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Relative influences of microhabitat incubation conditions and genetic parentage effects on lake sturgeon (*Acipenser fulvescens*) offspring traits during early ontogeny

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Abstract Knowledge on factors influencing traits during critical early growth periods is essential for predicting population persistence. Genetic effects and microhabitat stream conditions at female selected oviposition sites influence larval phenotypes. However, limited work has examined contributions of both factors across sequential ontogenetic stages for larvae of wild origin. Using a wild population of lake sturgeon (*Acipenser fulvescens*) from Black Lake, Michigan (USA), fertilized eggs were collected from stream substrate just prior to hatch at one-meter intervals along seven transect lines at an adult-selected spawning area. Microhabitat variables (depth, discharge, substrate size) were recorded at egg collection points. Body length, body area, and yolk-sac area were quantified for yolk-sac larvae ($N = 359$) at the time of hatch. Following the onset of exogenous feeding, larval growth was measured weekly for four weeks. Parentage was assigned using genetic-based analysis. Inter-individual variation in phenotypic traits quantified at hatch were attributed to stream microhabitat variables; mean depth had the largest influence. No additive genetic effects were detected at hatch. Post-emergence larval growth significantly varied within and among half-sibling groups with the greatest range in body size observed at 33 days post-hatch. Additive genetic variance and heritability increased with age. Results demonstrate that female-selected incubation habitats influenced traits at hatch for wild-origin fish, but effects do not persist to a sequential ontogenetic stage. Alternatively, growth after the onset of exogenous feeding was largely influenced by intrinsic (genetic) factors which must be considered when designing and implementing rehabilitation strategies for lake sturgeon and potentially other threatened riverine fishes.

Keywords Microhabitat variation · Substrate size · Discharge · Water depth · Heritability

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Introduction

Knowledge of underlying factors that contribute to growth and survival during early life stages is essential

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for predicting recruitment success and population resilience (Aubry et al. 2013; Withers et al. 2015). For many fish species, the critical period of development that is informative for predicting year class strength occurs when larvae shift from reliance on endogenous (yolk) reserves to exogenous feeding (Hjort 1914; Kamler 2008; Zarri and Palkovacs 2019). Predation and starvation have been identified as determinants of survival at this stage (Schiemer et al. 2003; Withers et al. 2015) with the risks associated with both differing among larvae based on body size. Larger fish are often better at identifying food sources, enduring periods without food, and escaping predators (Miller et al. 1988; Kamler 2008; Grutter et al. 2017; Jensen et al. 2018).

Body size during early life stages can vary due to several factors including genetic (non-environmental) sources, the environmental conditions under which larvae develop, and/or due to genotype-by-environment interactions (Monaghan 2008; Mitchell at al. 2013; Dammerman et al. 2015). Individuals of varying genotypes can have similar or differing phenotypes when reared under the same environmental conditions depending upon the degree of plasticity within the traits (Svanbäck and Schluter 2012). For broadcast spawning fish species that do not provide parental care, environmental conditions at maternally-selected oviposition sites can have a large influence on offspring phenotypes during critical early life periods (Rudolf and Rödel 2005; Refsnider and Janzen 2010; Lowerre-Barbieri et al. 2011). Females are expected to choose oviposition sites with conditions that are conducive to offspring growth and survival to maximize their own reproductive success (Kern et al. 2013); however, several factors including proximity of mates, predation risk to offspring, and microhabitat environmental conditions influence female oviposition site selection (Refsnider and Janzen 2010; Falcy 2015; Benjankar et al. 2016).

In stream systems, environmental conditions (e.g., temperature, discharge) can vary temporally and spatially (Fausch et al. 2002; Allan and Castillo 2007; McCluney et al. 2014) as well as on micro-geographic scales (Schiemer et al. 2003). Adults often shift their use of stream microhabitats (Kanno et al. 2012) during spawning, thereby potentially exposing offspring to a variety of rearing conditions. For polygamous, broadcast-spawning species like sturgeon, spatial variation in habitat use during spawning events (Caroffino et al. 2010; Dumont et al. 2011; Bocast et al. 2014) can result in larvae of the same or differing genotype to rear under varying environmental regimes (Duong et al. 2011; Dammerman et al. 2016), even within a small geographic area (e.g., within the same spawning site). Previous work has shown that stream conditions experienced prior to hatch can influence larval growth and behavior during sequential ontogenetic stages (Martell et al. 2005; Martell and Kieffer 2007; Wassink et al. 2020) for individuals from the same and different family (Dammerman et al. 2015, 2016). However, few studies have quantified the relative influences of multi-variate, stream incubation habitats combined with genetic family effects on phenotypic trait variation across sequential ontogenetic stages for wild-origin fishes including sturgeon.

Lake sturgeon (*Acipenser fulvescens*) are long-lived, potamodromous, iteroparous fish that are endemic to the Hudson Bay, Great Lakes, and Mississippi River basins (Pollock et al. 2015; Bruch et al. 2016). Listed as endangered or threatened in most states and provinces where they are present (Bruch et al. 2016), lake sturgeon populations have been numerically depressed due to overharvest, habitat loss and degradation, and limited recruitment (Hayes and Caroffino 2012). Adults reside in lakes except during the spawning season when they migrate to stream habitats to find mates (Pollock et al. 2015). Stream temperature and discharge conditions cue the timing of adult migrations as well as the timing and location of spawning within the spawning grounds (Forsythe et al. 2012a; Bruch et al. 2016). Females will spawn at multiple locations within a spawning site, spawning during numerous interactions with multiple males (Dammerman et al. 2019). Adults do not provide post-ovulatory care as the eggs incubate under site-specific conditions (Smith and King 2005; Duong et al. 2011). Spawning and egg incubation habitats are characterized by shallow depth containing cobble, pebble, and gravel substrate, which provide cover in the form of interstitial spaces for eggs and newly-hatched yolk-sac larvae (Forsythe et al. 2012a; Hastings et al. 2013). After hatch, yolk-sac larvae remain at the spawning grounds for approximately 6–15 days, dependent on temperature while absorbing endogenous yolk reserves, before dispersing downstream as exogenously-feeding larvae (Smith and King 2005; Duong et al. 2011).

Similar to other fishes, lake sturgeon mortality is high during critical early life stages (~99%; Forsythe et al. 2013). Long-term success of restoration programs depends on protection of spawning and rearing habitats

(Hayes and Caroffino 2012), and focusing recovery efforts on improving growth and survival during the larval and juvenile stages (Caroffino et al. 2010; Pollock et al. 2015). The objectives of the study described herein were to quantify microhabitat egg incubation conditions experienced by wild-origin offspring at an adult-selected spawning area, and determine the relative contribution of microhabitat incubation conditions and genetic (family) effects on traits at hatch and post-emergence growth.

Materials and methods

Study site

The study was conducted in 2013 on the Upper Black River (UBR), the largest tributary of Black Lake located in Cheboygan County, Michigan, USA (Fig. 1). Black Lake supports a well-studied population of lake sturgeon with an estimated size of 1100 adults (Baker and Scribner 2017). A mean of 300–350 adults annually migrate to the UBR over a 3–6 week period (Forsythe et al. 2012b) to spawn at various sites within a 1.50 km stretch of the river (Fig. 1). Shallow spawning sites (~1–3 m) and wadable stream conditions allow for daily monitoring of adult spawning activities and collection of gametes. Additionally, the Black Lake Streamside Rearing Facility located nearby (Fig. 1) provides the opportunity to rear captive individuals under stream conditions to monitor early development.

Egg collection and microhabitat variables

From the beginning of May to mid-June, adult lake sturgeon were sampled and monitored daily on the spawning grounds using methods described in Dammerman et al. (2019). At a well-established spawning site utilized on an annual basis (egg collection site, Fig. 1), river depth (m) was recorded daily using a staff gauge, and temperature (°C) and discharge (m^3/s) estimates were collected hourly using an Onset HOBO data logger (Cape Cod, Massachusetts, USA). Once spawning activities and egg deposition were observed at the spawning site, in situ developmental staging of the fertilized eggs on the substrate (Dettlaff et al. 1993; Eckes et al. 2015) and calculation of the cumulative thermal units (CTUs, the sum of mean daily water temperatures minus the constant, K, over a specific period of time as defined in Kempinger 1988) were conducted daily to accurately predict date of hatch. Fertilized eggs developed under site-specific conditions at the spawning site until one day prior to estimated hatch date.

On the day of collection (one day prior to predicted hatch date), seven transect lines (A-G) were placed at 5-m intervals along the stream bank parallel to the river (Fig. 2). The developing eggs were sampled at 1-m intervals along each transect line. A 3-m long metal pole with a 0.22 × 0.28-m rectangular metal frame attached to the bottom, and a Canon Powershot D10 underwater camera mounted 0.50 m above the rectangular frame, were used to characterize abiotic microhabitat variables and sample developing sturgeon eggs at each transect point. The rectangular frame (0.20 × 0.26 m) with 1-cm etched markings was placed on the substrate providing a consistent river area to be sampled at each point, and each photograph to cover a standard distance of 0.05 m^2.

