~ year – residence time	4	8292.41	0.00	0.17
Sperm concentration ~ year – residence time – interspawning interval	5	8293.14	0.73	0.12
Sperm concentration ~ year – residence time + upstream time	5	8293.62	1.20	0.09
Sperm concentration ~ year – residence time – intra-annual migrations	5	8293.83	1.41	0.08
Sperm concentration ~ year – residence time + fork length	5	8294.38	1.97	0.06
Sperm concentration ~ year – residence time – interspawning interval + upstream time	6	8294.45	2.04	0.06
Sperm concentration ~ year – residence time – interspawning interval – intra-annual migrations	6	8294.51	2.10	0.06
Sperm concentration ~ year – residence time – interspawning interval + fork length	6	8295.23	2.82	0.04
Sperm concentration ~ year – residence time – intra-annual migrations + upstream time	6	8295.39	2.98	0.04
Sperm concentration ~ year – residence time + upstream time + fork length	6	8295.54	3.13	0.04
Sperm concentration ~ year – residence time – intra-annual migrations + fork length	6	8295.76	3.35	0.03
Sperm concentration ~ year – residence time – interspawning interval – intra-annual migrations + upstream time	7	8296.19	3.78	0.03

Note: Models are arranged by ΔAIC_c score. All models with ΔAIC_c score < 4 were averaged.

Table 5. Factor loadings, correlation of factor loadings to principal components, eigenvalues, and variance explained for principal components analysis of sperm quality variables.

	Factor loadings (and correlation coefficients)							
	Motility	Velocity curvilinear	Velocity average path	Velocity straight line	Linearity	Eigenvalue	Variance (%)	Cumulative variance (%)
PC1	−0.638 (0.41)	−0.641 (0.35)	−0.425 (0.94)*	−0.003 (0.91)*	−0.000 (0.42)	3.024	60.48	60.48
PC2	−0.590 (0.41)	−0.721 (0.52)*	−0.307 (0.02)	0.193 (0.07)	−0.001 (0.50)*	1.509	30.17	90.65
PC3	−0.971 (0.18)	0.138 (0.09)	−0.098 (0.01)	−0.171 (0.01)	0.017 (0.02)	0.305	6.11	96.75
PC4	−0.953 (0.00)	0.262 (0.04)	−0.076 (0.03)	−0.133 (0.02)	−0.018 (0.08)	0.162	3.23	99.99
PC5	−0.647 (0.00)	0.700 (0.00)	0.121 (0.00)	0.279 (0.00)	0.002 (0.00)	0.001	0.01	100.00

*Correlation coefficients greater than 0.50 are considered strongly correlated (Afifi et al. 2004).

Table 6. General linear models explaining sperm quality variables explained by principal components (1 and 2) analysis as a function of lake sturgeon migratory behavior.