Just prior to egg collection, a photo was taken at each transect point to quantify mean substrate size. Point estimates of water depth (m) and water velocity (m/s) at the points were measured using a stadia rod and Marsh McBirney flow meter. Velocity estimates were converted to discharge (m^3/s) by multiplying velocity by the river cross-sectional area. Temperature was not measured during egg collection given that it was confounded by the time of sampling. Sturgeon eggs were collected at each point by swiftly sliding a metal rod back and forth against the substrate within the rectangular frame for ten seconds to dislodge the eggs. A Wildlife Supply Company triangular kick net (25.40 cm deep) was placed directly downstream of the rectangular frame to collect all dislodged eggs. Live eggs (Fig. 2) were transported to the Black Lake Streamside Rearing Facility and kept separate by transect point in heath trays until they began to hatch the following morning. Dead eggs were discarded to prevent microbial infections.

Estimating mean depth and mean discharge at transect points for the entire incubation period

Ten days after egg collection, water depth (m) and water velocity (m/s) were measured a second time at each of the transect points to determine the reliability in using the daily staff gauge and HOBO data logger to estimate mean depth and mean discharge at each transect point over the entire egg incubation period. Depth (m) and discharge (m^3/s, converted from velocity) point estimates taken on two separate occasions at the transect points were divided

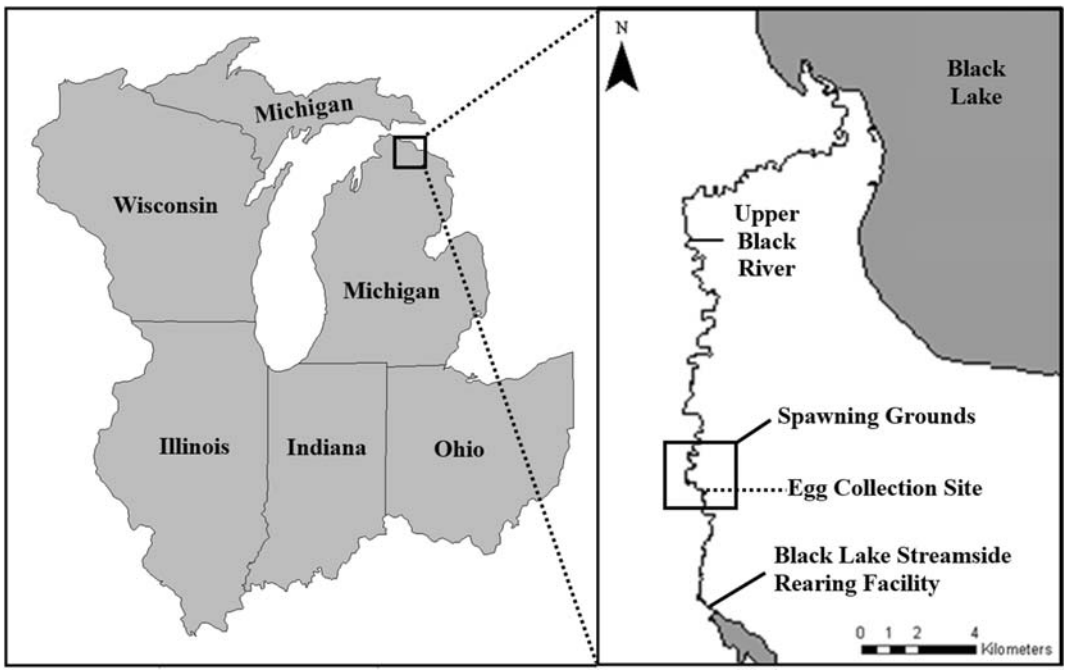

Fig. 1 The study location on the Upper Black River, the largest tributary of Black Lake, Michigan, USA. The adult-selected spawning grounds and the location where lake sturgeon eggs were collected in the study are shown

by the mean depth and mean discharge estimates recorded the same days using the staff gauge and HOBO data logger (Online Resource 1). Linear regression analysis on these ratios using the statistical program, R (version 3.1.2, R Development Core Team) revealed strong relationships ($R^2 > 0.94$) between the staff gauge/HOBO data and the point estimates (Fig. S1, Fig. S2, Online Resource 1). Thus, mean depth and mean discharge at each transect point for the entire egg incubation period were estimated using the ratios and the data recorded from the HOBO logger and staff gauge (see calculations in Table S1, Online Resource 1).

Estimating mean substrate size

Substrate photos collected at each transect point were analyzed using Image J software (version 1.34). The particle axis with the greatest linear distance was measured and recorded as the particle length (mm). Given the large number of particles in each photo, a

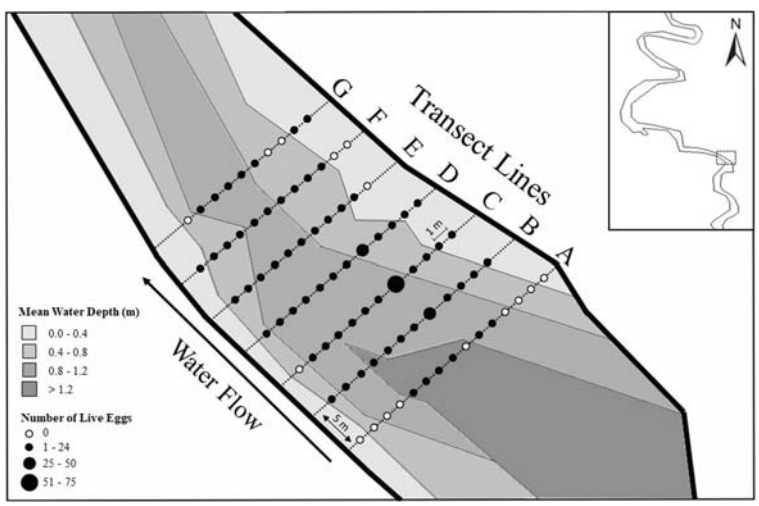

Fig. 2 Schematic diagram (not to scale) of the adult-selected spawning site where microhabitat variables (mean depth, discharge, and substrate size) were quantified along seven transect lines (A-G). Transect lines were placed 5 m apart. Fertilized lake sturgeon eggs were collected at 1-m intervals (circles) along each transect line. Circle sizes correspond to the relative number of live lake sturgeon eggs collected at each sampling point. Gray shading represents mean water depth at each of the transect points

preliminary analysis was conducted to determine whether grids could be used to estimate mean substrate size at each transect point. Ten percent of the substrate photos taken during egg collection were subsampled, and the lengths of all particles in the photo were measured. Using the same images, a 3 × 3 set of grids with each grid measuring 0.07 × 0.09 m (covering the total image area of 0.05 m^2) was placed over the image, and all particles within three randomly-selected grids were measured. Linear regression analysis in R indicated a strong relationship between the mean substrate size estimated from the grids and that estimated from the entire photo ($y = 1.53x - 1.32$, $R^2 = 0.95$). Thus, mean substrate size for each of the transect points was estimated by measuring all of the particles within three randomly-selected grids placed over the photo. Particles within each photo were classified based on the Wentworth (1922) Classification System as modified by Cummins (1962) where size categories included: sand/fine particles (>2 mm), gravel (2–16 mm), pebble (16–64 mm), cobble (64–256 mm), and boulders (>256 mm).

Quantifying phenotypic traits at hatch and post-emergence growth

At hatch, yolk-sac larvae (larvae with endogenous yolk-reserves that are not developmentally ready to exogenously feed) were randomly subsampled from each of the transect points where sturgeon eggs were collected due to space limitations in the Streamside Rearing Facility. Yolk-sac larvae were not sampled from transect points where the camera was out of water because substrate size could not be determined. Yolk-sac larvae were anesthetized with tricaine methanesulfonate (MS-222; 25.00 mg/mL) for approximately one-minute while being photographed. Image J software was used to quantify body length (mm), body area (mm^2), and yolk-sac area (mm^2; Dammerman et al. 2015). Yolk-sac larvae were randomized with respect to transect point and each was assigned to modified, liter-sized milk jugs (15.20 × 6.80 cm), which served as individual development chambers (Fig. S3, Online Resource 2). Each chamber contained one individual. Additionally, chambers contained gravel substrate to provide cover during endogenous yolk-sac absorption, mesh covering to allow water to flow out of the chambers but prevented fish escape, and independent water inputs allowing for continual water movement (~0.10 m/s). Chamber screens were cleaned multiple times daily to prevent algal accumulation. Chambers were monitored daily for fish emerging from the substrate.