Model	df	AIC_c	ΔAIC_c	$wAIC_c$
Principal component 1				
PC1 ~ residence time + intra-annual migrations	**4**	415.68	**0.00**	**0.16**
PC1 ~ residence time	3	415.73	0.05	0.16
PC1 ~ residence time – upstream time	4	416.67	0.99	0.10
PC1 ~ residence time + intra-annual migrations – upstream time	5	417.33	1.65	0.07
PC1 ~ residence time – interspawning interval	4	417.53	1.85	0.06
PC1 ~ residence time + intra-annual migrations – interspawning interval	5	417.55	1.87	0.06
PC1 ~ residence time + fork length	4	417.81	2.13	0.06
PC1 ~ residence time + intra-annual migrations + fork length	5	417.84	2.17	0.06
PC1 ~ residence time – interspawning interval – upstream time	5	418.58	2.90	0.04
PC1 ~ residence time – upstream time + fork length	5	418.83	3.16	0.03
PC1 ~ residence time + intra-annual migrations – interspawning interval – upstream time	6	419.28	3.60	0.03
PC1 ~ residence time + intra-annual migrations – upstream time + fork length	6	419.55	3.88	0.02
Principal component 2				
PC2 ~ residence time	**3**	344.22	**0.00**	**0.17**
PC2 ~ residence time – upstream time	4	344.34	0.12	0.16
PC2 ~ residence time – upstream time – intra-annual migrations	5	345.39	1.17	0.09
PC2 ~ residence time – intra-annual migrations	4	345.97	1.74	0.07
PC2 ~ residence time + interspawning interval	4	346.25	2.02	0.06
PC2 ~ residence time – upstream time + interspawning interval	5	346.34	2.12	0.06
PC2 ~ residence time + fork length	4	346.38	2.15	0.06
PC2 ~ residence time – upstream time – fork length	5	346.54	2.32	0.05
PC2 ~ residence time – upstream time – intra-annual migrations + interspawning interval	6	347.44	3.21	0.03
PC2 ~ 1 (null model)	2	347.52	3.30	0.03
PC2 ~ residence time – upstream time – intra-annual migrations + fork length	6	347.64	3.42	0.03
PC2 ~ residence time – intra-annual migrations + interspawning interval	5	348.04	3.81	0.02
PC2 ~ residence time – intra-annual migrations + fork length	5	348.15	3.93	0.02

Note: Models are arranged by ΔAIC_c score. All models with ΔAIC_c score < 4 were averaged.

When considered on its own, sperm concentration did not explain the number of larvae sired (GLM, $t = -1.17$, $p = 0.254$; Supplementary Table S5[1]) during the 2017 spawning season. Sperm concentration also did not explain RS during the 2018 spawning season (GLM, $t = 0.198$, $p = 0.845$; Supplementary Table S5[1]).

Discussion

Teleost fishes exhibit considerable variation in reproductive behavior (Taborsky 1998; Avise et al. 2002). Even among members of the same population, behavioral plasticity is also frequently evident, as demographic and environmental conditions vary spatially and temporally (Komers 1997). Behaviors exhibited during

Table 7. Negative binomial model explaining male lake sturgeon reproductive success as a function of lake sturgeon migratory behavior.

Model	df	AIC_c	ΔAIC_c	$wAIC_c$
2017				
Reproductive success ~ 1 (null model)	2	263.44	0.00	0.13
Reproductive success ~ female exposures	3	263.94	0.50	0.10
Reproductive success ~ female exposures – river residency	4	265.02	1.58	0.06
Reproductive success ~ – river residency	3	265.13	1.69	0.05
Reproductive success ~ – fork length	3	265.42	1.98	0.05
Reproductive success ~ intra-annual migrations	3	265.66	2.22	0.04
Reproductive success ~ – upstream time	3	265.68	2.23	0.04
Reproductive success ~ interspawning interval	3	265.70	2.26	0.04
Reproductive success ~ female exposures – fork length	4	266.19	2.75	0.03
Reproductive success ~ female exposures – upstream time	4	266.22	2.78	0.03
Reproductive success ~ female exposures – intra-annual migrations	4	266.30	2.86	0.03
Reproductive success ~ female exposures + interspawning interval	4	266.30	2.86	0.03
Reproductive success ~ – river residency – fork length	4	267.31	3.87	0.02
2018				
Reproductive success ~ female exposures + interspawning interval	4	259.56	0.00	0.16
Reproductive success ~ female exposures + interspawning interval + upstream time	5	259.82	0.27	0.14
Reproductive success ~ female exposures + interspawning interval + river residency	5	261.39	1.84	0.06
Reproductive success ~ female exposures + interspawning interval + upstream time + intra-annual migrations	6	261.53	1.97	0.06
Reproductive success ~ female exposures + interspawning interval + intra-annual migrations	5	261.55	1.99	0.06
Reproductive success ~ interspawning interval + upstream time	4	261.73	2.18	0.05
Reproductive success ~ female exposures + interspawning interval + fork length	5	261.74	2.18	0.05
Reproductive success ~ interspawning interval	3	262.25	2.70	0.04
Reproductive success ~ female exposures + interspawning interval + upstream time + fork length	6	262.27	2.71	0.04
Reproductive success ~ female exposures + interspawning interval + upstream time + river residency	6	262.28	2.73	0.04
Reproductive success ~ interspawning interval + upstream time + intra-annual migrations	5	262.64	3.08	0.03
Reproductive success ~ interspawning interval + river residency	4	262.83	3.27	0.03

Note: Models are arranged by ΔAIC_c score. All models with ΔAIC_c score < 4 were averaged.

migration and spawning that are tied to decisions associated with when and where to reproduce have substantial influence on reproductive effort and fitness consequences (Warren and Morbey 2012; Dammerman et al. 2019). In this study we show that male migratory and spawning behaviors were key components associated with current year reproductive investment, especially residence time in spawning areas and realized levels of female exposure, that in turn affected sperm concentration and quality. Detailed information on male behaviors were based on information pertaining to chronology and duration of key events obtained from passive RFID tag detection antennas deployed strategically throughout the Black River. Results demonstrating reproductive costs and benefits were concordant during consecutive years. A negative relationship between current reproductive investment and future reproductive investments is expected (Stearns 1989). Variation in reproductive effort reflected here as intra-annual versus interannual reproductive trade-offs can affect lifetime reproduction in lake sturgeon and long-lived iteroparous fish species generally (Parker 1990; Boschetto et al. 2011; Kekäläinen et al. 2015). Plasticity in migratory and spawning behavior within and among years, as demonstrated here, is likely to be increasingly important to population persistence in situations where formerly reliable cues are no longer predictive of positive fitness outcomes (Schlaepfer et al. 2002).

Migration and spawning behaviors incur benefits and costs

Animal migrations involve round-trip seasonal movements between spatially distinct areas that are used for different life events (Mueller and Fagan 2008). Migrations to breeding areas are energetically costly (Jonsson et al. 1997; Senner et al. 2020). The distance and terrain traversed can be a major component of the costs of current year reproduction and have even been documented to result in development of alternative reproductive traits that are associated with male RS (e.g., dorsal hump size and jaw length in Chinook salmon (*Oncorhynchus tshawytscha*) Kinnison et al. 2003) and egg size and number in female salmonids generally (Kinnison et al. 2001).

Previous studies of lake sturgeon spawning migratory behavior between Black Lake and Black River (Forsythe et al. 2012*a*) documented that over an 8-year period, the onset of migrations and spawning activities at spawning sites were associated with temperature, discharge, and lunar cycle. Where and when individuals spawned were highly repeatable for individuals across years (Forsythe et al. 2012*b*). Specifically, 72 h lagged effect of changes in environmental variables was found to be a reliable migratory cue and predictor of physical stream and evening light conditions conducive to successful spawning. Here we extend the analyses focusing on male migratory and spawning behavior that focus on male spawning ground occupancy as a measure of investment in current year reproduction.

Male river residence times during this study varied greatly within and between years (Fig. 2). For example, river residence time was highly variable among males present in the two main spawning run peaks in 2018 (Fig. 2). Intra-annual variation likely resulted from high late April snowfall, which delayed the onset of spawning by nearly 2 weeks relative to previous years (Figs. 3A–3D). Males spawning in the early 2018 period were afforded opportunities to spawn in areas several kilometres upstream from "traditional" spawning areas (Fig. 1). Males with prolonged river residence times were exposed to more spawning females (Fig. 4) and expressed lower sperm concentrations than males that spent less time in spawning areas of the river (Fig. 2), indicating duration of spawning ground occupancy is a reliable indicator of levels of reproductive activity. Data show that male behaviors were consistent with investment in current reproduction (i.e., duration of river occupancy and number of migratory bouts) and affected breeding opportunities in a single season as reflected in higher current year male RS (Supplementary Table S5[1]).