Individual development chambers were cleaned and rocks were removed when larvae volitionally emerged from the substrate to begin exogenously feeding after depleting yolk-sac reserves. All dead fish found in the substrate were discarded due to tissue degradation that precluded genetic analysis. Surviving larvae were anesthetized and photographed to determine post-emergence body length (mm). Larvae were placed back in the chambers without substrate, and were photographed weekly to quantify post-emergence growth. Larvae were fed brine shrimp nauplii (*Artemia* spp) three times daily to satiation for three weeks until transitioning to processed, frozen blood worms (Chironomid midge larvae) for the remainder of the growth period. Larvae that died during the growth period and did not have significant tissue degradation were preserved in 95% ethanol for genetic parentage analysis. Approximately 4 weeks post-emergence (e.g., just before larval growth exceeded development chamber rearing capacity), surviving larvae were removed from the chambers and a clip from the caudal fin (< 1-cm^2) was non-lethally taken for genetic parentage analysis. All fin clips were individually stored in 95% ethanol.

Genetic parentage analysis

DNA was extracted from larval fin clips using DNeasy(R) extraction kits (QIAGEN, Inc.), and quantified using a Nanodrop 1000 spectrophotometer (Thermo Fisher Scientific, Inc.). Larvae were genotyped at 12 microsatellite loci: AfuG68B (McQuown et al. 2002); AfuG68, AfuG74, AfuG9, AfuG63, AfuG56, AfuG195, AfuG160, AfuG112, AfuG204 (Welsh et al. 2003); Spl 120 (McQuown et al. 2000); and Aox 27 (King et al. 2001). Polymerase chain reaction and genotyping were conducted using methods described in Duong et al. 2011. Due to low DNA concentrations, 1.50 μL of a 10.00 ng/μL stock of forward and reverse primer were used to increase signals and cycle number was set to 35 for all loci during the annealing phase. All genotyping scores were assigned by two experienced lab personnel, and a 10% subset of the samples were re-genotyped to empirically estimate genotyping error. Genotyping error was calculated as the number of allelic errors divided by the total number of alleles that were genotyped.

Parentage analysis was conducted using the software programs CERVUS 3.0 (Kalinowski et al. 2007) and COLONY 2.0.5.8 (Jones and Wang 2010), with assignment of the most likely single parent or parental pair based on concordance between the two programs. For both programs, parentage analysis included all 262 adults sampled during the 2013 spawning run, an 85% adult capture rate (Dammerman et al. 2019), and an empirical genotyping error estimate of 0.40%. In CERVUS, simulations included 10,000 offspring with a strict level of 95% and a relaxed level of 80% to determine the confidence in parentage assignment based on the population estimates of allelic frequencies. Adults with the highest maximum likelihood score in COLONY and highest positive LOD score in CERVUS were assigned as the most likely candidate parents or parental pairs.

Statistical analysis of yolk-sac larval traits measured at hatch and post-emergence larval growth

All statistical analyses were performed in R (version 3.1.2). Multicollinearity between the microhabitat variables (mean depth, mean discharge, mean substrate size) was examined by fitting Eq. 1 and quantifying the variance inflation factors (vif) using the R package "car" (Fox and Weisberg 2011). Additionally, Pearson's correlations (r) were estimated between pairs of variables. The vif values and correlation estimates were both low ($vif < 1.22$, $r < 0.30$) indicating no issues with multicollinearity. A negative binomial regression fit with R package "MASS" (Venables and Ripley 2002) was used to determine whether the number of live, fertilized lake sturgeon eggs collected at each transect point was dependent on the three microhabitat variables. The model was fit as:

$$Number\ of\ Live\ Eggs = MeanDepth + MeanDischarge + MeanSubstrateSize + e \quad (1)$$

with e referring to the residual error. A negative binomial error distribution was used instead of a Poisson given the over-dispersion in the data. Simpler models were tested in a step-wise manner by eliminating one variable at a time. Likelihood ratio tests were used to determine the model of best fit.

Linear mixed-effect models were used to test for the effects of the microhabitat variables and genetic additive effects (e.g., family effects based on shared parentage) on the phenotypic traits measured at hatch (body length, body area, and yolk-sac area) for the yolk-sac larvae. The three hatch traits were analyzed separately using restricted maximum likelihood estimation and the R package "regress" (Clifford and McCullagh 2014). First, the three hatch traits were each independently fit to the full model:

$$Hatch\ Trait = MeanDepth + MeanDischarge + MeanSubstrateSize + GeneticRelationshipMatrix + e \quad (2)$$

The three microhabitat variables were fit as fixed effects. The term 'GeneticRelationshipMatrix' here refers to the A-matrix, or additive genetic relationship matrix, that contains mathematical values of relatedness (e.g., 0.25 for half-siblings, 0.5 for full-siblings) for every pair-wise individual comparison in the pedigree (Wilson et al. 2010). The pedigree was constructed through genetic parentage analysis, and fit here as a random effect ($GeneticRelationshipMatrix \sim N\left(0, A\sigma_A^2\right)$). This allows for the estimation of the additive genetic variance (V_A), or the measure of the additive effect genes have on an individual's phenotype. Lastly, e in the model refers to the residual error ($e \sim N\left(0, I\sigma_e^2\right)$). After initial fit to the full model (Eq. 2), each of the traits were then fit to all simpler models in a step-wise manner. Model of best fit was determined using likelihood ratio tests.

To determine whether the additive genetic and environmental effects co-varied with age, the post-emergence larval growth data was fit to a random regression animal model (Meyer and Hill 1997; Schaeffer 2004; Wilson et al. 2005) using the R package "pedigreemm" (Bates and Vasquez 2014). The model included a second-order polynomial regression for Age (days post-hatch), which models the additive genetic effect as an animal-specific quadratic function over time (with terms P0, P1, and P2), the three microhabitat variables as fixed effects, and weighted, heterogeneous residual variances. Typically, in an animal model framework, repeated measures of individuals requires inclusion of a 'permanent environmental effect' term to correct for correlations that an individual has with itself (e.g., non-genetic sources of fixed differences among individuals;

Wilson et al. 2010). Since convergence issues prevented inclusion of a 'permanent environmental effect' term that varied with age in the study, weight residual variances were used to reduce potential bias in the additive genetic variance estimates (Kruuk and Hadfield 2007; Wilson et al. 2010).

Weighted residual variances were generated by fitting four separate models, one for each age, with the population mean as the only fixed effect and the A-matrix ('GeneticRelationshipMatrix' term described above) as a random effect. The four sets of additive genetic and residual variances estimated from these models were used to assign weights for the polynomial model. Heterogeneous variances were used given that the residual variance is not always constant over time (Schaeffer 2004). However, a random regression animal model with homogenous variances was also fit, and compared to the heterogeneous model using Akaike Information Criterion (AIC) values. The simplest model with the lowest AIC value (≥2 apart) was chosen as the model of best fit. To determine how larval body length compared among related individuals (i.e., half-siblings and sibling groups), heritability (h^2) was estimated at each age by taking the additive genetic variance (V_A) divided by the sum of the additive variance and residual variances (V_R) estimated from the random regression animal model of best fit. Given the inability to model the permanent environmental effects, heritability estimated in the study represents the upper-limit (or highest possible value) of a narrow-sense heritability estimate.

Preliminary tests for the presence of maternal effects and spatial autocorrelation

For larvae that were assigned a mother during genetic parentage analysis, the presence of a maternal effect was tested by fitting models with female body size as an additional random effect. In all models, variances attributed to the maternal effect were negligible (0–1.71%) indicating little influence of maternal effects on the traits measured in the study. To test for the presence of spatial autocorrelation in the environmental covariates given the transect sampling design (Finley et al. 2018), traits were fit using Eq. 1, and semi-variograms of the residuals (Dormann et al. 2007) were plotted using the R package "geoR" (Ribeiro Jr and Diggle 2018). Visualizations of these plots indicated there was no evidence of spatial autocorrelation within the data; therefore, spatial effect terms were not needed in the final analysis of the traits.

Results

Fertilized egg collection

On May 3rd, 2013, adult lake sturgeon were observed spawning at a well-established spawning site (egg collection site, Fig. 1) in the UBR. On May 5th, developmental staging (Dettlaff et al. 1993; Eckes et al. 2015) of eggs present on the substrate confirmed fertilization. Fertilized eggs were predicted to hatch on May 9th based on staging and estimated CTUs (Kempinger 1988). On May 8th (one day prior to expected hatch), sturgeon eggs were collected along the seven transect lines at approximately 66.50 CTUs, which is within the range of CTUs at the time of hatch estimated in previous lake sturgeon studies on the UBR (Smith and King 2005; Dammerman et al. 2015). Of the 84 transect points sampled (Fig. 2), live, fertilized lake sturgeon eggs were collected from 68 different points (Fig. 2, Table 1). The number of live, fertilized lake sturgeon eggs collected at these points (Fig. 2) ranged from 0 to 73 with a total of 541 live, fertilized eggs collected along the seven transect lines. Most eggs were collected near the thalweg in the center of the river, and the largest proportion of live eggs (55%) was collected from transect lines C and D (Fig. 2).

Mean discharge for the transect points where eggs were collected was 0.75 m^3/s (SD, 0.28) ranging from 0.05 to 1.22 m^3/s. Mean substrate size was 11.74 mm (SD, 5.39) and ranged from 3.58 to 33.83 mm. Gravel was the most prevalent substrate type, but size varied among transect lines with some points containing predominantly pebble substrate (Table 1). Mean discharge had the largest effect influence and was positively related to the number of live lake sturgeon eggs collected from the transect points ($p < 0.01$;Table 2). Mean substrate size was included in the model of best fit, but the variable did not have a significant effect on its own ($p = 0.18$, Table 2). Mean depth at the transect points where eggs were collected was 0.79 m (SD, 0.29) ranging from 0.12 to 1.33 m and varied among transect lines (Table 1), but was not associated with the number of live eggs collected at each sampling point ($p = 0.29$).

Phenotypic traits measured at hatch

At hatch, 359 yolk-sac larvae were sampled from 68 of the transect points where fertilized eggs were collected due to space limitations (i.e., number of individual development chambers). The mean proportion of eggs sampled from each transect points was 76.80% (SD, 34.67). Mean body length at hatch was 13.02 mm (SD, 0.97), and ranged from 9.80 to 16.18 mm. Mean body area was 28.17 mm^2 (SD, 4.16), and ranged from 17.37 to 41.10 mm^2 among the transect lines (Fig. 3). Both body length and body area were associated with the three microhabitat variables quantified at each transect point. Mean depth and mean substrate size were negatively associated with body length and body area with depth having the largest influence (Table 3). Mean discharge was positively associated with body length and body area (Table 3). Yolk-sac area varied among yolk-sac larvae with a mean of 7.95 mm^2 (SD, 1.16) and ranged from 5.13 to 12.42 mm^2. Yolk-sac area was negatively dependent on mean depth and positively associated with mean discharge at the transect sampling points (Table 3), but did not vary due to mean substrate size. The additive genetic effect (i.e., genetic term) was not significant for the three phenotypic traits measured at the time of hatch ($p > 0.05$) and was dropped from the models.

Post-emergence larval growth and parentage analysis

Larvae were observed volitionally emerging from the substrate within the individual development chambers on May 20th, approximately 12 days post-hatch when CTU was 205.00. On the date of emergence, 334 larvae were photographed for a survival rate of 93.04% from hatch to time of emergence. Larvae were photographed again on May 27th (19 days post-hatch), June 3rd (26 days post-hatch), and June 10th (33 days post-hatch) before outgrowing the individual development chambers. A total of 44 larvae died during the post-emergence period. Viable fin clips were collected from 15 of these larvae for genetic parentage analysis. When the experiment concluded on June 10th, 290 larvae were alive for a survival rate of 86.83% in the chambers during the post-emergence growth period; fin clips were taken from all of these larvae for genetic parentage analysis.

The 305 fin clips collected from the larvae for parentage analysis were genotyped at 12 loci. A total of 11 loci were in Hardy-Weinberg equilibrium. Allelic diversity ranged from 2 to 11 with a mean of 5.25 alleles per locus. Expected heterozygosity for the 12 loci was 0.58. The combined, multi-locus, non-exclusion probability for the parent pairs was 8.46×10^{-5}. Ninety percent of the larvae ($N = 274$) were assigned at least one parent with a 75% degree of concordance in parental assignments between CERVUS and COLONY. Forty females were assigned offspring with a mean of 5.60 larvae (SD, 6.54) and a range of 1 to 27 offspring per female. A relationship was not observed between the number of offspring assigned and female body length ($R^2 < 0.001$, Fig. S4, Online Resource 2). Females had a mean of 4.45 mates (SD, 4.57) with mate number ranging from 1 to 19 males. Sixty-one males were assigned offspring with a mean of 4.30 larvae (SD, 3.56) and range of 1 to 15 larvae per male.

Mean growth from hatch (May 9th) to four weeks post-emergence (June 10th, age 33 days) was 28.38 mm (SD, 4.36, range of 11.85–39.34). A relationship was not observed between yolk-sac area at hatch and growth from hatch to the time of emergence ($R^2 = 0.03$, Fig. S5, Online Resource 2). Mean growth during the post-emergence growth period (May 20th – June 10th) was 18.71 mm (SD, 5.23, range 3.57–30.06). However, larvae showed considerable variation in body length with the inter-individual variation in size increasing with age (Fig. 4). The greatest range in larval body size was observed at 33 days post-hatch as the largest and smallest individuals differed in size by 26.38 mm (Fig. 4).

Similar larval growth trajectories with heterogeneous slopes were observed within and among half-sibling groups as individuals that were largest at the onset of exogenous feeding (12 days post-hatch) were not necessarily the largest at the end of the study (33 days post-hatch). For clarity and simplicity, larval growth trajectories from the two females that were assigned the most larvae during genetic parentage analysis are shown to demonstrate the pattern seen across maternal sibling groups (Fig. 5). Approximately 23% of the offspring assigned a mother in the study came from these two females (Fig. S6). A plot showing the larval growth trajectories for all forty females can be seen in Online Resource 2 (Fig. S7).

The random regression animal model with weighted, heterogeneous residual variances was the best fit for the post-emergence larval growth data (Table 4). Models

Table 1 Mean (standard deviation, range) estimates for the three microhabitat rearing conditions at the 68 transect points where live, fertilized lake sturgeon eggs were collected. Estimates are for the entire egg incubation period (3-May to 8-May). Mean depth and mean discharge were predicted from staff gauge and HOBO data logger measurements (Online Resource 1). Mean substrate size was estimated using digital photography. Microhabitat rearing conditions within a spawning site were quantified to determine what environmental conditions influence the location of adult lake sturgeon spawning

Transect line	# Sampling points	Mean depth (m)	Mean discharge (m^3/s)	Mean substrate size (mm)
A	6	1.23 (0.09, 1.08–1.33)	0.75 (0.11, 0.57–0.86)	13.99 (6.15, 9.12–25.56)
B	12	0.90 (0.29, 0.26–1.22)	0.68 (0.26, 0.11–1.00)	12.22 (5.47, 3.58–22.67)
C	11	0.80 (0.32, 0.14–1.06)	0.73 (0.25, 0.12–0.92)	9.51 (3.02, 5.22–14.38)
D	12	0.69 (0.30, 0.12–0.97)	0.68 (0.35, 0.05–0.98)	12.94 (4.40, 6.74–21.11)
E	10	0.74 (0.18, 0.36–0.95)	0.82 (0.29, 0.15–1.07)	10.40 (4.92, 5.57–21.73)
F	10	0.64 (0.19, 0.29–0.87)	0.75 (0.29, 0.07–1.00)	12.34 (8.08, 6.73–33.83)
G	7	0.68 (0.26, 0.25–0.89)	0.89 (0.37, 0.25–1.22)	10.58 (3.74, 7.75–14.82)

containing any of the three microhabitat variables had higher AIC values than models that excluded the variables (Table S3, Online Resource 3). The weighted, heterogeneous residual variance model was also a better fit for the data when compared to the homogeneous residual variance model (delta AIC = 60.856). The polynomial terms obtained from the model of best fit were: P0 = 1.74, P1 = 23.78, P2 = 9.53. Residual (V_R) and additive genetic (V_A) variances estimated for each age from the model outputs varied from 0.44 to 35.05, increasing with age. Heritability (h^2) for body length also increased with age ranging from 0.80 to 0.85 (Table 4).

Discussion

Microhabitat conditions within adult selected oviposition sites affect offspring growth and development in a variety of species (Refsnider and Janzen 2010). However, knowledge regarding the persistent effects of these environmental variables on larval trait variation across sequential ontogenetic stages is limited. In this study on a threatened population of lake sturgeon, quantification of microhabitat variables at an adult-selected spawning area, captive rearing of wild-produced larvae, and genetic-based parentage analysis allowed for the determination of how microhabitats and genetic effects influenced larval phenotypes at hatch and post-emergence.

Microhabitat variables influence adult spawning behavior and larval traits measured at hatch

The positive relationship between mean discharge and the number of fertilized eggs collected in the stream reinforces the importance of this stream variable on lake sturgeon early life history. Eggs were collected from sites where mean discharge was less than 1.10 m^3/s (velocity less than 0.86 m/s), which allows for successful mixing of sperm and eggs during broadcast spawning events while not requiring adults to expend excessive energy staying positioned near mates. Additionally, adequate flows help keep the adhesive surface of incubating eggs clear of sediment and debris reducing the occurrence of microbial infections (Fujimoto et al. 2013).