The number of larvae sired by males increased with increasing river residence times. This indicated that males that expended greater effort in current year reproduction in terms of prolonged time in the spawning areas realized higher RS than males residing for a shorter period. Interestingly, males that made multiple mi-

grations from the lake to the spawning grounds did not have lower sperm concentration, nor did this behavior enhance male RS. Thus, there is variability in how males expend resources to current reproduction, reflected in plasticity in migratory behaviors employed. Clearly, in the currency of current male RS, there is a more efficient strategy. Staying in the spawning area longer incurs greater rewards in terms of female exposures and offspring sired than making multiple migratory bouts, though both behaviors incur costs in terms of future reproductive events (interspawning interval, Table 7, Supplementary Table S5[1]). Given that in the UBR, there is a 43% chance that males spawning in consecutive years and a 57% chance of spawning semiannually (Pledger et al. 2013), the vast majority of males in the population spawned over the 2 years of the study. Additional work would be useful to document potential compensatory mechanisms to ascertain the full impact of current versus future trade-offs by documenting interspawning interval and RS over longer time periods.

Male RS is generally determined by successfully producing progeny with multiple mates (Trivers 1972; Price 1984; Rowe et al. 1994). Results indicate that greater access to females is afforded to males that expend resources to stay on the spawning grounds for prolonged periods of time. Quantifying the variability in migratory and reproductive effort and fitness consequences is important, especially in species of conservation concern. Long-term studies conducted in populations where the vast majority of the sexually mature individuals are tagged and observed is logistically difficult, but important. Additional work would be useful to document potential compensatory mechanisms to ascertain the full impact of current versus future trade-offs over longer periods of time and across years characterized by more extreme environmental variability over multiple male reproductive events.

Sperm concentration and quality

Studies in fishes characterized by external fertilizations indicate that male sperm quality (i.e., concentration and motility) relative to competing males is a reliable predictor of male RS regardless of reproductive tactic employed or degree of spawning synchrony (Egeland et al. 2015). Sperm concentration and sperm quality data in this study indicated that arriving at the spawning grounds and residing during periods where spawner availability is low may be beneficial to the current year RS. This is evidenced in Fig. 3, which shows males that migrate from the lake to the spawning grounds multiple times are present during times when OSR is comparatively low.

Whereas sperm concentration provides a single parameter related to sperm quality and reproductive potential, sperm velocity (Gage et al. 2004; Liljedal et al. 2008; Fitzpatrick et al. 2009; Gasparini et al. 2010) and duration of motility have also been associated with RS (Boschetto et al. 2011). The use of CASA provided a multivariate measure to quantify how migratory and spawning behaviors contributed to intermale variability. River residence times were strongly negatively associated with sperm concentration (Table 4, Supplementary Table S3[1]) and sperm quality (Table 4, Supplementary Table S3[1]) as shown by multivariate ordination of composite sperm quality traits of individual males (PC1 and PC2; Table 5).

If spawning was the predominate cause for reduced sperm concentration and quality, the expectation would be that multiple intra-annual migrations in a season would result in strong negative association between sperm concentration and quality and the number of migratory events in a season. While an increasing number of intra-annual migrations showed an intermediate positive association with PC1 and PC2 (Table 6, Supplementary Table S3[1]), and thus a negative association with sperm quality (Table 4), this association was not evident when considering sperm concentration in 2017 and 2018 (Table 4, Supplementary Table S4[1]). A likely explanation is that males with longer residence times invested heavily in current year reproduction by attempting to mate with as many females as possible, even as the number of males relative to females increased (Fig. 3). This relationship was evident in Fig. 4, where increasing number of intra-annual migrations did not increase male exposure to females in 2018, but a clear association between river residence time and female exposure was noted.