Table 2 Coefficient estimates, standard errors (SE), *p* values, and 95% confidence intervals (CI) from the negative binomial regression of best fit showing the expected change in the log number of live, fertilized lake sturgeon eggs collected due to the microhabitat variables quantified at each transect point. Microhabitat variables within the stream were quantified to determine what environmental components influence the number of lake sturgeon eggs present in a given location on the spawning grounds

Variable	Component	Estimate	SE	P value	95% CI
Number of Live Eggs Collected	Intercept	−0.05	0.55	0.933	(−1.07, 0.99)
	Mean Discharge	2.24	0.55	<0.001	(1.23, 3.25)
	Mean Substrate Size	0.03	0.02	0.179	(−0.02, 0.08)

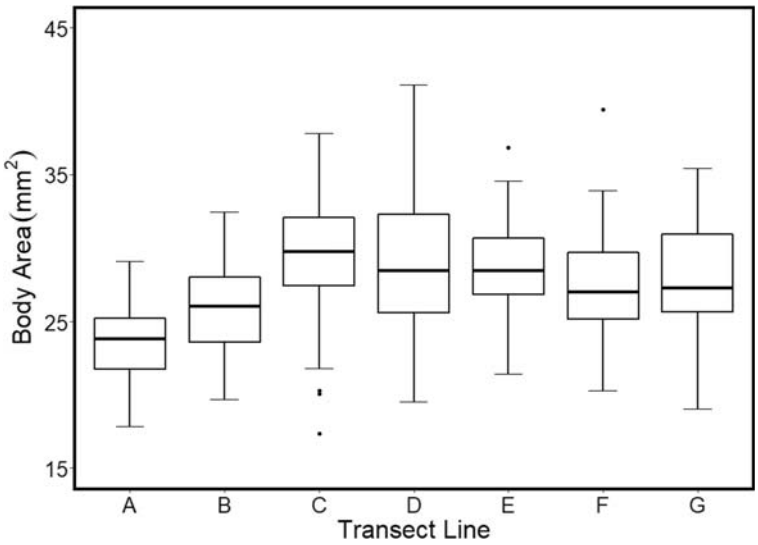

Fig. 3 Box and whisker plots (median, range, quantiles) showing body area at hatch for lake sturgeon yolk-sac larvae that were collected as fertilized eggs along seven transect lines from an adult-selected spawning area. The three microhabitat variables (depth, discharge, and substrate size) experienced during egg incubation had a statistically significant influence on the trait

Egg surfaces clear of debris promotes gas exchange in and out of the egg (Kemp et al. 2011; Siddique et al. 2014). Therefore, sufficient gas exchange during the embryonic stage may explain the positive relationship between discharge and the three phenotypic traits measured at hatch. For example, Green et al. (2006) documented larger body length and body area at hatch for tropical anemonefish (*Amphiprion melanopus*) that incubated near the interior of a clutch where gas exchange was presumed to be higher as opposed to the peripheral micro-environments.

Numerous studies have documented adult preferences for gravel or pebble substrate at spawning sites for sturgeon (McAdam 2011; Boucher et al. 2014; Pollock et al. 2015) and other broadcast spawning fishes that lack parental care (e.g., *Alosa fallax*, Gerkens and Thiel 2001; *Cyprinella lutrensis*, Durham and Wilde 2008; *Sander vitreus*, *Sander canadensis*, Bozek et al. 2011). In this study on lake sturgeon, gravel being the predominant substrate type at the transect points and inclusion of substrate size in the model of best fit for the number of eggs collected was not surprising. Interstitial spaces protect eggs from being scoured (Caroffino et al. 2010) and provide cover for yolk-sac larvae (Hastings et al. 2013). Lack of these interstitial habitats during rearing decreases survival, reduces growth, and

Table 3 Coefficients, standard errors (SE), p values, and 95% confidence intervals (CI) estimated from the models of best fit for the three phenotypic traits measured at hatch for yolk-sac larvae. Models were fit to examine whether stream habitat variables influenced phenotypes at the time of hatch

Hatch traits	Fixed effect	Estimate	SE	*P*-value	95% CI
Body Length	Intercept	13.64	0.33	<0.001*	(13.00, 14.29)
	Mean Depth	−1.08	0.27	<0.001*	(−1.62, −0.55)
	Mean Discharge	0.76	0.27	0.006*	(0.22, 1.30)
	Mean Substrate	−0.03	0.01	0.010*	(−0.05, −0.01)
Body Area	Intercept	30.09	1.41	<0.001*	(27.32, 32.87)
	Mean Depth	−3.85	1.17	0.001*	(−6.16, −1.54)
	Mean Discharge	3.48	1.17	0.003*	(1.18, 5.77)
	Mean Substrate	−0.13	0.05	0.006*	(−0.22, −0.04)
Yolk-sac Area	Intercept	7.40	0.27	<0.001*	(6.87, 7.93)
	Mean Depth	−0.20	0.29	0.488	(−0.78, 0.37)
	Mean Discharge	0.87	0.31	0.005*	(0.27, 1.47)

*Indicates the variable was statistically significant ($p < 0.05$)

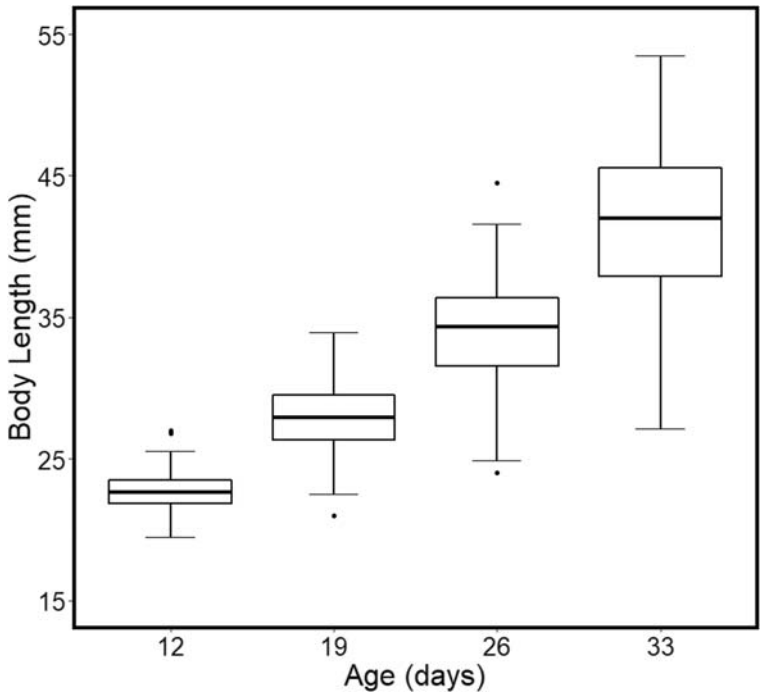

Fig. 4 Box and whisker plots (median, range, quantiles) for larval body length during the post-emergence growth period. Exogenously-feeding larvae showed considerable variation in size with the greatest range observed at 33 days post-hatch. Growth varied due to additive genetic effects, but no effect was detected for the three microhabitat stream variables experienced during egg incubation

delays gut development for larval sturgeon (Baker et al. 2014; Boucher et al. 2014). The negative relationships between body length and body area at hatch with mean substrate size documented in the study suggests that some eggs may have been affected from incubating at sites that lacked sufficient interstitial spaces. Although photographs of the substrate were taken for analysis, the mean substrate type quantified for the entire photo was assumed to be the substrate that all eggs incubated on given the inability to distinguish the exact location of every egg in the photograph.

As broadcast spawners, sturgeon can successfully reproduce across a range of water depths if flow rates allow for successful mixing of eggs and milt. Thus, water depth has been cited as a relatively unimportant cue in comparison to other cues for spawning adults (Parsley et al. 1993; Roseman et al. 2011). This study on lake sturgeon is consistent with the literature as depth

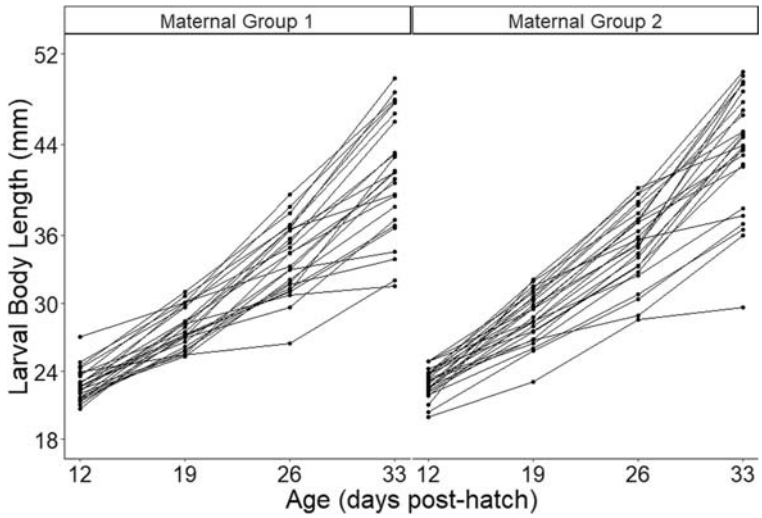

Fig. 5 Individual growth curves for exogenously-feeding larvae from two maternal sibling groups that were assigned nearly 23% of the total offspring during genetic parentage analysis. Larval body length was measured four times during the 33-day post-emergence growth period, and significantly varied within and among maternal groups

Table 4 Additive genetic variances (V_A) and residual variances (V_R) estimated at each age (days post hatch) from the random regression animal model of best fit. Heritability (h^2) was estimated as $h^2 = V_A/(V_A + V_R)$

Age (days)	V_A	V_R	h^2
12	1.74	0.44	0.80
19	4.50	1.00	0.82
26	14.19	2.89	0.83
33	35.05	6.37	0.85

was not associated with the number of live sturgeon eggs collected along the transect lines. Despite this lack of importance, water depth has been consistently reported and/or modeled in numerous studies detailing suitable spawning and rearing habitat for lake sturgeon (Bruch and Binkowski 2002; Pollock et al. 2015; Baril et al. 2017) as well as other sturgeon species (Billard and Lecointre 2001; Flowers et al. 2009; Paragamian et al. 2009; McDonald et al. 2010; Yi et al. 2010). Collectively, studies cite that because water depths at available spawning habitats vary greatly among populations, depth information is more informative when taken in consideration with other critical habitat variables (e.g., flow, temperature). Thus, the negative relationship of depth with the three phenotypic traits measured at hatch in this study is not particularly meaningful without also considering the influence of flow or substrate. Regardless, lake sturgeon spawning habitat preferences of moderate velocities (0.15–1.40 m/s), depths less than 6-m, and gravel to cobble substrates (Hay-Chmielewski and Whelan 1997; Chiotti et al. 2008; Pollock et al. 2015; Bruch et al. 2016) were also observed in this study on the Black Lake sturgeon population. Collectively, these three variables have direct effects on larval phenotypes that are tied to survival during critical early life stages.

Additive genetic effects influence post-emergence larval growth

Growth during early life stages is predicted to vary due to intrinsic and extrinsic factors including genetic effects and environmental rearing conditions (Kamler 2008; Garrido et al. 2015). Despite affecting traits at the time of hatch, the three microhabitat stream variables experienced during egg incubation did not have a persistent effect on growth for exogenously-feeding larvae. Alternatively, a significant proportion of the variation in growth rate observed was due to additive genetic effects, which have been shown to vary with ontogeny given that selection regimes are often age-specific (Wilson and Réale 2006). The increase in additive genetic variance (and thus heritability) with increasing age is consistent with results by Yongsheng et al. (2011), who measured juvenile body length for full-sibling families of Japanese flounder (*Paralichthys olivaceus*) during early ontogeny. Additionally, results are concordant with a general trend noted for fish in the literature (Kinghorn 1983; Nilsson 1994; Choe and Yamazaki 1998), presumably due to the "timing hypothesis" or "variance compounding" where traits expressed later in life show more variance due to the cumulative effects of allelic variants and any new gene expression (Houle 1998; Wilson et al. 2005).

Despite being reared independently in this study, larval growth trajectories varied considerably among individuals after the onset of exogenous feeding with size heterogeneity being the greatest at the end of the experiment (33 days post-hatch). Baras and Lucas (2010) note the same pattern in dorado (*Brycon moorei*) where individuals reared in isolation following hatch differed in size by approximately 17 cm at 36 days post-hatch. Paired with the lack of persistent microhabitat effects, results from this study on lake sturgeon suggest that larvae reared under the same environmental conditions (e.g., within a hatchery environment) will still show individual variation in growth due to inherent, genetic differences. Similar results have been noted by Martins et al. (2005) for larval African catfish (*Clarias gariepinus*) and Wang et al. (1998) for hybrid sunfish (*Lepomis cyanellus* x *L. macrochirus*) where individually-housed fish showed variation in growth despite rearing under "optimal conditions" without competition for resources; the authors concluded that the factors driving these individual differences must be genetically-based. Examples of these genetic-based factors associated with differential larval growth in fishes include metabolic rates, digestive capabilities, starvation thresholds, and food conversion efficiencies (Letcher et al. 1996; Campeas et al. 2009; Garrido et al. 2015). Although none of these factors were measured in this study on lake sturgeon, observed growth trajectories indicate that not only may these factors vary among larvae in the same cohort, but also among larvae within the same sibling groups. Thus, individuals with the same genotype may inherently differ in growth and

potentially survival due to differential utilization of diets in a captive setting (Castanheira et al. 2017) and presumably the wild.

Heritability estimates quantified for body length during the post-emergence growth period were higher than estimates reported for body length at hatch and growth from hatch to emergence estimated in previous studies on the sturgeon population on Black Lake (Dammerman et al. 2015, 2016). Although heritability can increase with age (Wilson et al. 2005) and weights were assigned to the heterogeneous residual variances, the inability to model the 'permanent environmental effects' term in the random regression model could have inflated the V_A (and thus heritability) estimates in the study. Thus, h^2 estimates are being reported with the understanding that they represent the upper limit of a heritability estimate and provide a modest insight into the potential ability of the trait to genetically respond to selection.

Conclusions and future directions

The results of this study has important implications for both lake sturgeon rehabilitation strategies and riverine fishes in general. Protection of spawning and rearing habitats requires a detailed understanding of what environmental variables are important for spawning success and are conducive to growth and survival during critical early life stages. For broadcast spawning species like sturgeon, maintaining sufficient water depths, adequate flows to ensure fertilization success and egg viability, and suitable substrate with ample interstitial spaces are essential habitat requirements for spawning adults, eggs, and yolk-sac larvae. These variables can directly influence phenotypes at hatch thereby driving early life survival in riverine fishes. Additionally, intrinsic factors can play a primary role in determining larval growth after the onset of exogenous feeding. Given that size is an important indicator of overwinter survival, which is a known driver of recruitment for many fishes (Hurst and Conover 1998; Fullerton et al. 2000; Biro et al. 2004), rehabilitation programs like those implemented for lake sturgeon must consider the combined influence of external and intrinsic factors when designing effective stocking strategies aimed at optimizing growth in hatchery programs (Volkman et al. 2004).

Additional observations during the post-emergence growth period would benefit this study by allowing 'permanent environmental effects' to be modeled and more precise heritability estimates to be quantified. These types of observations would provide a greater understanding of how post-emergence larval growth will respond to selection thereby providing further insight into potential population changes in genotypic (family) composition, population levels of genetic diversity, and resilience. In addition to identifying intrinsic factors, future work could include examining in-stream microhabitat variables that potentially influence post-emergence growth such as the spatial distribution of aquatic macro-invertebrates, which are important prey species for juvenile lake sturgeon (Pollock et al. 2015). Studies such as these would provide insight into whether size differences observed in the study during captive rearing are indicative of size differences present among wild larvae that remain in the stream during the exogenous feeding period. Collectively, knowledge gained could provide greater understanding of the factors driving recruitment or affecting potential population persistence, thereby providing guidance for rehabilitating and protecting wild, threatened riverine fish populations.

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Authors' contributions The authors agree that each individual listed in the author list: 1) made substantial contributions to the conception or design of the work; or the acquisition, analysis, or interpretation of data; or the creation of new software used in the work; 2) drafted the work or revised it critically for important intellectual content; 3) approved the version to be published; and 4) agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Data availability Datasets used in the manuscript will be made available on Dryad after acceptance for publication.

Compliance with ethical standards

Conflicts of interest/competing interests The authors have no conflicts of interest or competing interests regarding the manuscript content.

Ethics approval All procedures performed in the study involving animals were conducted under animal use and care procedure number (03/14–042-00), and were in accordance with the ethical standards of the Michigan State University Institutional Animal Care and Use Committee.

Consent to participate Not applicable as this research did not involve human participants.

Consent for publication The authors all agree with the content of the manuscript, give explicit consent to submit for publication, and have permission from responsible authorities at Michigan State University (where the work was carried out) to submit this manuscript for publication.

Code availability ImageJ is freely available on the NIH website (https://imagej.nih.gov/ij/). R is freely available for download on The R Project website (https://www.r-project.org/). R code used for analyses will be made available on Dryad after manuscript is accepted for publication.