Even within a species there is tremendous variability in reproductive patterns and phenotypes (Taborsky 1998). Sperm competition where sperm of two or more males have the opportunity to fertilize the same ova (or many extruded gametes; Parker 1970) is commonly observed (Birkhead and Møller 1998), including in freshwater fishes (Egeland et al. 2015), especially those species that do not use nests but expend gametes over broad areas (Levitan 2005). Casselman et al. (2006) found that sperm concentration was positively related to fertilization success in walleye (*Sander vitreus*) and many other fish species that exhibit external fertilization (Neff et al. 2003). Sperm velocity is also important to fertilization success (Gage et al. 2004). This study did not observe males engaged in intrasexual competition, nor prespawning site selection and spatial positioning proximal to females (Oliveira et al. 2001; Neff et al. 2003) to synchronize sperm release with release of female eggs. For example, Yeates et al. (2007) reported declines in male fertilization success due to lack of ejaculate synchrony in Atlantic salmon (*Salmo salar*). Population demographic characteristics can also be important, for example, in situations where skewed OSRs can increase the intensity of intrasexual competition and the variance in individual RS (Emlen and Oring 1977). Further observation of Black River lake sturgeon while on the spawning grounds would allow greater clarity about actual reproductive tactics employed and relative success.

Larger male body size can confer advantages during intrasexual competition to establish breeding territories (Anderson et al. 2010). There was no evidence that river residence time nor the number of intra-annual spawning migrations varied consistently among males of different body size (a surrogate of age) in either 2017 or 2018. This suggested that male priority of access to females as a function of size or age may be ameliorated by migratory and spawning behaviors that increase duration of time in spawning areas interacting with females. Given the high levels of promiscuity by members of both sexes (Duong et al. 2011*a*; Dammerman et al. 2019) and evidence of sperm depletion in this study, timing migration to coincide with large aggregations of female would be a successful strategy. Results were somewhat surprising due to assumed increased testes size of large relative to small males, and tremendous range in male body size on the spawning areas (101 to 168 cm TL across both years, mean ± SD = 138 ± 13 cm). Cornwallis and Birkhead (2007) found that dominant (i.e., larger) males produced more sperm than subordinate (smaller) males, but sperm concentration of subordinate males remained more constant over a larger number of mating events. In contrast, sperm traits have been documented to differ between young and old males (Sharma et al. 2015; Vega-Trejo et al. 2019), attributed to male aging. Assuming male lake sturgeon can at least partially regenerate sperm (e.g., within a reproductive season), the reproductive senescence theory predicts that costs of reproduction over multiple reproductive events should lead to a decline in ejaculate quality and age-dependent differences in the ability of males to replenish sperm.

Lake sturgeon spawn in flowing waters of intermediate depth and velocity (Peterson et al. 2007). In the Black River population, Dammerman et al. (2019) found that the number of attending males was best associated with female RS, suggesting that depensatory forces including low spawner abundance and male (and thus sperm) abundance are important for fertilization assurance. Characteristics of lake sturgeon sperm would thus also be important for male RS as has been documented in other fish species.

Within a spawning season, males face trade-offs between sperm allocations to current versus future mating attempts. There are other factors to consider regarding sperm quality variation. Schütz et al. 2017 found that males use different tactics to success-

fully fertilize gametes. Specifically, male may adjust spawning bout duration and sperm ejaculate amounts when exposed to males of different quality and when females are present in greater abundance. Trade-offs may occur among different measures of sperm quality. Taborsky et al. (2018) documented trade-offs between measures of sperm performance and endurance that were optimized in opposing directions in different life history phenotypes of the cichlid fish *Lamprologus callipterus*. Measures of other parameters would be useful for lake sturgeon or other broadcast spawning species, including male position and distance from females as gametes are released, as well as stream discharge and numbers and qualities of competing males.

Factors influencing sperm concentration

The reduction in sperm concentration during a spawning season has been well documented for teleost fishes (Buyukhatipoglu and Holtz 1984; Piironen 1985; Christ et al. 1996). Previous sturgeon studies (Bruch and Binkowski 2002; Dumont et al. 2011; Thiem et al. 2013) found that long residence times are the result of sustained spawning efforts allowing males to breed several times in a single season. Bruch and Binkowski (2002) found that sperm concentration diminished as the spawning season progressed. Bruch and Binkowski (2002) attributed the reduction in sperm concentration to number of spawning events in a season, rather than a consequence of increased river residency, which though unreported were likely to be correlated. Our data reveal that behaviors including duration of river occupancy and number of migratory events were reliable surrogates of the level of investment in current reproduction. These behaviors were related to the number of breeding opportunities in a single season as reflected in female exposures (Fig. 4) and higher current year male RS, but at a cost of lower probability of spawning in consecutive years (longer interspawning interval resulting in higher RS; Supplementary Table S5[1]).

Implications of findings to long-lived iteroparous species

Life histories represent suites of traits that affect probabilities of survival and reproductive output through life (Partridge and Harvey 1988). Given that resources available for growth, survival, and reproduction are finite, theory classically held that selection would impose trade-offs associated with optimal allocation of resources at each age through life (Gadgill and Bossert 1970). Conditional, age-specific mortality schedule differences in adults would dictate different reproductive allocation schedules (Schaffer 1974; Charlesworth and Leon 1976).

For lake sturgeon, adult survival is extremely high; therefore, trade-offs are unlikely to involve elevated probability of mortality resulting from enhanced current year reproductive effort. The benefit of added investment in current reproduction in long-lived iteroparous species is likely a trade-off with expectations of future RS (Pianka and Parker 1975), as described in this study based on probabilities of male spawning in consecutive years. Further study would be valuable to evaluate how variability in migratory behavior adversely affects future reproductive effort over longer time periods.

Associations between physical environmental features and biotic responses

Findings from this study demonstrate the complexity of environmental conditions within a spawning period, among years, and male spawning behaviors and the influence that male behavior has on sperm concentration and quality. Spawning adults generally enter rivers when migratory conditions are favorable (Jonsson and Jonsson 2009). Environmental conditions to some extent dictate the reproductive synchrony and spatial juxtaposition of males and therefore affect male reproduction (Schuster and Wade 2003). We documented that variability in male spawning behaviors, including upstream migration time, duration of river residence, and the number of intra-annual migrations, varied with environmental conditions (principally river discharge and temperature; Fig. 3). For lake sturgeon in the UBR, Forsythe et al. (2012*a*) documented that water temperature and river discharge were highly predictive of the daily number of spawning adults arriving on the spawning grounds. Discharge is often the primary factor controlling when salmonids enter rivers, whereas increases or decreases in discharge appear to be important for the timing of the ascent (Jonsson 1991).

This study contributes understanding to male migratory and reproductive behaviors that affect male RS. Although males and females make equal contributions to offspring genotypes, the majority of life history theory has focused on the age-specific biology of females. The focus on females has been primarily motivated by the relative ease of documentation of the direct connection of female offspring number to population dynamics. In contrast, male RS is more difficult to document and is widely believed to be influenced by the number of females successfully mated (Bateman 1948) and by female quality, typically expressed by the traits of mated females (Arnold and Duvall, 1994). Additionally, results in this study indicate that male RS is heavily dependent on female availability. OSRs were consistently male-biased each year and throughout the spawning season due to differences between males and females in the interspawning interval. Males exhibited behaviors including prolonged time in spawning areas that increase current year reproductive effort. However, the rewards, in terms of RS, were not comparable (i.e., compared with engaging in multiple migratory bouts). For populations in which females of reproductive age are in low abundance (i.e., male-biased OSRs) and where females are sexually receptive over a prolonged period, males may have to expend considerable resources to successfully mate (Schuster and Wade 2003; Richard et al. 2005). Male behaviors that affect access to females via intra- or intersexual interactions based on duration and synchrony of female receptivity may not guarantee successful egg fertilization (Perrone and Zaret 1979). If findings of reproductive trade-offs described here hold over longer interspawning intervals, the disparities in lifetime fitness could be exaggerated.

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