References

Allan JD, Castillo MM (2007) Stream ecology: structure and function of running waters. Springer, Dordrecht

Aubry LM, Rockwell RF, Cooch EG, Brook RW, Mulder CPH, Koons DN (2013) Climate change, phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. Glob Change Biol 19:149–160

Baker EA, Scribner KT (2017) Cohort-specific estimates of first-year survival are positively associated with size at stocking for lake sturgeon *Acipenser fulvescens* (Rafinesque 1817) stocked in black Lake, Michigan, USA. J Appl Ichthyol 33: 892–897

Baker DW, McAdam DSO, Boucher M, Huynh KT, Brauner CJ (2014) Swimming performance and larval quality are altered by rearing substrate at early life stages in white sturgeon, *Acipenser transmontanus* (Richardson, 1836). J Appl Ichthyol 30:1461–1472

Baras E, Lucas MC (2010) Individual growth trajectories of sibling *Brycon moorei* raised in isolation since egg stage, and their relationship with aggressive behaviour. J Fish Biol 77: 985–997

Baril A-M, Buszkiewicz JT, Biron PM, Phelps QE, Grant JWA (2017) Lake sturgeon (*Acipenser fulvescens*) spawning habitat: a quantitative review. Can J Fish Aquat Sci:1–9

Bates D, Vasquez AI (2014) Pedigreemm: pedigree-based mixed-effects models. R package version 0.3–3. https://CRAN.R-project.org/package=pedigreemm

Benjankar R, Tonina D, Marzadi A, McKean J, Isaak DJ (2016) Effects of habitat quality and ambient hyporheic flows on salmon spawning site selection. J Geophys Res Biogeosci 121:1222–1235

Billard R, Lecointre G (2001) Biology and conservation of sturgeon and paddlefish. Rev Fish Biol Fish 10:335–392

Biro PA, Morton AE, Post JR, Parkinson EA (2004) Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). Can J Fish Aquat Sci 61:1513–1519

Bocast C, Bruch RM, Koenigs RP (2014) Sound production of spawning lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in the Lake Winnebago watershed, Wisconsin, USA. J Appl Ichthyol 30:1186–1194

Boucher MA, McAdam SO, Shrimpton JM (2014) The effect of temperature and substrate on the growth, development and survival of larval white sturgeon. Aquac 430:139–148

Bozek MA, Baccante DA, Lester NP (2011) Walleye and sauger life history. In: Barton BA (ed) Biology, management, and culture of walleye and sauger. USA pp, American Fisheries Society, Bethesda, Maryland, pp 233–301

Bruch RM, Binkowski FP (2002) Spawning behavior of lake sturgeon (*Acipenser fulvescens*). J Appl Ichthyol 18:570–579

Bruch RM, Haxton TJ, Koenigs R, Welsh A, Kerr SJ (2016) Status of lake sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. J Appl Ichthyol 32:162–190

Campeas A, Brun-Bellut J, Baras E, Kestemont P, Gardeur JN (2009) Growth heterogeneity in rearing sea bass (*Dicentrarchus labrax*): test of hypothesis with an iterative energetic model. An 3(9):1299–1307

Caroffino DC, Sutton TM, Elliott RF, Donofrio MC (2010) Predation on early life stages of lake sturgeon in the Peshtigo River, Wisconsin. Trans Am Fish Soc 139:1846–1856

Castanheira MF, Conceicao LEC, Millot S, Rey S, Begout ML, Damsgard B, Kristiansen T, Hoglund E, Overli O, Martins CIM (2017) Copings styles in farmed fish: consequences for aquaculture. Rev Aqua 9:23–41

Chiotti JA, Holtgren JM, Auer NA, Ogren SA (2008) Lake sturgeon spawning habitat in the big Manistee River, Michigan. North Am J Fish Manag 28:1009–1019

Choe MK, Yamazaki F (1998) Estimation of heritabilities of growth traits, and phenotypic and genetic correlations in juvenile Masu salmon *Oncorhynchus masou*. Fish Sci 64(6):903–908

Clifford D, McCullagh P (2014) The regress package R package version 1.3-15

Cummins KW (1962) An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. Am Midl Naturalist 67:477–504

Dammerman KJ, Steibel JP, Scribner KT (2015) Genetic and environmental components of phenotypic and behavioral trait variation during lake sturgeon (*Acipenser fulvescens*) early ontogeny. Environ Biol Fish 98:1659–1670

Dammerman KJ, Steibel JP, Scribner KT (2016) Increases in the mean and variability of thermal regimes result in differential phenotypic responses among genotypes during early ontogenetic stages of lake sturgeon (*Acipenser fulvescens*). Evol Appl 9(10):1258–1270

Dammerman KJ, Webb MAH, Scribner KT (2019) Riverine characteristics and adult demography influence female lake sturgeon (*Acipenser fulvescens*) spawning behavior, reproductive success, and ovarian quality. Can J Fish Aquat Sci 76: 1147–1160

Dettlaff TA, Ginsburg AS, Schmalhausen OI (1993) Sturgeon fishes: developmental biology and aquaculture. Springer-Verlag, Berlin

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30(5):609–628

Dumont B, D'Amours J, Thibodeau S, Dubuc N, Verdon R, Garceau S, Bilodeau P, Mailhot Y, Fortin R (2011) Effects of the development of a newly created spawning ground in the des Prairies River (Quebec, Canada) on the reproductive success of lake sturgeon (*Acipenser fulvescens*). J Appl Ichthyol 27:394–404

Duong TY, Scribner KT, Crossman JA, Forsythe PS, Baker EA (2011) Environmental and maternal effects on embryonic and larval developmental time until dispersal of lake sturgeon (*Acipenser fulvescens*). Can J Fish Aquat Sci 68:643–654

Durham BW, Wilde GR (2008) Composition and abundance of drifting fish larvae in the Canadian River, Texas. J Freshw Ecol 23(2):273–280

Eckes OT, Aloisi DB, Sandheinrich MB (2015) Egg and larval development index for lake sturgeon. NA J Aquac 77:211–216

Falcy MR (2015) Density-dependent habitat selection of spawning Chinook salmon: broad-scale evidence and implications. J Anim Ecol 84:545–553

Fausch KD, Torgersen CE, Baxter CV, Li HW (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6):483

Finley AO, Forsythe PS, Crossman JA, Baker E, Scribner KT (2018) Assessing impact of exogenous features on biotic phenomena in the presence of spatial dependence: a lake sturgeon case study in natural stream settings. PLoSONE 13(12):e0204150

Flowers HJ, Pine WE III, Dutterer AC, Johnson KG, Ziewitz JW, Allen MS, Parauka FM (2009) Spawning site selection and potential implications of modified flow regimes on viability of gulf sturgeon populations. Trans Am Fish Soc 138:1266–1284

Forsythe PS, Crossman JA, Bello NM, Baker EA, Scribner KT (2012a) Individual-based analyses reveal high repeatability in timing and location of reproduction in lake sturgeon (*Acipenser fulvescens*). Can J Fish Aquat Sci 68:1–13

Forsythe PS, Scribner KT, Crossman JA, Ragavendran A, Baker EA, Davis C, Smith KK (2012b) Environmental and lunar cues are predictive of timing of river entry and spawning site arrival in lake sturgeon. K Fish Biol 81:35–53

Forsythe PS, Scribner KT, Crossman JA, Ragavendran A, Baker EA (2013) Experimental assessment of the magnitude and sources of lake sturgeon egg mortality. Trans Am Fish Soc 142:1005–1011

Fox J, Weisberg S (2011) An R companion to applied regression, Second edn. Sage, Thousand Oaks

Fujimoto M, Crossman JA, Scribner KT, Marsh TL (2013) Microbial community assembly and succession on lake sturgeon egg surfaces as a function of simulated spawning stream flow rate. Microb Ecol 66:500–511

Fullerton AH, Garvey JE, Wright RA, Stein RA (2000) Overwinter growth and survival of largemouth bass: interactions among size, food, origin, and winter severity. Trans Am Fish Soc 129:1–12

Garrido S, Ben-Hamadou R, Santos AMP, Ferreira S, Teodósio MA, Cotano U, Irigoien X, Peck MA, Saiz E, Ré P (2015) Born small, die young: intrinsic, size-selective mortality in marine larval fish. Sci Rep 5:17065

Gerkens M, Thiel R (2001) Habitat use of age-0 twaite shad (Alosa fallax Lacepede, 1803) in the tidal freshwater region of the Elbe River, Germany. Bull Fr Pêche Piscic 362-363:773–784

Green BS, Anthony KRN, McCormick MI (2006) Position of egg within a clutch is linked to size at hatching in a demersal tropical fish. J Exp Mar Biol Ecol 329:144–152

Grutter AS, Blomberg SP, Fargher B, Kuris AM, McCormick MI, Warner RR (2017) Size-related mortality due to gnathiid isopod micropredation correlates with settlement size in coral reef fishes. Coral Reefs 36:549–559

Hastings RP, Bauman JM, Baker EA, Scribner KT (2013) Post-hatch dispersal of lake sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) yolk-sac larvae in relation to substrate in an artificial stream. J Appl Ichthyol 29(6):1208–1213

Hay-Chmielewski EM, Whelan GE (1997) Lake sturgeon rehabilitation strategy. Special report 18, fisheries division, Michigan Department of Natural Resources, Ann Arbor

Hayes DB, Caroffino DC (2012) Michigan's Lake sturgeon rehabilitation strategy. Michigan Department of Natural Resources, Fisheries Division Special Report 62, Lansing

Hjort, J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports Et Proces-Verbaux Volume XX

Houle D (1998) How should we explain variation in the genetic variance of traits? Genetica 103:241–253

Hurst TP, Conover DO (1998) Winter mortality of young-of-the-year Hudson River striped bass (*Morone saxatilus*) – size dependent patterns and effects on recruitment. Can J Fish Aquat Sci 55(5):1122–1130

Jensen AJ, Finstad B, Fiske P (2018) Evidence for the linkage of survival of anadromous Arctic char and brown trout during winter to marine growth during the previous summer. Can J Fish Aquat Sci 75:663–672

Jones OR, Wang JL (2010) COLONY: a program for parentage and sibship inference from multilocus genotype data. Mol Ecol Res 10:551–555

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol 16: 1099–1006

Kamler E (2008) (2008) resource allocation in yolk-feeding fish. Rev Fish Biol Fish 18:143–200

Kanno Y, Schmidt CU, Cook SB, Mattingly HT (2012) Variation in microhabitat use of the threatened spotfin chub (*Erimonax monachus*) among stream sites and seasons. 21: 363–374

Kemp P, Sear D, Collins A, Naden P, Jones I (2011) The impacts of fine sediment on riverine fish. Hydrol Process 25:1800–1821

Kempinger JJ (1988) Spawning and early life history of Lake sturgeon in the Lake Winnebago system, Wisconsin. Am Fish Soc Symp 5:110–122

Kern MM, Nassar AA, Guzy JC, Dorcas ME (2013) Oviposition site selection by spotted salmanders (*Ambystoma maculatum*) in an isolated wetland. J Herpetol 47(3):445–449

King TL, Lubinski BA, Spidle AP (2001) Microsatellite DNA variation in Atlantic sturgeon (*Acipenser oxyrinchus*) and cross-species amplification in the Acipenseridae. Cons Genet 2:103–119

Kinghorn BP (1983) A review of quantitative genetics in fish breeding. Aquac 31:283–304

Kruuk LEB, Hadfield JD (2007) How to separate genetic and environmental causes of similarity between relatives. J Evol Biol 20:1890–1903

Letcher BH, Rice JA, Crowder LB, Rose KA (1996) Variability in survival of larval fish: disentangling components with a generalized individual-based model. Can J Fish Aquat Sci 53:787–801

Lowerre-Barbieri SK, Brown-Peterson NJ, Murua H, Tomkiewicz J, Wyanski DM, Saborido-Rey F (2011) Emerging issues and methodological advances in fisheries reproductive biology. Mar Coast Fish: Dyn Manag Ecosyst Sci 3:32–51

Martell DJ, Kieffer JD (2007) Persistent effects of incubation temperature on muscle development in larval haddock (*Melanogrammus aeglefinus* L.). J Exp Biol 210:1170–1182

Martell DJ, Kieffer JD, Trippel EA (2005) Effects of temperature during early life history on embryonic and larval development and growth in haddock. J Fish Biol 66:1558–1575

Martins CIM, Schrama JW, Verreth JAJ (2005) Inherent variation in growth efficiency of African catfish *Clarias gariepinus* (Burchell, 1822) juveniles. Aquac 36:868–875

McAdam SO (2011) Effects of substrate condition on habitat use and survival by white sturgeon (*Acipenser transmontanus*) larvae and potential implications for recruitment. Can J Fish Aquat Sci 68(5):812–822

McCluney KE, Poff NL, Palmer MA, Thorp JH, Poole GC, Williams BS, Williams MR, Baron JS (2014) Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river bains with human alterations. Front Ecol Environ 12(1):48–58

McDonald R, Nelson J, Paragamian V, Barton G (2010) Modeling the effect of flow and sediment transport on white sturgeon spawning habitat in the Kootenai River, Idaho. J Hydraul Eng 136(12):1077–1092

McQuown EC, Sloss BL, Sheehan RJ, Rodzen J, Tranah GJ, May B (2000) Microsatellite analysis of genetic variation in sturgeon: new primer sequences for Scaphirhynchus and Acipenser. Trans Am Fish Soc 129:1380–1388

McQuown EC, Gall GAE, May B (2002) Characterization and inheritance of six microsatellite loci in lake sturgeon. Trans Am Fish Soc 131:299–307

Meyer K, Hill WG (1997) Estimation of genetic and phenotypic covariance for longitudinal data by restricted maximum likelihood. Livest Prod Sci 47:185–200

Miller TJ, Crowder LB, Rice JA, Marschall EA (1988) Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can J Fish Aquat Sci 45(9):1657–1670. https://doi.org/10.1139/f88-197

Mitchell TS, Warner DA, Janzen FJ (2013) Phenotypic and fitness consequences of maternal nest-site choice across multiple early life stages. Ecology 94(2):336–345. https://doi.org/10.1890/12-0343.1

Monaghan P (2008) Early growth conditions, phenotypic development and environmental change. Philos Trans R Soc B 363:1635–1645

Nilsson J (1994) Genetics and growth of juvenile Arctic char. Trans Am Fish Soc 123:430–434

Paragamian VL, McDonald R, Nelson GJ, Barton G (2009) Kootenai River velocities, depth, and white sturgeon spawning site selection – a mystery unraveled? J Appl Ichthyol 25(6):640–646

Parsley MJ, Beckman LG, McCabe GT (1993) Spawning and rearing habitat use by white sturgeon in the Columbia River downstream from McNary dam. Trans Am Fish Soc 122:217–227

Pollock MS, Carr M, Kreitals NM, Phillips ID (2015) Review of a species in peril: what we do not know about lake sturgeon may kill them. Environ Rev 23:30–43

Refsnider JM, Janzen FJ (2010) Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. Ann Rev Ecol Evol Syst 41:39–57

Ribeiro PJ Jr, Diggle PJ (2018) geoR: analysis of geostatistical data. R package version 1:7–5.2.1 https://CRAN.R-project.org/package=geoR

Roseman EF, Manny B, Boase J, Child M, Kennedy G, Craig J, Soper K, Drouin R (2011) Lake sturgeon response to a spawning reef constructed in the Detroit river. J Appl Ichthyol 27:66–76

Rudolf VHW, Rödel MO (2005) Oviposition site selection in a complex and variable environment: the role of habitat quality and conspecific cues. Oecol 142:316–325

Schaeffer LR (2004) Application of random regression models in animal breeding. Livest Prod Sci 86:35–45

Schiemer F, Keckeis H, Kamler E (2003) The early life history stages of riverine fish: ecophysiological and environmental bottlenecks. Comp Biochem Physiol Part A 133:439–449

Siddique MAM, Psenicka M, Cosson J, Dzyuba B, Rodina M, Golpour A, Linhart O (2014) Egg stickiness in artificial reproduction of sturgeon: an overview. Rev Aquac 6:1–12

Smith KM, King DK (2005) Dynamics and extent of larval lake sturgeon *Acipenser fulvescens* drift in the upper Black River, Michigan. J Appl Ichthyol 21:161–168

Svanbäck R, Schluter D (2012) Niche specialization influences adaptive phenotypic plasticity in the threespine stickleback. Am Nat 180(1):50–59

Venables WN, Ripley BD (2002) Modern applied statistics with S, Fourth edn. Springer, New York

Volkman ET, Pangle KL, Rajchel DA, Sutton TM (2004) Hatchery performance attributes of juvenile Lake sturgeon fed two natural food types. NA J Aquac 66(2):105–112

Wang N, Hayward RS, Noltie DB (1998) Variation in food consumption, growth, and growth efficiency among juvenile hybrid sunfish held individually. Aquac 167:43–52

Wassink L, Huerta B, Li W, Scribner K (2020) Interaction of egg cortisol and offspring experience influences stress-related behaviour and physiology in lake sturgeon. Anim Behav 161:49–59

Welsh AB, Blumberg M, May B (2003) Identification of microsatellite loci in lake sturgeon, *Acipenser fulvescens*, and their variability in green sturgeon, *A. medirostris*. Mol Ecol Notes 3:47–55

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30:377–392

Wilson AJ, Réale D (2006) Ontogeny of additive and maternal genetic effects: lessons from domestic mammals. Am Nat 167:E23–E38

Wilson AJ, Kruuk LEB, Coltman DW (2005) Ontogenetic patterns in heritable variation for body size: using random regression models in a wild ungulate population. Am Nat 166:E177–E192

Wilson AJ, Reale D, Clements MN, Morrissey MM, Postma E, Walling CA, Kruuk LEB, Nussey DH (2010) An ecologist's guide to the animal model. J Anim Ecol 79:13–26

Withers JL, Sesterhenn TM, Foley CJ, Troy CD, Höök TO (2015) Diets and growth potential of early stage larval yellow perch and alewife in a nearshore region of southeastern Lake Michigan. J Gt Lakes Res 41(3):197–209

Yi Y, Wang Z, Yang Z (2010) Two-dimensional habitat modeling of Chinese sturgeon spawning sites. Ecol Model 221(5):864–875

Yongsheng T, Tianjun X, You L, Songlin C (2011) Estimates of genetic and phenotypic parameters for weight and length in Paralichthys olivaceous (Temminck et Schlegel). Act Oceanol Sin 30(6):58–64

Zarri LJ, Palkovacs EP (2019) Temperature, discharge, and development shape the larval diets of threatened green sturgeon in a highly managed section of the Sacramento River. Ecol Freshw Fish 28(2):257–265